Species Status Assessment Report for the Gopher Tortoise (*Gopherus polyphemus*)

Version 0.4

Adult gopher tortoise. Image credit: Jeffrey M. Goessling, Ph.D.

August 2021

U.S. Fish and Wildlife Service
Southeast Region
Atlanta, GA

ACKNOWLEDGEMENTS

This document was prepared by Jo Emanuel (U.S. Fish and Wildlife Service (USFWS) - Florida Ecological Services), Lourdes Mena (USFWS – Florida Ecological Services). John Tupy (USFWS – Mississippi Ecological Services), Michael Marshall (Texas A&M Natural Resources Institute), Brian Folt (University of Florida), Michelina Dziadzio (Florida Fish and Wildlife Conservation Commission), and Mathew Hinderliter (USFWS - Ecological Services).

We would also like to recognize and thank the following individuals who provided substantive information and/or insights for our SSA: Jane Cook and Haven Barnhill.

Additionally, valuable input into the analysis and reviews of a draft of this document were provided by Conor McGowan. We appreciate their input and comments, which resulted in a more robust status assessment and final report.

Suggested reference:

U.S. Fish and Wildlife Service. 2021. Species status assessment report for the Gopher Tortoise (*Gopherus polyphemus*), Version 0.4. August 2021, Atlanta, GA.

VERSION UPDATES

The changes from Version 0.1 (May 2021 – Internal Review) included minor grammatical and formatting changes.

The changes from Version 0.2 (June 2021 – Expert Review) included minor grammatical and formatting changes, addition of citations, incorporation of recipient sites, re-run of the future conditions modeling, and addition of pertinent information throughout the document.

The changes from Version 0.3 (Peer and Partner Review) included minor grammatical and formatting changes, addition of citations, minor map and table revisions, and addition of pertinent information throughout the document.

EXECUTIVE SUMMARY

The Species Status Assessment (SSA) reports the results of the comprehensive status review for the gopher tortoise (*Gopherus polyphemus*). For the purpose of this assessment, we define viability as the ability of the gopher tortoise to sustain resilient populations in the wild over time. Using the SSA framework, we consider what the species needs to maintain viability by characterizing the status of the species in terms of its resiliency, redundancy, and representation (USFWS 2016, entire; Wolf et al. 2015, entire). This SSA provides a thorough assessment of biology and natural history and assesses demographic risks, stressors, and limiting factors in the context of determining the viability for the species.

The gopher tortoise is a burrowing reptile species generally associated with southern pine tree species occurring in the Southeastern Atlantic and Gulf Coastal Plains, from Southeastern South Carolina to extreme Southeastern Louisiana. Typical gopher tortoise habitat consists of an open canopy with diverse herbaceous vegetation on well-drained xeric soil with widely spaced trees and shrubs. These systems depend on frequent disturbance, primarily from fire, for the perpetuation and maintenance of species composition and structure within the natural community.

For the gopher tortoise to maintain viability, its populations or some portion thereof must be resilient. The best available information regarding the gopher tortoise and gopher tortoise habitat indicates that habitat loss, degradation, and fragmentation (due to land use changes), climate change, and habitat management are the most significant factors influencing gopher tortoise viability. Other factors influencing viability include road mortality, disease, human harvesting and rattlesnake roundups, predation, invasive flora and fauna, and other conservation measures, including relocation, translocation, and headstarting programs.

For this assessment, we defined populations for the species as contiguous areas surrounding known gopher tortoise burrows with habitat conducive to survival, movement, and inter-breeding

among individuals within the area. Using spatial survey data from across the range of the gopher tortoise, we delineated populations at two spatial scales: local populations and landscape populations, as defined below.

- **Local population**: geographic aggregations of individuals that interact significantly with one another in social contexts that make reproduction significantly greater between individuals within the aggregation than with individuals outside of the aggregation. Operationally delineated by identifying aggregations of individuals or burrows where individuals were clustered together within a 1,968 feet (600 m) buffer to the exclusion of other adjacent individuals or burrows. We delineated 656 local gopher tortoise populations with available spatial data.
- **Landscape population**: a series of local populations that are connected by some form of movement; individuals within a landscape population are significantly more likely to interact with other individuals within the landscape population than individuals outside of the landscape population. Operationally delineated by identifying local populations connected by habitat within 8,202 feet (2.5 km) buffer around each local population. We delineated 253 landscape populations with available spatial data.

We lack consistent and reliable estimates of density, sex ratios, recruitment, dispersal, habitat, and management effort for all populations, thus we qualitatively assessed resiliency by evaluating the estimated abundance of adult gopher tortoises as a metric for categorical levels of resiliency: high (greater than or equal to 250), moderate (51-249), and low (less than 50). Currently, there are an estimated 149,152 gopher tortoises from 656 spatially delineated local populations across the range of the species, with local abundance categories as follow: 360 low, 169 moderate, and 127 high.

To assess representation for gopher tortoise, we delineated five analysis units based on the results of a recent genetics study (Galliard et al. 2017, entire), physiographic regions, and the input of species experts. We evaluated current representation by examining the number of populations and their associated resiliency within the five population analysis units across the species' range. We report redundancy for gopher tortoise as the total number and resiliency of populations and their distribution within and among representative units. Although representation and redundancy have likely decreased significantly relative to the historical distribution of the species, there are still many resilient populations distributed across the range of the species, contributing to future adaptive capacity (representation), and buffering against the potential of future catastrophic events. Because the species is widely distributed across its range, it is highly unlikely any single event would put the species as a whole at risk, although the western most portions of the range are likely more vulnerable to such catastrophes given that most of the populations present in this unit are of low resiliency.

To assess viability for the gopher tortoise, we developed an analytical framework that integrates projections from multiple models of future anthropogenic and climatic change to project future trajectories/trends of gopher tortoise populations and identify stressors with the greatest influence on future population persistence. The modeling framework estimates the change in population growth and persistence probability of populations while accounting for geographic variation in life history, by linking intrinsic factors (demographic vital rates) to four extrinsic anthropogenic factors that are hypothesized to threaten gopher tortoise population persistence (climate warming, sea-level rise, urbanization, and shifts in habitat management).

Six scenarios of future climate warming, sea-level rise, urbanization, and habitat management were used to simulate population growth and extinction risk for gopher tortoises for 80 years into the future. Specifically, we created three scenarios with different levels of stressors (low stressors, medium stressor, and high stressors) that experienced habitat management consistent with contemporary target management goals. We then used the medium stressor values and built three additional models that varied in habitat management treatments, ranging from 'more management' conditions to worsening ('less management') and much worse ('much less management') conditions (Table ES-1).

Table ES-1.

Scenarios	Climate warming (deg C)	Sea-level rise (m)	Urbanization	Management
Low stressors	1.0	0.54 m	P = 0.95	Status quo
Medium stressors	1.5	1.83 m	P = 0.50	Status quo
High stressors	2.0	3.16 m	P = 0.20	Status quo
More management	1.5	1.83 m	P = 0.50	More
Less management	1.5	1.83 m	P = 0.50	Less
Much less management	1.5	1.83 m	P = 0.50	Much less

To assess future redundancy, resiliency, and representation of the gopher tortoise, we used population projections to estimate changes in gopher tortoise populations in the future under each of the six scenarios. We assessed the **resiliency** of future populations to changing environments by estimating persistence probability, categorized as 'extremely likely to persist', 'very likely to persist', 'more likely than not to persist', and 'unlikely to persist', and simulating the number of populations predicted to persist at the end of the projection. We assessed **redundancy** by measuring predicted changes in the total number of individuals, local populations, and landscape populations in the future. We summarized population trends by estimating population growth rate as increasing (greater than 1.00), stable (equals 1.00), or decreasing (less than 1.00). We evaluated how **representation** is predicted to change in the future by examining how population growth of total population size, number of populations, and number of landscape populations will vary by the five population genetic groups of tortoises across the species' range. For each scenario, we summarized the results among all populations across the species' range, but also by genetic units.

Overall projections suggest that extinction risk for the gopher tortoise is relatively low in the future. Of the individuals, local populations, and landscape populations modeled (a small subset of populations likely to occur across the landscape), mean projections among scenarios for 80 years in the future suggested the presence of 47,202–50,846 individuals (females) among 188–198 local populations within 106–114 landscape populations. The persistence of relatively large numbers of individuals and populations suggests resiliency of the species in the face of global change, and redundancy to buffer from future catastrophic events. The spatial distribution of populations predicted to persist in the future are distributed evenly among genetic analysis units, which suggests the persistence of genetic representation in the future as well.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS 2

VERSION UPDATES 3

EXECUTIVE SUMMARY 3

TABLE OF CONTENTS 6

LIST OF TABLES 8

LIST OF FIGURES 11

CHAPTER 1 – INTRODUCTION 18

CHAPTER 2 – SPECIES BIOLOGY AND INDIVIDUAL NEEDS 24

2.1 Taxonomy 24

2.2 Species Description 25

2.4 Life History 27

2.6 Population Dynamics 37

2.7 Resource Needs and Habitat 40

CHAPTER 3 – FACTORS INFLUENCING VIABILITY 46

3.1. Habitat Loss and Fragmentation 46

3.1.1. Historical Loss of Longleaf Pine and Longleaf Restoration 47

3.1.2 Fragmentation and Urbanization 49

3.1.3. Solar Farms 52

3.1.4. Agricultural Lands 53

3.2. Road Effects and Mortality 54

3.3. Climate Conditions 57

3.4. Disease 60

3.5. Human Harvesting and Other Activities 63
3.5.1. Human Harvest 63
3.5.2. Rattlesnake Roundups 63
3.6. Predation 64
3.7. Non-native and Invasive Species 66
3.7.1. Invasive Flora 66
3.7.2. Invasive Fauna 67
3.8. Habitat Management 69
3.8.1. Prescribed Fire 71
3.8.2. Herbicide Applications 73
3.8.3. Mechanical Vegetation Management 75
3.8.4. Timber Management 76
3.9. Conservation Measures 79
3.9.1. Federal and State Protections and Conservation 79
3.9.2. Florida Gopher Tortoise Management Plan and Permitting Guidelines 82
3.9.3. Relocation, Translocation, Recipient Sites, and Headstarting 83
3.9.5. Conservation Agreements 89
3.9.6. Conservation Strategies, Best Management Practices, and Other Conservation Initiatives and Guidelines 90
3.9.7. Conservation Lands 91
3.9.9. Private Lands Conservation Efforts 95
3.10. Summary of Factors Influencing Viability 102
CHAPTER 4 – POPULATION AND SPECIES NEEDS AND CURRENT CONDITION 103
4.1. Introduction 103
4.2. Delineating populations 107
4.3. Delineating representative units 111
4.4. Current resiliency 114
4.4.1. Population factors 115
4.4.2. Habitat and management factors 122
4.5. Current resiliency results 130
4.6. Current representation and redundancy 140
CHAPTER 5 – FUTURE CONDITIONS AND VIABILITY 143
5.1 Models and scenarios 143

5.1.1. Model Structure 143
5.1.2. Demographic parameters 144
5.1.3. Modeling threats 149
5.1.4. Scenarios and population projection structure 156
5.2 Model results 158
5.3. Summary of future conditions and viability 170
Literature Cited 175
APPENDIX A 212
APPENDIX B 224

LIST OF TABLES

Table 3. 1-Human population estimates and future projections (including percentage increases) for six states within historical range of the gopher tortoise (Blanchard 2007, p. 7; Culver College of Business 2021, unpaginated; FEDR 2018, unpaginated; Georgia Census 2021, unpaginated; Population Projections 2021, unpaginated; SCBCB 2009, p. 2; U.S. Census Bureau 2021, unpaginated). 51

Table 3. 2-Gopher Tortoise Project Boundary: WLFW and LLPI Totals by Practice and Year.. 80

Table 4. 1-Site specific data population factors and current resilience for spatially delineated local populations of gopher tortoise. 119

Table 4. 2-County level data population factors (presence of juveniles, estimated number of burrows, and estimated abundance) derived from landowner questionnaire, organized by analysis unit. 121

Table 4. 3-Estimates of known occupied habitat (habitat included within local population boundaries) and potential habitat (habitat located outside of local population boundaries), by analysis unit, as predicted by the HSI model. Total habitat is the sum of occupied and potential habitat... 126

Table 4. 4-Estimates of low, moderate, and high suitability habitat based on responses to landowner survey. Total habitat is the sum of low, moderate, and high suitability habitat. 126

Table 4. 5-Acres burned (prescribed fire and wildfire), rangewide, and by analysis unit, for the years 1994-2019. Data obtained from the Tall Timbers Southeast fire history dataset............. 127

Table 4. 6-Midstory management, including acres burned and acres managed by other means (e.g. chemical and mechanical) between October 2018-Septemeber 2019, as reported by ALRI (2019)... 128

Table 4. 7-Midstory management, including acres burned and acres managed by other means (e.g. chemical and mechanical), by agency, for FY2021, as reported by the gopher tortoise CCA report (2021). Data cover only the candidate portion of the gopher tortoise range. *Other includes Poarch Band of Creek Indians, Longleaf Alliance, Jones Center, Alabama Forestry Commission, National Park Service, and Georgia Power. 129

Table 4. 8-Results provided by respondents to the landowner questionnaire, by analysis unit, including acres burned, estimated burn frequency in years, and whether other practices beneficial to gopher tortoises are implemented on the property... 130

Table 4. 9-Number of local populations and current resilience of gopher tortoise, by analysis unit; includes spatially explicit and county level data. 131

Table 5. 1-Demographic parameter estimates used to model and project baseline population demographics of gopher tortoises (Gopherus polyphemus) in conservation lands across the

species' range. N is the number of studies used to estimate a mean value for simulation modeling. 145

Table 5. 2-Six scenarios of future climate warming, sea-level rise, urbanization, and habitat management used to simulated population growth and extinction risk for gopher tortoises for 80 years into the future. Scenarios vary in the magnitude of threat influences on gopher tortoise demography; threat levels included three levels of climate warming (1.0, 1.5, and 2.0 degrees C increase; 33.8, 34.7, 35.6 degrees F, respectively)), three levels of sea-level rise (intermediate-high [1.83 m/6.00 ft], high [2.55 m/8.37 ft], and extreme [3.16 m/10.37 ft] scenarios), three levels of urbanization scenarios predicted by the SLEUTH model [Terando et al. 2014] at probability thresholds of 0.9 (conservative prediction), 0.5 (moderate prediction), and 0.1 (aggressive prediction), and four levels of changes in habitat management (no changes, less management predicted by RCP4.5 [Kupfer et al. 2020], much less management predicted by RCP8.5 [Kupfer et al. 2020], and improved management [the opposite of the effect predicted by RCP4.5 in Kupfer et al. 2020]). 156

Table 5. 3-Simulated population projections for gopher tortoises under six scenarios of future change. Columns summarize the initial number (in 2020), future predicted number, and population growth rate (λ) for the total population size, number of populations, and number of landscape populations for six scenarios projected 40, 60, and 80 years into the future. See Table 5.2 for descriptions of scenarios and parameters. 161

Table 5. 4- Predicted population persistence probabilities categories for gopher tortoise populations in year 2100 under six future scenarios varying in the magnitude of future stressors; numbers represent number of local gopher tortoise populations, whereas numbers in parentheses represent the percentage of populations that fall into each category Persistence categories are Extremely Likely Extant (p > 95.0%), Very Likely Extant (p= 80.0–94.9%), More Likely Than Not Extant (p= 50.0–79.9%), and Unlikely Extant (p< 50.0%; i.e., extirpated). See Table 2 for descriptions of scenarios and their parameters. 163
Table 5. 5-Simulated population projections for gopher tortoise populations in each of the five analysis units (Gaillard et al. 2017). Six scenarios of predicted future change were projected 80 years into the future; results are summarized by the initial number, future predicted number, and population growth rate (λ) for the total population size, number of local populations, and number of landscape populations in each analysis unit. See Table 5.2 for descriptions of scenarios and parameters. 166

Table 5. 6-Simulated population projections for gopher tortoises under scenarios varying in immigration rate. Columns summarize the initial number (in 2020), future predicted number, and population growth rate (λ) for the total population size, number of populations, and number of landscape populations for four scenarios projected 80 years into the future. Each scenario models stressors and management actions using input values from the 'medium stressors' scenario from

Table 5.2, and the 'intermediate immigration' scenario has the same input values the 'medium stressors' scenario from Table 5.2; see Table 5.2 for more information about input parameters. 169

LIST OF FIGURES

Figure 1. 1-SSA Framework .... **Error! Bookmark not defined.**

Figure 2. 1-Gopher tortoise adult (Left), subadult (Center), and hatchling (Right). Image credit: Michelina Dziadzio Florida Fish and Wildlife Conse. 25

Figure 2. 2-Distribution of the gopher tortoise across the Southeastern United States. 27

Figure 2. 3-Gopher tortoise burrow showing sandy apron and mouth/entrance (left) and gopher tortoise eggs in a nest excavated in a burrow apron (right). Image credit: Michelina Dziadzio. . 32

Figure 2. 4-Diagram of a gopher tortoise burrow showing a gopher tortoise near the end chamber, commensal species using side chambers, and casual visitants near the burrow opening. Image source: Dr. Walter Auffenberg, Florida Museum of Natural History (Auffenberg 1969). 43

Figure 2. 5-Images showing active gopher tortoise burrows, one in an open-canopy pine area (left) and the other showing gopher tortoise tracks (right) in a recently planted pine stand. Image credit: Angela Larsen-Gray. 44

Figure 3. 1-Factors influencing the viability of the gopher tortoise. 46

Figure 3. 2-Locations and relative size of existing longleaf acreages of Significant landscapes for Longleaf Conservation. Source: The Conservation Fund. 49

Figure 3. 3-Location of solar power plants within the range of the gopher tortoise. 53

Figure 3. 4-Interstates and major freeways and highways occurring across the range of the gopher tortoise in Florida, Georgia, Louisiana, Mississippi, Alabama, and South Carolina. 55

Figure 3. 5-Images showing gopher tortoise burrow on road right-of-way (left) and road killed gopher tortoise (right). Image credit: Randy Browning (left) and Jeffrey M. Goessling, Ph.D. (right). 56

Figure 3. 6-Image of an adult gopher tortoise with nasal discharge associated with active Upper Respiratory Tract Disease (URTD). Image credit: Jessica McGuire. 61

Figure 3. 7-Image of predated gopher tortoise nest (left) and hatchling gopher tortoise predated by raccoon (right). Image credit: Michelina Dziadzio. 66

Figure 3. 8-Image of a heavy infestation of cogongrass (*Imperata cylindrica*). Image credit: Mississippi Forestry Commission 67

Figure 3. 9-Gopher tortoise known occurrence location (yellow) and unknown (gray) on NCASI Member Company lands. Data compiled here includes informal and formal surveys, burrow observations, presence at a stand level, and tortoise sightings. Unknown counties (gray) do not imply absence on NCASI Member Company lands as some counties do not contain Member Companies, some Member Company land in some counties may not include gopher tortoise habitat, and not all Member Company lands had survey data (NCASI 2020, p. 8). 97

Figure 3. 10-Gopher tortoise conservation occurs through collaboration among several entities. Large private working forest owners and managers (blue) complete gopher tortoise conservation within their own organizations but also collaborate with environmental non-governmental organizations (ENGOs), government agencies, and universities (yellow). Furthermore, private forest owners and managers cooperate with each other via the National Alliance of Forest Owners (NAFO), the National Council for Air and Stream Improvement, Inc. (NCASI), and the Wildlife Conservation Initiative (orange) to ensure gopher tortoise conservation efforts happen throughout the species' range. Lastly, forest certification programs (orange) provide further assurances that at-risk species conservation (including gopher tortoise conservation) will continue to be a priority on private forests. Entities listed do not represent an exhaustive list of cooperators and partners. Source: NCASI 99

Figure 3. 11-Gopher tortoise conservation delivery network for small family forests. Source: AFF 101

Figure 4. 1-Location of counties with gopher tortoises present (grey) and with responses to the private landowner questionnaire (with hatching). 106

Figure 4. 2-Process for delineating local (600 meter/1,968 feet buffer) and landscape populations (2500 meter/8,202 feet buffer) using burrow locations for gopher tortoises. 110

Figure 4. 3-Location of spatially delineated local populations (left panel) and landscape populations (right panel) across the range of the gopher tortoise. 111

Figure 4. 4-Sampling locations and subsequent genetics units from genetics study by Galliard et al. 2017.. 113

Figure 4. 5-Analysis units used as units of representation for the gopher tortoise in this Species Status Assessment. Analysis units include Western (Unit 1), Central (Unit 2), West Georgia (Unit 3), East Georgia (Unit 4), and Florida (Unit 5). 114

Figure 4. 6-Influence diagram depicting population factors contributing to viability of gopher tortoise... 116

Figure 4. 7-Location and associated resilience (red = low; blue = moderate; green = high) for spatially delineated local populations of gopher tortoise.. 119

Figure 4. 8-*From Crawford et al. 2020:* Relationships from the best-fitting model between habitat suitability and environmental predictors, by ecoregion group (top right), for the gopher tortoise. Although relationships varied by ecoregion, gopher tortoise habitat suitability tended to increase with the amount of well-drained soil, compatible land cover (e.g., evergreen forests, scrub/shrub), and fire frequency. 123

Figure 4. 9-*From Crawford et al. 2020:* Influential environmental, landscape, and biophysical attributes for gopher tortoise suitable habitat and presence at a site, as identified in questionnaires of 16 experts. Attributes are generally ordered from highest (top rows) to lowest (bottom rows) influence on habitat suitability and species presence. Definitions for attribute rankings: Highly – attributes must occur at a site for the species to be present; Somewhat – attributes occurring on the landscape greatly increase the likelihood of species being present, but species may occasionally use landscapes without these attributes; Slightly – attributes occurring on the landscape slightly or variably increase the likelihood of species being present, but species may use landscapes without these attributes... 124

Figure 4. 10-Location of suitable habitat (green) from the Habitat Suitability Index model (Crawford et al. 2020) and suitable soils (grey). 125

Figure 4. 11-location of protected areas and local gopher tortoise populations with associated current resilience, by analysis unit; includes spatially explicit and county level data............... 132

Figure 4. 12-Location and associated resilience (red = low; yellow = moderate; green = high) for local populations of gopher tortoise in analysis unit 1. 133

Figure 4. 13-Location and associated resilience (red = low; yellow = moderate; green = high) for local populations of gopher tortoise in analysis unit 2. 135

Figure 4. 14-Location and associated resilience (red = low; yellow = moderate; green = high) for local populations of gopher tortoise in analysis unit 3. 136

Figure 4. 15-Location and associated resilience (red = low; yellow = moderate; green = high) for local populations of gopher tortoise in analysis unit 4. 138

Figure 4. 16-Location and associated resilience (red = low; yellow = moderate; green = high) for local populations of gopher tortoise in analysis unit 5. 140

Figure 4. 17-Resiliency of gopher tortoise local populations summarized by analysis unit. 142

Figure 5. 1-Effect of mean annual temperature (MAT; degrees C) on (A) maturity age (MA), (B), fecundity, and (C) annual apparent survival probability (φ) of gopher tortoise (Gopherus polyphemus) populations. Geographic variation in biotic conditions (e.g., MAT) predict significant variation in maturity age and fecundity (P < 0.05) but not in annual apparent survival probability. 159

Figure 5. 2- Persistence probabilities of gopher tortoise (*Gopherus polyphemus*) local populations (left) and landscape populations (right) predicted by a future scenario of less habitat management with medium stressor (Table 2) projected 80 years into the future. Symbols are colored by persistence probability categories: Extremely Likely Extant (> 95.0%), Very Likely Extant (= 80.0–94.9%), More Likely Than Not Extant (= 50.0–79.9%), and Unlikely Extant (< 50.0%; i.e., extirpated). See Table 5.2 for descriptions of scenarios and their parameters. 164

Figure 5. 3-Current (left) and future predicted abundance (right) of gopher tortoise (*Gopherus polyphemus*; right inset) populations in the Southeastern United States that were modeled to predict future population growth and extinction risk for the species under scenarios of global change. Each circle represents a local population and circles are colored by analysis units. Symbol size reflects a log-transformed scale of population size; the left panel shows population size estimated during a survey during 2010–2020; the right panel shows predicted population size under a future scenario of 'medium stressors with less management' (Table 2). Abundance of populations during 2010–2020 was estimated from analysis of data from burrow surveys,

burrow scope surveys, or line-transect distance sampling (LTDS) at each the site within the last ten years. 168

LIST OF ACRONYMS

Act	Endangered Species Act
AFB	Air Force Base
AFF	American Forest Foundation
ALRI	America's Longleaf Restoration Initiative
ASL	Above Sea Level
BMP	Best Management Practices
CCA	Candidate Conservation Agreement
CCAA	Candidate Conservation Agreement with Assurances
CFR	Code of Federal Regulations
DNA	Deoxyribonucleic Acid
DoD	Department of Defense
Forest Service	United States Forest Service
FNAI	Florida Natural Areas Inventory
FWC	Florida Fish and Wildlife Conservation Commission
FR	Federal Register
FY	Fiscal year
GDNR	Georgia Department of Natural Resources
GTC	Gopher Tortoise Council
INRMP	Integrated Natural Resources Management Plan
LIT	Local Implementation Team
LTDS	Line Transect Distance Sampling
MOA	Memorandum of Understanding
MVP	Minimum Viable Population
NCASI	National Council for Air and Stream Improvement
NF	National Forest
NOAA	U.S. National Oceanic and Atmospheric Administration
NRCS	Natural Resources Conservation Service
NWR	National Wildlife Refuge
RCP	Representative Concentration Pathway
Service	United States Fish and Wildlife Service
SFI	Sustainable Forestry Initiative
SLEUTH	Slope, Land use, Exclusion, Urban, Transportation, and Hill-shade model
SLR	Sea Level Rise
SSA	Species Status Assessment
SERPPAS	Southeast Regional Partnership for Planning and Sustainability
URTD	Upper Respiratory Tract Disease
U.S.	United States
U.S.C.	United States Code
USDA	United States Department of Agriculture
WLFW	Working Lands for Wildlife
WMA	Wildlife Management Area

CHAPTER 1 – INTRODUCTION

The gopher tortoise (*Gopherus polyphemus*) is a burrowing reptile species generally associated with southern pine tree species including longleaf pine (*Pinus palustris*), loblolly pine (*P. taeda*), slash pine (*P. elliottii*). Natural community associations include xeric oak (*Quercus* spp.) uplands including sandhills and scrub, longleaf pine savannas (i.e., Red Hills region), xeric hammocks, pine flatwoods, dry prairie, coastal grasslands and dunes, mixed hardwood-pine communities, and a variety of disturbed (ruderal) plant communities, occurring in the Southeastern Coastal Plain from Southeastern South Carolina to extreme Southeastern Louisiana (Auffenberg and Franz 1982, entire; Kushlan and Mazzottii 1984, entire; Diemer 1986, p. 125; Diemer 1987, p. 72; Breininger et al. 1994, entire). Typical gopher tortoise habitat consists of an open canopy with diverse herbaceous vegetation on well-drained xeric soil with widely spaced trees and shrubs. These systems depend on frequent disturbance, primarily from fire, for the perpetuation and maintenance of species composition and structure within the natural community.

Historically, lightning induced fires and later anthropogenic use of fire burned the landscape. Currently most natural fires are actively suppressed (via firefighting efforts), resulting in many areas that are overgrown and ultimately degraded (Wear and Greis 2002, 9. 135). Although current gopher tortoise management includes use of prescribed fire, many areas remain fire suppressed.

On July 7, 1987, the gopher tortoise was listed as a threatened species in the western portion of its range, from the Tombigbee and Mobile Rivers in Alabama west to southeastern Louisiana on the lower Gulf Coastal Plain under the Endangered Species Act of 1973, as amended (Act; 16 U.S.C. 1531-1543) (52 FR 25376-25380). A Recovery Plan was subsequently completed in 1990 (Service 1990, entire). On January 18, 2006, the U.S. Fish and Wildlife Service (Service), was petitioned to list the gopher tortoise in the eastern portion of its range as threatened under the Endangered Species Act of 1973, as amended (16 U.S.C. 1531-1543). On September 9, 2009, the Service published a 90-day finding (74 FR 46401) that the petition presented substantial scientific and commercial information indicating that listing may be warranted and that the Service would initiate a status review. As part of the 12-month finding published on July 27, 2011, the Service determined that the species warranted listing under the Act as threatened but listing was precluded in the eastern portion due to higher priority actions (76 FR 45130).

The Species Status Assessment (SSA) compiles the best available information and data regarding the species' biology and factors that influence the species' viability. The gopher tortoise SSA is a summary of the information assembled and reviewed by the Service and incorporates the best scientific and commercial data available. This SSA documents the results of the comprehensive status review for the entire range of the gopher tortoise and serves as the scientific document that informs future agency decisions for this species.

The SSA framework (Service 2016, entire) is intended to be an in-depth review of the species' biology and threats, an evaluation of its biological status, and an assessment of the resources and conditions needed to maintain the species' long-term viability. The intent is for the SSA to be easily updated as new information becomes available and to support all functions of the Endangered Species Program. As such, the SSA report is a living document that may be used to inform Endangered Species Act decision making, such as listing, recovery, Section 7, Section 10, and reclassification decisions (the latter four decision types are only relevant should the species warrant listing under the Act). Therefore, we have developed this SSA to summarize the most relevant information regarding life history, biology, and factors influencing viability for the gopher tortoise. Additionally, we describe the current condition and forecast the possible response of the species to various factors and environmental conditions into the future to formulate a risk profile for the gopher tortoise.

This SSA is intended to provide the biological support for the decision on whether to propose to list or reclassify the species as threatened or endangered and, if so, to determine whether it is prudent to designate critical habitat in certain areas. Importantly, the SSA is not a decisional document by the Service; rather, it provides a review of available information strictly related to the biological status of the gopher tortoise. The listing decision will be made by the Service after reviewing this document and all relevant laws, regulations, and policies, and the results of a proposed decision will be announced in the *Federal Register,* with appropriate opportunities for public input.

The objective of this SSA is to thoroughly describe the viability of the gopher tortoise based on the best scientific and commercial information available. Through this description, we determined what the species needs to support viable populations, its current condition in terms of those needs, and its forecasted future condition under plausible future scenarios. In conducting this analysis, we took into consideration likely changes in the environment – past, current, and future – to help understand what factors drive the species' viability at multiple spatial and temporal scales.

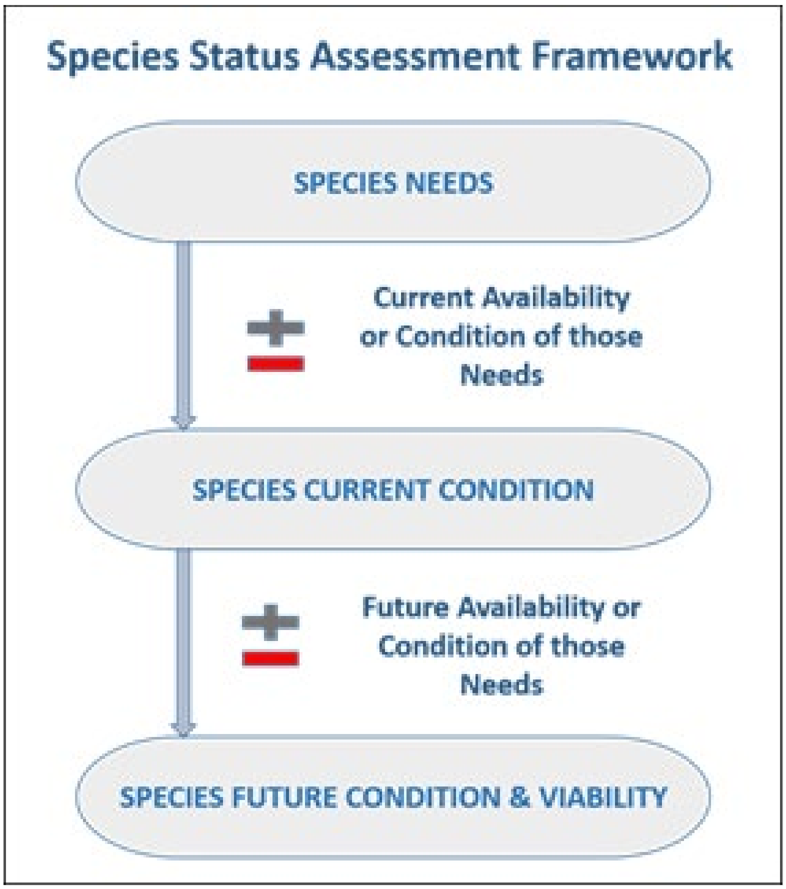


Figure 1. 1-SSA Framework

For the purpose of this assessment, we define 'viability' as the ability of a species to sustain populations in the wild over time. Viability is not a specific state, but rather a continuous measure of the likelihood that the species will sustain populations over time (Service 2016, p. 9). Using the SSA framework (Figure 1.1), we consider what the species needs to maintain viability by characterizing the status of the species in terms of the 3Rs: resiliency, redundancy, and representation (Wolf et al. 2015, entire; Service 2016, entire).

Resiliency is the ability of a species to withstand environmental stochasticity (normal, year-to-year variations in environmental conditions such as temperature and rainfall), periodic disturbances within the normal range of variation (fire, floods, storms), and demographic stochasticity (normal variation in demographic rates, such as survival and fecundity) (Redford et al. 2011, p. 40). Simply stated, resiliency is the ability to sustain populations through the natural range of favorable and unfavorable conditions.

We can best gauge resiliency by evaluating population-level characteristics such as: demography (abundance and the components of population growth rate—survival, reproduction, and migration), genetic health (effective population size and heterozygosity), connectivity (gene flow and population rescue), and habitat quantity, quality, configuration, and heterogeneity. Also, for species prone to spatial synchrony (regionally correlated fluctuations among populations), distance between populations and degree of spatial heterogeneity (diversity of cover types or microclimates) are also important considerations.

Redundancy is the ability of a species to withstand catastrophes by possessing numerous populations distributed in space. Catastrophes are stochastic events that are expected to lead to population collapse regardless of population health and for which adaptation is unlikely (Mangel and Tier 1993, p. 1083). We can best gauge redundancy by analyzing the number and distribution of populations relative to the scale of anticipated species-relevant catastrophic events. The analysis entails assessing the cumulative risk of catastrophes occurring over time. Redundancy can be analyzed at a population or regional scale, or for narrow-ranged species, at the species level. Redundancy is assessed by characterizing the number of resilient populations across a species' range. The more resilient populations a species has, distributed over a larger area, the better the chances that the species can withstand catastrophic events.

Representation is the ability of a species to adapt to both near-term and long-term changes in its physical (climate conditions, habitat conditions, habitat structure, etc.) and biological (pathogens, competitors, predators, etc.) environments. This ability to adapt to new environments—referred to as adaptive capacity—is essential for viability, as species need to continually adapt to their continuously changing environments (Nicotra et al. 2015, p. 1269). Species adapt to novel changes in their environment by either [1] moving to new, suitable environments or [2] by altering their physical or behavioral traits (phenotypes) to match the new environmental conditions through either plasticity or genetic change (Beever et al. 2016, p. 132; Nicotra et al. 2015, p. 1270). The latter (evolution) occurs via the evolutionary processes of natural selection, gene flow, mutations, and genetic drift (Crandall et al. 2000, p. 290-291; Sgro et al. 2011, p. 327).

We can best gauge representation by examining the breadth of genetic, phenotypic, and ecological diversity found within a species and its ability to disperse and colonize new areas. In assessing the breadth of variation, it is important to consider both larger-scale variation (such as morphological, behavioral, or life history differences which might exist across the range and environmental or ecological variation across the range), and smaller-scale variation (which might include measures of inter-population genetic diversity). In assessing the dispersal ability, it is important to evaluate the ability and likelihood of the species to track suitable habitat and climate over time. Lastly, to evaluate the evolutionary processes that contribute to and maintain adaptive capacity, it is important to assess [1] natural levels and patterns of gene flow, [2] degree of ecological diversity occupied, and [3] effective population size. In our SSAs, we assess all three facets to the best of our ability based on available data.

To evaluate the current and future viability of the gopher tortoise, we assessed a range of conditions to characterize the species' 3Rs. This SSA provides a thorough account of known biology and natural history and assesses the risk of threats and limiting factors affecting the future viability of the species.

This SSA includes: (1) a description of gopher tortoise resource needs at both individual and population levels; (2) a characterization of the historical and current distribution of populations across the species' range; (3) an assessment of the factors that contributed to the current and future status of the species and the degree to which various factors influenced viability; and (4) a synopsis of the factors characterized.

CHAPTER 2 – SPECIES BIOLOGY AND INDIVIDUAL NEEDS

In this chapter, we provide biological information about the gopher tortoise*,* including its taxonomic history, morphological description, historical and current distribution and range, and known life history. We then outline the resource needs of individuals.

2.1 Taxonomy

The gopher tortoise is one of six living North American tortoise species and the only one indigenous to the Southeastern United States (Ernst and Lovich 2009, p. 581; Edwards et al. 2016, p. 131); the other congeneric species are found in western North America. First described by F.M. Daudin in 1802, *G. polyphemus* is classified as belonging to Class Reptilia, Order Testudines, and Family Testudinidae. Two of the most recent changes affecting the genus *Gopherus* are the reclassification of the desert tortoise (*G. agassizii*) into two species (Murphy et al. 2011, entire) – Agassiz's desert tortoise (*G. agassizii*) and Morafka's desert tortoise (*G. morafkai*) – and the subsequent reclassification of *G. morafkai* into two species as well (*G. morafkai* and *G. evgoodei*) (Edwards et al. 2016, entire). Recent morphological and genetic studies have reinforced the traditional assignment of all species into genus *Gopherus* (Crumly 1994, pp. 12-16). Allozyme differentiation has indicated that *G. polyphemus* is most closely related to *G. flavomarginatus* and is thus placed in a clade (genetically related group) distinct from the clade containing *G. berlandieri* and *G. agassizii* (Morafka et al. 1994, p. 1669).

The taxonomic status of the gopher tortoise throughout its range is considered valid (Integrated Taxonomic Information System 2021, p. 1). There is no taxonomic distinction between the gopher tortoise in the western and eastern portions of its range or at any level of geographic subdivision. We are aware of no efforts to reclassify the species.

2.2 Species Description

The gopher tortoise (Figure 2.1) typically has a domed, brown to grayish-black carapace approximately 10-15 inches (in; 25-38 centimeters; cm) in length and weighing approximately 9-13 pounds (lbs; 4.08-5.9 kilograms; kg) (Ernst et al. 1994, p, 466; Bramble and Hutchison 2014, p. 4). The plastron is yellowish and hingeless (Ernst et al. 1994, p. 466). A fossorial species (a species adapted to digging and living primarily underground), its hind feet are often described as elephantine or stumpy (round and pad-like), and the forelimbs are shovel-like, with claws used for digging (Ernst et al. 1994, p. 469). In comparison to females, males are smaller; usually have a larger gland under the chin, a longer gular projection, and more deeply concave plastron (Ernst et al. 1994, p. 466). Hatchlings are about 2 inches (51.4 cm) in length, with a softer, yellow-orange shell (Iverson 1980, p. 357; Butler et al. 1995, p. 174). Hatchling gopher tortoises are classified as those less than 2.4 inches (60 millimeters) in straight-line carapace length (CL), juveniles as those greater than 2.4 inches to 5.1 inches (60 millimeters to 130 millimeters) in CL, subadults as those greater than 5.1 inches to 8.6 inches (130 mm - 219 mm) in CL, and adults as those tortoises 8.7 inches (220 mm) in CL or greater (Landers et al. 1982, entire).

Figure 2. 1-Examples of typical size and coloration of gopher tortoise adult (Left), subadults (Center), and hatchlings (Right). Image credit: Michelina Dziadzio

2.3 Range and Distribution

The gopher tortoise occurs in the Southeastern Atlantic and Gulf Coastal Plains from southern South Carolina west through Georgia, the Florida panhandle, Alabama, and Mississippi to eastern Louisiana, and south through peninsular Florida (Figure 2.2; Auffenberg and Franz 1982, p. 95). The range of the gopher tortoise generally aligns with the historic range of the longleaf pine ecosystem (Auffenberg and Franz 1982, pp. 99-120). The eastern portion of the gopher tortoise's range includes Alabama (east of the Tombigbee and Mobile Rivers), Florida, Georgia, and southern South Carolina. The western range, west of the Tombigbee River in Alabama, Mississippi, and Louisiana, is currently listed as threatened under the Act (Figure 2.2). The core of the current distribution of the gopher tortoise occurs in the eastern portion of the range and includes peninsular Florida and southern Georgia. The gopher tortoise is more widespread and abundant in the core of its distribution, where these areas have been referred to as the "central" portion of the tortoise's geographic extent previously in the literature (Tuberville et al. 2009, p. 12) and more recently as east Georgia, west Georgia and peninsular Florida genetic units (Gaillard et al. 2017, pp. 500-502). It is estimated that approximately 86 percent of the forest area in the south is in private ownership and approximately 80 percent of the gopher tortoise range occurs in private ownership, with the remainder owned or managed by local, state, federal, or private conservation entities (Wear and Greis 2013, p. 103; NRCS 2018, p. 2).

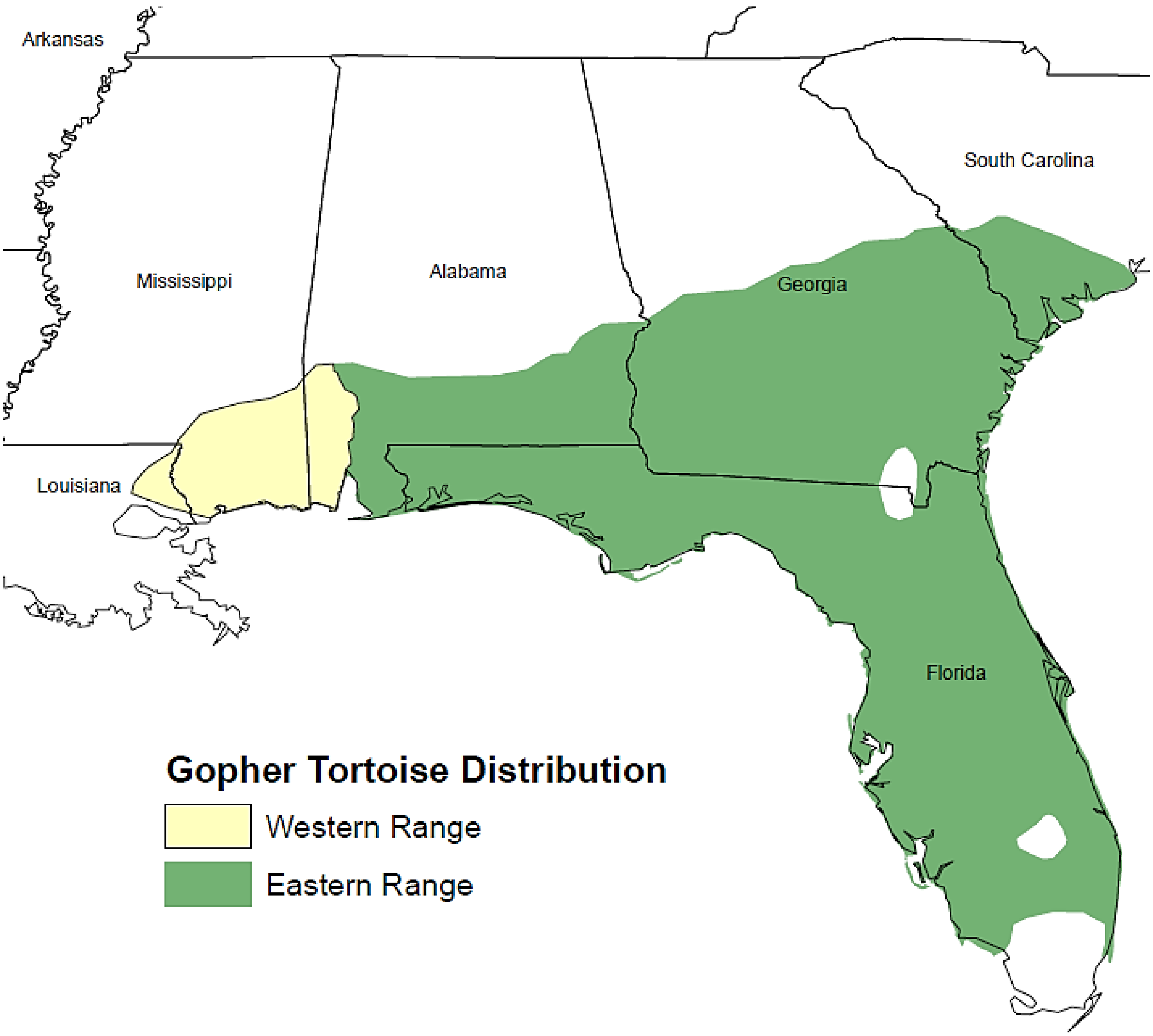


Figure 2. 2-Distribution of the gopher tortoise across the Southeastern United States.

2.4 Life History

Some of the challenges for the conservation of this species lie in its life history traits; specifically, the late age of reproductive maturity (estimated to be between 12 – 20 years), low reproductive output (estimated to be between 4 – 8 eggs/clutch), and long lifespan (generally estimated at 50–80 years) (Service 2013, p. 21). Below is a synthesis of the current state of knowledge of gopher tortoise life history.

Activity

Tortoises spend most of their time within burrows and emerge during the day to bask, feed, and reproduce (Service 2013, p. 21). Tortoises are active above ground when daytime temperatures range from 75 - 87 °Fahrenheit (F) (23.9 - 30.6 °Celsius; C) (McRae et al. 1981, pp. 167-168). Daily active periods are typically unimodal in spring and fall, with bimodal periods (early to mid-morning, middle to late afternoon) during the hotter temperatures of summer. Daily activity above ground becomes significantly reduced by the end of the growing season during October as temperatures begin to cool (McRae et al. 1981, p. 167-168). Gopher tortoises throughout most of the range shelter within their burrows during the dormant season, become torpid, do not eat, and rarely emerge, except on warm days to bask in sunlight at the burrow entrance (Service 2008, p. 10). Gopher tortoises become active again in April or when air temperatures are above 73.4 °F (23 °C) (Douglass and Layne 1978, p. 364; Butler et al. 1995, pp. 175-177). One exception is in southern Florida, where the gopher tortoise is active every month of the year, though winter activity is restricted to warm (> 69.8 °F [21°C]) days (Douglass and Layne 1978, pp. 361-364; Moore et al. 2009, pp. 390-391; Castellon et al. 2018, pp. 9-10).

In a study that examined gopher tortoise populations on fire maintained longleaf pine stands, females may use an average of 5 burrows per year, while males occupy an average of 10 burrows per year (Ott-Eubanks et al. 2003, p. 318). In lower quality habitat, tortoises may use many more burrows and incur more significant energy expenditures, ultimately leading to low population densities and increased clumping of individuals into small enclaves (Ott-Eubanks et al. 2003, pp. 319-320). Males tend to use more burrows and move more frequently among their different burrows than females as they seek breeding opportunities (McRae et al. 1981, p. 174; Diemer 1992a, p. 285; 1992b, p. 162; Smith 1995, p. 12; Ott-Eubanks et al. 2003, p. 318).

Tortoises select and prefer burrow sites in open canopy areas where sunlight reaches the ground (Boglioli et al. 2000, pp. 703-704; Rostal and Jones 2002, pp. 484-485; McIntyre et al. 2019, p. 287). Such sites reflect areas where herbaceous forage plants are more abundant and for females, sunlight and soil temperatures for egg incubation are more suitable. Also, males select sites and burrows that increase their proximity to females and breeding opportunities (Boglioli et al. 2000, pp. 703-704; Ott-Eubanks et al. 2003, pp. 318-319). The repeated use and travel to the same burrows by individual tortoises on relatively pristine sites in some studies suggests that tortoises know the geography of their home range, burrows, and the location of neighboring tortoises (Ott-Eubanks et al. 2003, p. 318). In habitat of exceptionally poor quality, small groups of gopher tortoises will restrict movements to a few burrows and socialize only with a few neighboring individuals (Guyer et al. 2012, pp. 131–132). Burrow site selection within populations in coastal or other geographically isolated areas may be influenced by environmental conditions, such as storms and drought (Kushlan and Mazzotti 1984, p. 237; Waddle et al. 2006, pp. 282 – 283, Blonder et al. 2021, pp. 9–11)

Diet and Foraging

Gopher tortoises were found to mostly forage on foliage, seeds, and fruits of grasses and forbs, generally in an area of about 150 feet (45.7 meters; m) surrounding burrows (McRae et al. 1981, p. 169). Although they feed primarily on broadleaf grasses, wiregrass (*Aristida stricta var. beyrichiana*), asters, legumes, and fruit, they are known to eat more than 300 species of plants (Garner and Landers 1981, pp. 123–130; Ashton and Ashton 2004, pp. 33-35; Richardson and Stiling 2019, pp. 387-388). The diet of adults resembles that of a generalist herbivore, with at least some preference for certain plants over others, and may also include insects and carrion (Macdonald and Mushinsky 1988, pp. 349-351; Birkhead et al. 2005, p. 155; Richardson and Stiling 2019, pp. 387–388). Legumes are thought to be particularly important for re-conditioning females after egg laying, and it has been shown that clutch sizes and percent of gravid females were lowest in areas with low percent cover of legumes (White 2009, p. 12). In a study on patterns of gastrolith ingestion by adult female gopher tortoises, over 85% of gravid tortoises contained shell and stone gastroliths while only 5% of non-gravid female tortoises had shells and stones in the gut, suggesting opportunistic intake of calcium-rich gastroliths may provide important nutritional supplements for reproductive female gopher tortoises (Moore and Dornburg 2014, p. 57). Juvenile gopher tortoises tend to forage on fewer plant species, eat fewer grasses, and select more forbs, including legumes, than adults (Garner and Landers 1981, p. 131; Mushinsky et al. 2003, p. 352).

Reproduction and Growth

Gopher tortoises mostly breed from May through October (Landers et al. 1980, p. 355; McRae et al. 1981, pp. 172-173; Taylor 1982, entire; Diemer 1992a, pp. 282-283; Ott-Eubanks et al. 2003, p. 317). However, gopher tortoise populations in south Florida show courtship behavior year-round and have an extended reproductive season, producing young over a much longer period than other populations further north (Moore et al. 2009, p. 391). Females ovulate during the spring, but likely store sperm so that active breeding during ovulation may not always be required for fertilization (Ott et al. 2000, p. 308). Males travel to female burrows and copulation occurs above ground, often at the burrow entrance, more frequently during July to September, a period of peak sex and adrenal steroid hormones (Ott et al. 2000, p. 299; Ott-Eubanks et al. 2003, p. 318).

Females may mate with several males during a single mating season and males may search for prolonged periods for receptive females (Boglioli et al. 2003, p. 849; Johnson et al. 2009, p. 217). The multiple paternities of about 30 percent of the clutches in a Florida gopher tortoise population was confirmed to indicate males fertilizing multiple clutches and females with multiple mates. Paternity analysis of the above study also suggested that larger males may have a reproductive advantage over smaller males in mating with females (Colson-Moon 2003, pp. 38-40). Mean body mass of males mounting females did not differ from the mean mass of all other males from a study of 20 females that received 286 visits from males in a large population in southwestern Georgia (Boglioli et al. 2003, pp. 848-849). Local gopher tortoise populations have been described as colonies, with aggregations of burrows in which dominant males competitively and behaviorally exclude other males at female burrows to maintain a loose female harem as a mating system (Douglass 1986, pp. 175-176). However, recent literature has failed to support the conclusion that the term colony is appropriate for gopher tortoises or that the breeding system is consistent with defense of a harem. Instead, the activities are most consistent with scramble competition (Boglioli et al. 2003, p. 849; Johnson et al. 2009, p. 217). Tuberville et al. (2011, p. 181) compared successful mating (in terms of number of known offspring sired) of relocated males to resident males and found that size was unlikely to be the only or primary cue used by females in choosing males. Johnson et al. (2009, p. 217) found that males appear to chase other males during mating season, but females never do. In addition, aggregations of burrows in some areas and study sites may be an artifact of fragmentation and the concentration of burrows in the available remaining habitat (Mushinsky and McCoy 1994, pp. 44-45; Boglioli et al. 2003, p. 849). Outside influences such as geographic or environmental factors often play a role in shaping differences of behavior in local breeding populations.

Rangewide, average clutch size varies from about four to eight eggs/clutch (Ashton et al. 2007, p. 357). Clutch size generally is positively correlated with adult female size (Diemer and Moore 1994, p. 132; Smith 1995, pp. 22-23; Rostal and Jones 2002, p. 482). Female gopher tortoises with lower body condition scores and lower plasma phosphorus levels were less likely to have eggs (White 2009, pp. 84-97). Average clutch size in the western range, from 4.8 - 5.6 eggs/clutch, is comparably low (Seigel and Hurley 1993, p.6; Seigel and Smith 1996, pp. 10-11; Tuma 1996, pp. 22-23; Epperson and Heise 2003, pp. 318-321). Studies have examined the percentage of females gravid per year (Diemer and Moore 1994, pp. 133-134; Smith et al. 1997a, p. 598), however, it was unknown whether non-gravid females either did not ovulate or deposited their clutch before researchers caught them.

Female gopher tortoises usually lay eggs from mid-May through mid-July, and incubation lasts 80 - 110 days (Diemer 1986, p. 127). Tortoises may nest in the soil at the entrance of a burrow (Figure 2.3; Butler and Hull 1996, p. 16; Smith et al. 1997a, p. 599), or in other open sandy areas, when available (Landers et al. 1980, p. 357).. In an analysis of 19 gopher tortoise populations from across the geographic range, larger clutches were produced in areas that were more southern, warmer, had greater site productivity, and were less seasonal (Ashton et al. 2007, p. 359). In Mississippi, nests are up to 16 cm (6.3 in) in depth and located about 46 cm (18.1 in) from the opening of the burrow (Epperson and Heise 2003, p. 318). Incubation at temperatures from 27°C to 32°C (80.6°F to 89.6°F) is required for successful development and hatching (DeMuth 2001, pp. 1611-1613; Rostal and Jones 2002, p. 482). Sex determination is temperature dependent for gopher tortoises, with lower temperatures producing more males and higher temperatures producing more females. The pivotal temperature for a 1:1 sex ratio has been observed to be 29.3°C (84.7°F) (DeMuth 2001, pp. 1612-1613).

Figure 2. 3-Gopher tortoise burrow showing sandy apron and mouth/entrance (left) and gopher tortoise eggs in a nest excavated in a burrow apron (right). Image credit: Michelina Dziadzio.

Nest depredation by vertebrates can be a substantial threat to some gopher tortoise populations (See Chapter 3 below). A study in southern Georgia, found approximately 90 percent of nests were destroyed by predators (Landers et al. 1980, p. 355, 358), while in a controlled study in southwest Georgia, a nest predation rate of 65 percent was observed (Smith et al. 2013, p. 4). In a smaller study from southern Alabama, about 46 percent of nests (n = 11) were destroyed by raccoons (*Procyon lotor),* Virginia opossums *(Didelphis virginiana)*, and nine-banded armadillos (*Dasypus novemcinctus)* (Marshall 1987, pp. 29-32). Egg hatching success at experimentally protected nests has ranged from 28-97 percent in Florida and Georgia (92 percent, Arata 1958, pp. 276-279; 86 percent, Landers et al. 1980, p. 359; 28 percent, Linley 1986, p. 23; 67 to 97 percent, Smith 1995, p. 25; 80.6 percent, Butler and Hull 1996, p. 16). In Mississippi, mean hatching success from protected nests in the field has ranged from 28.8-56 percent (Epperson and Heise 2003, p. 319; Noel et al. 2012, pp. 328-329).

Hatchlings excavate themselves from the nest and typically emerge from the middle of August through September (Epperson and Heise 2003, p. 319). Hatchlings and yearlings (zero to one year old) may temporarily shelter in adult burrows, bury under sand or leaf litter, or excavate a small burrow nearby (Douglass 1978, pp. 413-415; Wilson 1991, pp. 377-378; Butler et al. 1995, pp. 175-179; Pike 2006, pp. 70-73).

Gopher tortoise growth is most rapid during the juvenile stage, becoming slower at the onset of adulthood and reproductive maturity, followed by little or no adult growth, particularly later in maturity (Mushinsky et al. 1994, p. 122). Generally, tortoises become adults between 9 to 20 years of age, although reproductive maturity is determined by size rather than age. Growth rates and sizes at sexual maturity can vary among populations and habitat quality (Landers et al. 1982, pp. 104-105; Mushinsky et al. 1994, pp. 123-125).

Home range and Movement

Hatchling and yearling gopher tortoises initially move up to about 50 feet (15 m) from their nest to establish their first burrow, from which they will subsequently excavate and use about five burrows in a home range as small as about 0.5 acres (0.2 hectares; ha), to as large as 11.8 acres (4.8 ha) (Wilson 1991, p. 39; Butler et al. 1995, pp. 177-178; Epperson and Heise 2003, pp. 320-321; Pike 2006, pp. 70-72). On average, yearling gopher tortoises move relatively short distances to establish new burrows, although they are known to have traveled up to 1,485 ft (450 m) to new burrows (Butler et al. 1995, p. 178; Epperson and Heise 2003, pp. 320). Hatchlings and yearlings may also take shelter beneath litter and woody debris (Diemer 1992b, p. 163, pp. 178-179). Yearling and juvenile gopher tortoises typically forage within about 23 feet (7 m) of their burrow (McRae et al. 1981, pp. 175-176; Butler et al. 1995, pp. 178-179; Epperson and Heise 2003, pp. 320-321).

The burrows of a gopher tortoise represent the general boundaries of a home range, which is the area used for feeding, breeding, and sheltering (McRae et al. 1981, p. 176). The home range area tends to vary with habitat quality, becoming larger in areas of poor quality (Auffenberg and Iverson 1979, pp. 559-561; Castellon et al. 2012, p. 159; Guyer et al. 2012, p. 130). Males typically have larger home ranges than females (McRae et al. 1981, p. 175; Guyer et al. 2012, p. 130; Castellon et al. 2018, pp. 11–12). Mean home ranges of individual tortoises in Mississippi, Alabama, Florida, and Georgia have varied from 0.15–39.8 acres (0.06–16.1 ha) for males and 0.1–20.8 acres (0.04 – 8.4 ha) for females (McRae et al. 1981, pp. 175–176; Diemer 1992b, pp. 160-161; Tuma 1996, pp. 28-43; Ott-Eubanks et al. 2003, pp. 315–316; Guyer et al. 2012, pp. 128-129; Castellon et al. 2018, p. 17). In comparison to females, male gopher tortoises use more burrows, and during breeding season, move among burrows more frequently over longer distances (McRae et al. 1981, p. 174; Auffenberg and Iverson 1979, pp. 548–549; Diemer 1992b pp. 160-162; Smith 1995, p. 108; Tuma 1996, pp. 28-43; Ott-Eubanks et al. 2003, pp. 115-117; Guyer et al. 2012, pp. 128-129; Castellon et al. 2018, p. 17).

Home ranges are larger in the western portion of the range than those typically observed for tortoises in Alabama, Georgia, and Florida, most likely due to habitat quality differences (Lohoefener and Lohmeier 1984, p. 1-25; Epperson and Heise 2003, p. 315; Richter et al. 2011, p. 408). Gopher tortoise movements increase as herbaceous biomass and habitat quality decrease (Auffenberg and Iverson 1979, p. 558; Auffenberg and Franz 1982, p. 121. Castellon et al. 2018, p. 18). It is common for peripheral populations to differ from populations found in a species' core range where the habitat quality tends to be higher (Prieto-Ramirez et al. 2020, pp. 2–3), which may influence tortoise average home range size and movements but also highlights the species' plasticity.

As distances increase between gopher tortoise burrows, isolation among gopher tortoises also increases due to the decreasing rate of visitation and breeding by males to females (Boglioli et al. 2003, p. 848; Guyer et al. 2012, p. 131). Using extensive data from individual gopher tortoise inter-burrow movements and home range size, most breeding population segments have been found to consist of burrows no greater than about 549 feet (167 m) apart, (Ott-Eubanks et al. 2003, p. 320). Other studies and data show that gopher tortoises rarely move long distances from their burrows when mating (Guyer and Johnson 2002, pp. 6-8; Guyer et al. 2012, p. 131), though males will move longer distances from their burrows, up to 1,640 feet (500 meters), to a female burrow for mating opportunities. Gopher tortoises have been observed to move distances of over 4,921 feet (1,500 m) throughout multiple years (McRae et al. 1981, p.172; Diemer 1992b, p. 163; Castellon et al 2018, p. 20), however movements of this distance are not considered to be normal movements within a home range.

2.5 Genetics

Genetic flow in gopher tortoise populations is known to be influenced by distance, geographic features, and human influence by transporting tortoises across the range. There have been several phylogeographic studies of the gopher tortoise including mitochondrial DNA (Osentoski and

Lamb 1995 entire; Clostio 2012, entire) and microsatellites (Schwartz and Karl 2005, entire; Ennen et al. 2012, pp. 112 - 122; Clostio et al. 2012, entire; Gaillard et al. 2017, entire). Several studies showed genetic assemblages across the geographic range (Osentoski and Lamb 1995, p. 713; Ennen et al. 2012, pp.113-120; Clostio et al. 2012, pp. 617-620; Gaillard et al., 2017, pp. 501-503) but these studies were not entirely congruent in their delineations of western and eastern genetic assemblages. Recent microsatellite analysis suggests there are five main genetic groups, delineated by the Tombigbee and Mobile rivers, Apalachicola and Chattahoochee rivers, and the transitional areas between several physiographic province sections of the Coastal Plains (i.e., Eastern Gulf, Sea Island, and Floridian), and the authors suggest use of these groups as management units for conservation planning (Gaillard et al. 2017, pp. 505 - 507). In addition to the five genetic groups suggested by Gaillard et al. (2017), two additional genetic groups were loosely delineated by the Pascagoula and Chickasawhay rivers, and four genetic groups within the Florida region that seemed to reflect the influence of the local physiography (e.g., Atlantic Coast Ridge) (Gaillard et al. 2017, pp. 497-509).

A phylogenetic break (difference in genetics) had been reported between the western and eastern portions of the tortoise’s range based on a 712 base pair portion of a mitochondrial gene (Ennen et al. 2012, pp. 113-116). However, the phylogenetic break did not entirely correspond to a particular geographic barrier because shared haplotypes from the eastern and western portions of the tortoise’s range were found in the panhandle of Florida and in Georgia populations (Ennen et al. 2012, pp. 113-116). Research using another mitochondrial gene similarly found no shared haplotypes across the Mobile and Tombigbee Rivers (Clostio et al. 2012, pp. 619-620) but a recent study that genotyped 933 tortoises across the species’ range recognizes five groups (or regions) delineated by the Tombigbee-Mobile Rivers, Apalachicola-Chattahoochee Rivers, and the transitional areas between several physiographic province sections of the Coastal Plains (i.e., Eastern Gulf, Sea Island, and Floridian) (Gaillard et al. 2017, entire). In addition, the periphery of the range is identified as having lower genetic diversity relative to the core and genetic admixture at sampling sites along the boundaries of the genetically defined groups (Gaillard et al. 2017, p. 509).

There are several smaller scale genetic analyses that have been conducted to better understand local and regional genetic variation in gopher tortoises. In the Florida panhandle, mitochondrial DNA analysis found minimal genetic diversity among six populations and suggested that gene flow occurred among these populations (Sinclair-Winters et al. 2011, pp. 153–155), which would be contrary to the findings of Clostio et al. (2012, pp. 617-618) and consistent with Ennen et al. (2012, p. 113). Subsequent analysis compared the above-referenced Florida panhandle genetics with those collected by Schwartz and Karl (2005, entire) and found a genetic break between peninsular Florida and the Florida panhandle, as did Osentoski and Lamb (1995, pp. 713-714), but these data indicated genetic exchange across the panhandle of Florida from Wakulla County to Escambia County, with no significant break at the Apalachicola River as suggested by Clostio et al. (2012, p. 618). Microsatellite DNA markers and mitochondrial DNA were used to determine whether gopher tortoise populations on Camp Shelby, Mississippi, were spatially structured, if spatial structure was affected by military activity and habitat quality, and whether there was a correlation between geographic distance and genetic relatedness (Richter et al. 2011, entire). Results indicated that there was genetic structure within these populations, and that genetic diversity and gene flow were affected by habitat quality and land use. Genetic distance did not seem to correlate with geographic distance (Richter et al. 2011, p. 412).

Analyses of mitochondrial DNA and nuclear DNA microsatellite markers showed that four gopher tortoise populations in Mississippi have lower genetic diversity than some populations in the eastern portion of the tortoise's range (Ennen et al. 2010, p. 34). This lower genetic variation and heterozygocity suggests either a prior population bottleneck, a historical persistence of the western populations with naturally low genetic diversity, or the fact that western sites are located on the periphery of the range (Ennen et al. 2010, p. 35; Ennen et al. 2011, p. 210; Gaillard et al. 2017, p. 509).

The last decade of genetic research has shown that genetic diversity exists among individuals in a population, among populations and across the range (Ennen et al. 2010, entire; Clostio et al. 2012, entire; Gaillard et al. 2017, entire). The most recent rangewide genetic analysis also confirmed that the periphery of the range has lower levels of genetic diversity relative to the core but also showed genetic admixture between units (Gaillard et al. 2017, p. 507). Evidence of tortoises with ancestry from different genetic sites is most likely due to the decades of tortoises being moved by humans (Gaillard et al. 2017, pp. 504-505). Gene flow is asymmetric from the Central genetic sites (Alabama) to the peripheral sites and gene flow is higher from the Central genetic sites (Alabama) to the Western site (western range). The Florida and the Western Georgia genetic sites has had low genetic flow in the Florida panhandle area (Gaillard et al 2017, pp. 504-509).

2.6 Population Dynamics

As long-lived animals, gopher tortoises naturally experience delayed sexual maturity, low reproductive rates, high mortality at young ages and small size-classes, and relatively low adult mortality. The growth and dynamics of populations are stochastically affected by natural variation due to demographic rates, the environment, catastrophes, and genetic drift (Shaffer 1981, pp. 131-132). Factors affecting population growth, decline, and dynamics include the number or proportion of annually breeding and egg-laying females (breeding population size), clutch size, nest depredation rates, egg hatching success, mortality (hatchling/yearling, juvenile-subadult, adult), the age or size at first reproduction, age- or stage-class population structure, maximum age of reproduction, and immigration/emigration rates.

These factors and data have been evaluated in several investigations of population viability to estimate the probabilities of gopher tortoise population extinction over time and the important factors affecting persistence (Cox et al. 1987, pp. 24-34; Cox 1989, p. 10; Lohoefener and Lohmeier 1984, entire; Miller 2001, entire; Epperson and Heise 2001, pp. 37-39; Wester 2004, pp. 16-20; McDearman 2006, entire; Tuberville et al. 2009, entire). These gopher tortoise population models and simulations varied with regard to specific objectives, model structure, transparency, simulation time, and actual demographic parameters. Nevertheless, the various projections of population growth, decline, and persistence time in different scenarios are plausible.

Using demographic data from various tortoise populations in Florida, it has been shown that more than 90 percent of simulated populations with 50 annually breeding individuals can persist up to 200 years under favorable habitat and management conditions, and a threshold of 130-150 tortoises were needed for persistence under moderate conditions (Cox et al. 1987, pp. 27-29). Favorable conditions reflected relatively high adult survival and fecundity in areas maintained by prescribed fire and protected from human encroachment and development. Populations of this size and demographic characteristics were considered the smallest potentially viable by their definition of persistence for at least 200 years. However, in another viability analysis using a different model with slightly different demographic parameters, it was reported that larger populations of about 200 gopher tortoises were required to achieve a 0.9 or greater probability of persisting for 200 years (Cox et al. 1994, p. 29).

Populations as small as 50 tortoises, exhibited positive growth rates and persistence, as modeled with VORTEX (Lacy and Pollak 2014, entire) by Miller (2001, p. 13) using demographic data from Florida. The potential effect of upper respiratory tract disease (URTD) was evaluated by increasing annual mortality as compared to a baseline model. URTD reduced the stochastic population growth rate, particularly in the panhandle population models, to such an extent that populations declined to eventual extirpation (Miller et al. 2001, pp. 26-27). An assumption was also made that a severe localized outbreak of URTD would only occur every 50 years (Miller et al. 2001, p. 28). Because this parameter was based on little quantifiable information, precise conclusions for how URTD impacts populations could not be made. However, this analysis highlights a need to better understand the extent with which URTD impacts gopher tortoise populations, and its frequency of occurrence.

The potential additive effects of fire ant (*Conomyrma* spp., *Solenopsis invicta*) predation on hatchling mortality was simulated, based on field and experimental data for clutch size, hatching success, and predation in the western range from study sites at Camp Shelby and DeSoto National Forest, Mississippi (Epperson and Heise 2001, entire). Without fire ants, the annual multiplicative population growth rate (lambda) was 1.018, with stable, slightly growing populations. With fire ants, lambda was 0.977, with a declining population trend and eventual extirpation. In subsequent VORTEX modelling, it was found that if the mortality from fire ant depredation is additive to other mortality sources, then all populations with an initial size from 10 to 200 gopher tortoises were extirpated within 200 years, with a mean time to extirpation from 32.2 to 80.9 years (McDearman 2006, pp. 6–7).

Population dynamics of turtles, as long-lived animals, have commonly been considered sensitive to demographic changes in adult survival and, in some cases, juvenile survival (Gibbons 1987, entire; Congdon et al. 1993, entire; Heppell 1998, entire). Likewise, models and simulations of gopher tortoise populations are most sensitive to adult, hatchling, and juvenile survival rates (Miller 2001, entire; Epperson and Heise 2001, entire; Wester 2005, entire). For example, the small but positive population growth rates modeled for a stable base population became negative when mortality of the 3–4 + year age class increased from 3.0 to 5.0 percent, or the yearling (0–1 year age class) mortality increased from 95 to 97 percent (Miller 2001, p. 10; McDearman 2006, p. 7). Hatchling survivorship has been shown to be the most critical life history stage driving viability of gopher tortoises due to the very small likelihood that hatchlings survive to their second year (Tuberville et al. 2009, p. 33). A 5 percent decrease (from 96 percent in the baseline model to 91 percent) in hatchling mortality was sufficient to shift the population growth rate from slowly declining (–1.5 percent) to slowly increasing (+1.1 percent) and to eliminate the probability of extinction within the 200 years (Tuberville et al. 2009, p. 33).

Changes in other vital parameters also affect population growth, although generally not to the proportionate extent of mortality (McDearman 2006, p. 7). The finite rate of increase changed from 1.002 to 1.006 when the minimum age of first reproduction was reduced from 20 to 17 years, and independently, average clutch size was increased from 4.79 to 5.60 (Table 2, McDearman 2006, p. 20). An increase in juvenile (0–1 year) mortality from 94.89 percent to 96.89 percent effectively reduced successful reproduction for each female by 40 percent and eliminated population growth, leading to long-term decline and/or extirpation (Miller 2001, entire).

Highly accurate measurements and assessments of sensitive demographic parameters affecting population growth and viability likely will be difficult to attain with confidence, particularly in small populations. Studies from large populations or cross-sectional studies from several populations may be required, if environmental heterogeneity can be controlled. With uncertainty in measuring key demographic and environmental factors, the goals and objectives for establishing viable populations and habitat should include larger populations than those identified as minimally viable.

The effects of geographic location and habitat quality on population growth rates for tortoises have been investigated (Tuberville et al. 2009, pp. 17-22). All model scenarios resulted in population declines of 1–3 percent per year and varied as a function of both location and habitat quality. Populations in the southern portion of the range were the most stable, whereas populations at the edge of the range were the least stable, particularly when found in marginal habitat (Tuberville et al. 2009, p 17). This highlights the importance of habitat management in stabilizing population growth for the species. While gopher tortoise populations may not persist if habitat quality remains poor for long periods of time, populations of at least 100 gopher tortoises were found to be reasonably resilient to variations in habitat quality and geographic location, but only populations of at least 250 tortoises were found to be able to persist for 200 years (Tuberville 2009 et al., p. 19).

A Gopher Tortoise Council (GTC) workshop defined minimum viable population (MVP) in terms of acceptable benchmarks for the purpose of conservation and recovery efforts and did not determine absolute minimum thresholds (GTC 2013, entire). Viability, as used under the MVP definition, is more of a "rule of thumb" for conservation planning purposes, and thus does not exactly align with the definition of viability used in this SSA (see Chapter 1, pages 7-8). A viable tortoise population, according to GTC MVP guidelines, was defined as consisting of at least 250 adult tortoises, at a density of at least 0.4 tortoises per ha, with an even sex ratio and evidence of all age classes present, on a property with at least 100 ha of high quality, well-managed tortoise habitat (GTC 2013, pp. 2-3). A primary support population was defined as consisting of 50-250 adult tortoises and these are considered as candidates of reaching viability through habitat restoration, natural recruitment increases, or population augmentation. A secondary support population was defined as <50 tortoises that have more constraints to reaching viability, but are important for education, community interest, and augmentation, and can persist long-term with rigorous habitat management and/or connectivity with other populations (GTC 2014, p. 4). It should be noted that support populations may persist for a long period of time under high-quality habitat conditions (Folt et al. 2021, p. 13), but are likely more vulnerable to stochastic events than populations that meets the minimum viable population MVP threshold (Miller et al. 2001, p. 28; GTC 2014, p. 4). In fact, a recent study from Conecuh NF demonstrated that some small populations remain stable or growing over a thirty-year period (Folt et al. 2021, entire).

2.7 Resource Needs and Habitat

Gopher tortoise habitat requirements include sufficient areas of open pine or other uplands where adequate sunlight reaches the forest floor to stimulate the growth and development of the herbaceous plant stratum for forage, with sufficient warmth for basking and the incubation of eggs (Landers 1980, p. 8; Lohoefener and Lohmeier 1981, entire; Auffenberg and Franz 1982, pp. 99, 104-107, 111, 120; Jones and Dorr 2004, p. 461; McDearman 2006, p. 2; McIntyre et al. 2019, p. 287). Low food availability negatively affects tortoise population densities and can be caused by plant growth suppression due to accumulated leaves, litter, low light associated with canopy closure (Landers and Speake 1980, p. 522), due, in turn to lack of regular disturbance such as prescribed fire. Longleaf pine and other open pine systems, sandhills, scrub (e.g., oak-palmetto, coastal, rosemary), xeric hammock, and ruderal (disturbed; e.g., roadsides, rights-of-way, grove/forest edges, fencerows, and clearings) plant communities most often provide the conditions necessary to support gopher tortoises (Auffenberg and Franz 1982, p. 99).

In the western fringe of the range, soils are loamy and contain more clay (Lohoefener and Lohmeier 1981, p. 240; Auffenberg and Franz 1982, pp. 114-115, Mann 1995, pp. 10–11). Higher clay content in soils may contribute to lower abundance and density of tortoises such as in Mississippi versus the eastern portion of the range (Estes and Mann 1996, p. 24; Jones and Dorr 2004, p. 461). Xeric (dry) conditions are less common west of the Florida panhandle (Craul et al. 2005, pp. 11-13). Ground cover in the Coastal Plains can be separated into two general regions, with the division in the central part of southern Alabama and northwest Florida. To the west, bluestem (*Andropogon* spp.) and panicum (*Panicum* spp.) grasses predominate (Mann 1995, p. 11); to the east, wiregrass (*Aristida stricta*) is most common (Boyer 1990, p. 3). However, gopher tortoises do not necessarily respond to specific plants but rather the physical characteristics of habitat (Diemer 1986, p. 126). Historically, gopher tortoises occurred in open longleaf pine forests, savannas, and xeric grasslands that covered the coastal plain in the Southeastern United States, and while some areas of habitat might have had wetter soils at times and been somewhat cooler, these areas were generally xeric, open, and diverse (Ashton and Ashton 2008, p. 73).

In addition to meeting foraging needs, gopher tortoises require a sparse canopy and litter-free ground for nesting (Landers and Speake 1980, p. 522). In Florida, the number of active burrows per gopher tortoise was found to be lower where canopy cover was high (McCoy and Mushinsky 1988, p. 35). Females require almost full sunlight for nesting (Landers and Buckner 1981, p. 5) because eggs are often laid in the burrow apron or other warm, sunny areas for appropriate incubation (Landers and Speake 1980, p. 522).

At one site in southwest Georgia, most gopher tortoises were found in areas with 30 percent or less canopy cover (Boglioli et al. 2000, p. 703). However, more extensive examination of the same site revealed that canopy cover alone may not always be indicative of gopher tortoise habitat (McIntyre et al. 2019, p. 288 – 289). Ecotones created by clearing were also favored by gopher tortoises in north Florida (Diemer 1992b, p. 162). When canopies become too dense, usually due to fire suppression, gopher tortoises tend to move into ruderal habitats such as roadsides with more herbaceous ground cover, lower tree cover, and significant sun exposure (Garner and Landers 1981, p. 122; McCoy et al. 1993, p. 38; Baskaran et al. 2006, p. 346). In Georgia, open-canopy pine areas were more likely to have burrows, support higher burrow densities, and have more burrows used by large, adult gopher tortoises than closed-canopy forests (Hermann et al. 2002, p. 294). Historically, open-canopied southern pine forests were maintained by frequent, lightning generated fires. Subsequently, in addition to prescribed fire, grazing, mowing, roller chopping, timber harvesting, and selective herbicide application may be used in the restoration, enhancement, and maintenance of some gopher tortoise habitat (Cox et al. 2004, p. 10; Ashton and Ashton 2008, p. 78; GDNR 2014, unpaginated; Rautsaw et al. 2018, p. 141).

Burrows

The burrows of a gopher tortoise (Figure 2.4) are the center of normal feeding, breeding, and sheltering activity. As mentioned above, gopher tortoises excavate and use more than one burrow for shelter beneath the ground surface. Burrows, which may extend for more than 30 feet, provide shelter from canid predators, fire, winter cold and summer heat (Hansen 1963, p. 359; Landers 1980, p. 6; Wright 1982, p. 50; Diemer 1986, p. 127; Boglioli 2000, p. 699). Digging burrows benefits the surrounding habitat by returning leached nutrients to the surface (Auffenberg and Weaver 1969, p. 191; Landers 1980, p. 2), and increasing the heterogeneity (diversity) of the habitat in the vicinity of the burrow (Kaczor and Hartnett 1990, p. 107). Burrows can also serve to shelter seeds from fires (Kaczor and Harnett 1990, p. 108). Many organisms adapted to hot summers and cool winters use gopher tortoise burrows for refuge (Landers and Speake 1980, p. 515). An estimated 60 vertebrates and 302 invertebrates share tortoise burrows (Jackson and Milstrey 1989, p. 87). Gopher tortoise burrows not only provide other species shelter from extreme environmental conditions and predation but may also be used as feeding or reproduction sites, and as permanent microhabitats for one or all life stages (Jackson and Milstrey 1989, p. 86).

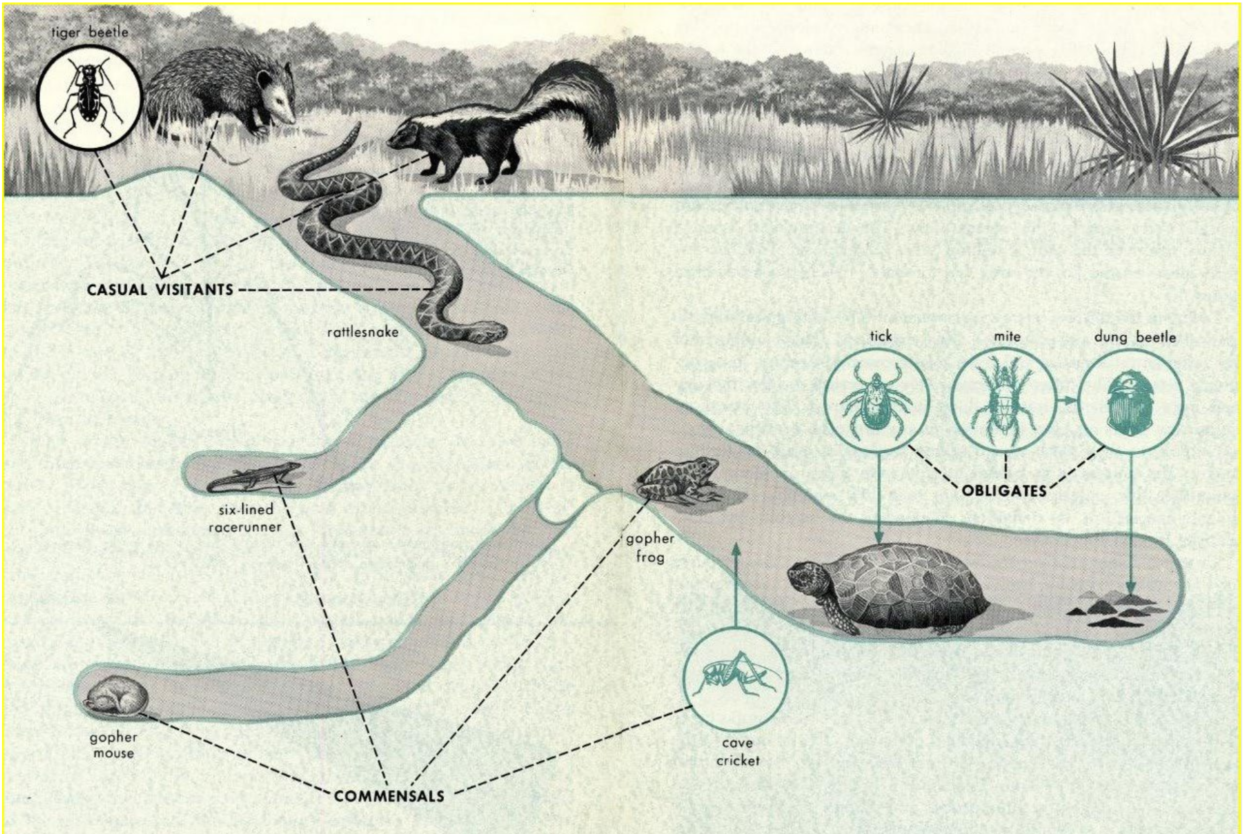


Figure 2. 4-Diagram of a gopher tortoise burrow showing a gopher tortoise near the end chamber, commensal species using side chambers, and casual visitants near the burrow opening. Image source: Dr. Walter Auffenberg, Florida Museum of Natural History (Auffenberg 1969).

In poor quality habitat where shrubs and hardwoods have encroached, gopher tortoises tend to excavate and use fewer burrows, likely due to limited availability of sites that are sufficiently open. The term “active burrow” is applied to burrows exhibiting indications they are likely inhabited by a gopher tortoise. Characteristics of active burrows (Figure 2.5) include fresh soil excavated from the interior of the burrow, deposited on the apron at the burrow entrance; tortoise feces on the apron or near the burrow entrance; and presence of eggshells and tracks (Auffenberg and Franz 1982, p. 76; Estes and Mann 1996, p. 11). Inactive burrows, which do not display conditions of recent use and occupancy by a gopher tortoise, are considered to be used as part of the annual home range of one or more gopher tortoises but are not currently occupied by a gopher tortoise. Indicators of inactive burrows include suitable size and shape of the burrow entrance; a recognizable apron of bare soil with or without encroachment of grasses or shrubs; and small amounts of leaf litter in the entrance that have not been moved by a gopher tortoise (Auffenberg and Franz 1982, p. 76; Estes and Mann 1996, p. 11). Abandoned burrows are unlikely to be used by a gopher tortoise and, normally, exhibit indications of erosion, a loss of shape and structure, and no apron. Occupancy of gopher tortoise burrows cannot be confirmed based on these characteristics.

Figure 2. 5-Images showing active gopher tortoise burrows, one in an open-canopy pine area (left) and the other showing gopher tortoise tracks (right) in a recently planted pine stand. Image credit: Angela Larsen-Gray.

Sand texture is most important in the formation of the burrow apron, which impedes rain from entering the burrow (Landers 1980, p. 6). Sand depth is also important because soil layers underlying it, such as clay, can impede digging and influence burrow depth (Baskaran et al. 2006, p. 347). Burrows in clay-type soils are more susceptible to regular winter flooding (Means 1982, p, 524). Additionally, burrows are shorter in clay soils, and clay soils may adversely affect nest success because these soils reduce exchange of oxygen and carbon dioxide (Wright 1982, p. 21; Ultsch and Anderson 1986, p. 790; Smith et al. 1997a, p. 599). Larger diameter burrow openings tend to result in longer burrows (Hansen 1963, p. 355). Burrows are usually distributed on higher ridge tops and their depths are sometimes limited by the water table (Baskaran et al. 2006, p. 346).

Tortoises select and prefer burrow sites in open canopy areas where sunlight reaches the ground (Boglioli et al. 2000, p. 703; Rostal and Jones 2002, p. 485). Such sites reflect areas where herbaceous plants for food are more abundant on the forest floor and, for females, sunlight and soil temperatures for egg incubation are more suitable. Also, males select sites and burrows that increase their proximity to females and breeding opportunities (Ott-Eubanks et al. 2003, p. 318; Boglioli et al. 2003, p. 849). The repeated use and travel to the same burrows by individual tortoises in stable habitat reveal that tortoises know the geography of their home range, burrows, and the location of neighboring tortoises (Ott-Eubanks et al. 2003, p. 318).

CHAPTER 3 – FACTORS INFLUENCING VIABILITY

Gopher tortoise life history, habitat needs, potential influencing factors (negative and positive) that are likely to affect the viability (Figure 3.1) of the species currently and into the future are identified and discussed in this chapter. Specific information and metrics associated with the current condition of gopher tortoise populations and habitat are discussed in Chapter 4.

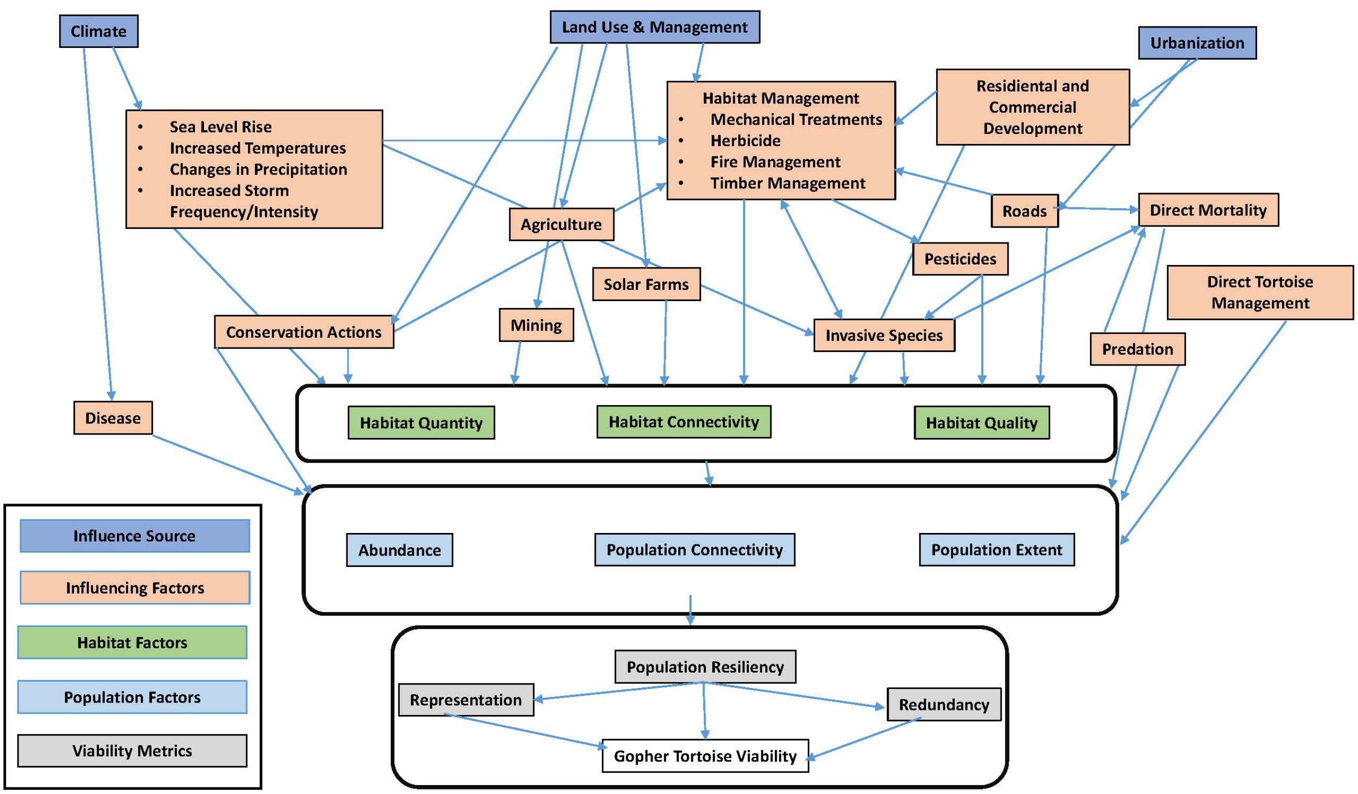


Figure 3. 1-Factors influencing the viability of the gopher tortoise.

3.1. Habitat Loss and Fragmentation

Gopher tortoise habitat comprises well-drained sandy soils (burrowing, sheltering, and breeding), with an open canopy, sparsely vegetated midstory, and abundant herbaceous groundcover (feeding). Gopher tortoise habitat occurs in a variety of upland natural communities such as sandhill, scrub, pine flatwoods (mesic and scrubby), xeric hammock, coastal habitats, and anthropogenic landscapes such as rights-of-way, pasturelands and planted pine stands. At a landscape scale, large swaths of interconnected, high quality habitat patches are likely to support viable populations, and ultimately lead to high resiliency of the species. Historically, open canopy conditions were maintained by frequent fires. Currently, habitat management is accomplished using prescribed fire, mechanical treatments (including timber harvesting), and herbicides. Habitat management activities may be implemented singularly or in combination (e.g., roller chopping followed by prescribed fire).

Urbanization and major roads (development; Auffenberg and Franz 1982, p. 112; Diemer 1986, p. 128; Diemer 1987, p. 74-75; Enge et al. 2006, p. 4), incompatible and/or insufficient habitat management, and certain types of agriculture (Lohoefener and Lohmeier 1984, pp. 2–6; Auffenberg and Franz 1982, p. 105; Hermann et al. 2002, pp. 294-295) can negatively impact gopher tortoises and gopher tortoise habitat. Invasive species can influence gopher tortoises either through direct impacts (e.g., predation; Mann 1995, p. 24;Engeman et al. 2009, p. 84; Engeman et al. 2011, p. 607; Dziadzio et al. 2016b, p. 531; Bartoszek et al. 2018, pp. 353-354) or alterations to habitat structure and/or function (Lippincott 1997, pp. 48-65; Bastios 2007, p. 24).

Climate change has the potential to negatively impact habitat through the loss of habitat due to sea level rise (Hayhoe et al. 2018, entire), limitations on number of suitable burn days due to changes in temperature (Kupfer et al. 2020, entire), precipitation, increased flooding due to predicted increases in the severity of hurricanes (Castellon et al. 2018, pp. 11-14), and human migration from inundated coastal areas, to inland areas, with subsequent impacts to gopher tortoises (Ruppert et al. 2008, p. 127).

Conservation of habitat through land acquisition and conservation actions on public and private lands and the retention of private forest lands, reduces the severity of some of these threats by providing protection of habitat across the landscape, maintaining connectivity between habitat patches, and increasing the opportunity for beneficial habitat management actions.

3.1.1. Historical Loss of Longleaf Pine and Longleaf Restoration

While gopher tortoises do occur and persist in open canopy stands of several southern pine species, gopher tortoises were historically associated with longleaf pine systems. Longleaf pine ecosystems are fire-dependent and once dominated the Coastal Plain of the Atlantic and Gulf coast regions, from Virginia to Texas (Ware et al. 1993, p. 447). Longleaf pine forests once covered an estimated 92 million acres (37 million ha) (Frost 1993, p. 20). By the 20th century, longleaf pine communities declined to less than 3 million acres due to forest clearing and conversion for agriculture, conversion from longleaf to other pine species, and development (Landers et al. 1995, p. 39). As a result of fire suppression and exclusion in many areas, currently, only an approximate 3 percent of remaining longleaf acres is in relatively natural condition (Simberloff 1993, p. 3; Frost 1993, p. 17; Jensen et al. 2008, p. 16).

America's Longleaf Restoration Initiative (ALRI) is a collaborative effort involving multiple public and private partners actively supporting efforts to restore and conserve longleaf pine ecosystems with a goal to increase longleaf coverage on the landscape to 8.0 million acres (3.2 million ha) (ALRI 2021, unpaginated). These efforts are focused within "significant landscapes" where Local Implementation Teams (LITs) are leading conservation efforts by coordinating partners, developing priorities, and fundraising to implement on-the-ground conservation (Figure 3.2). Several LITs are working within the range of the gopher tortoise to help restore longleaf pine on habitat utilized by gopher tortoises.

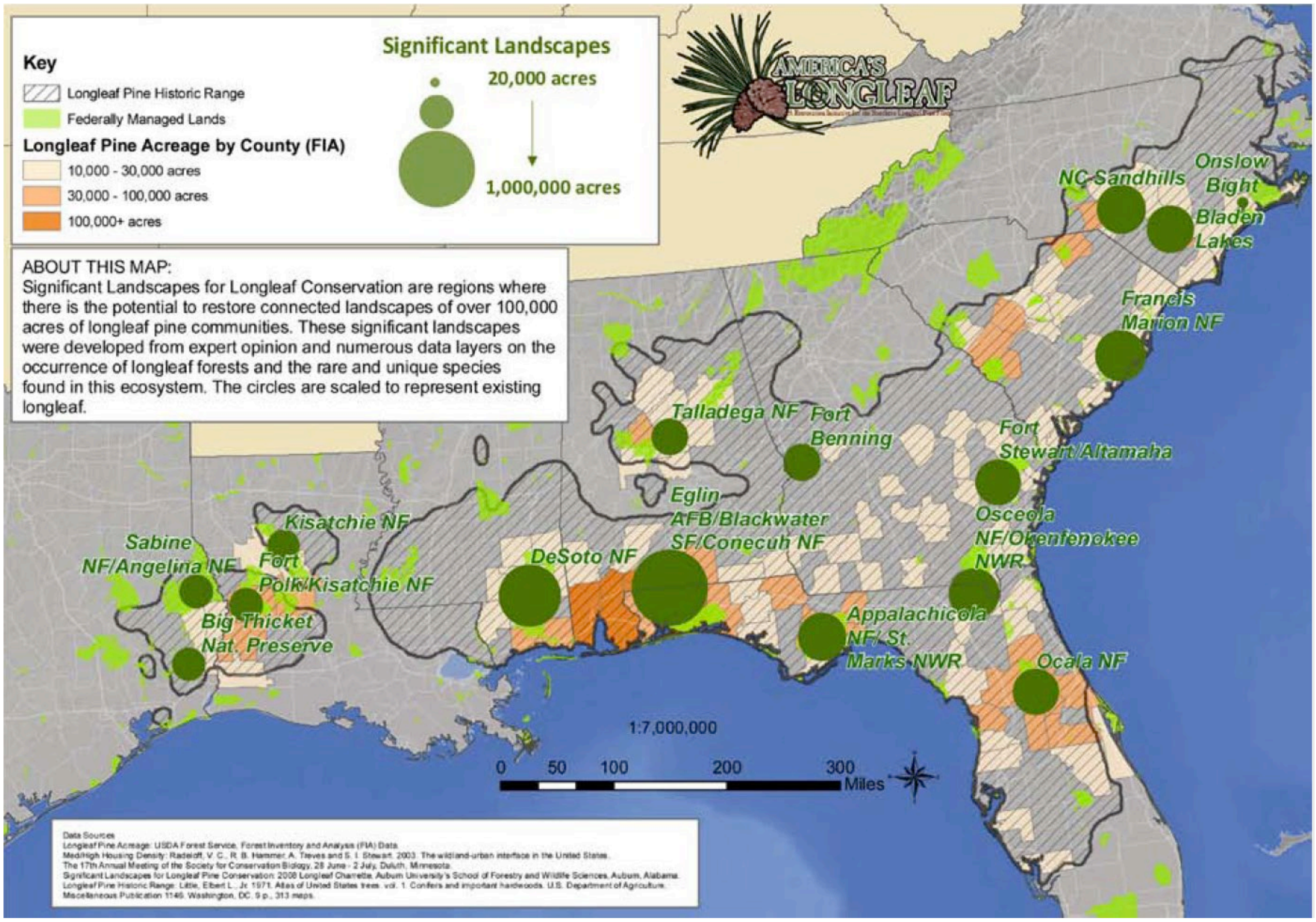


Figure 3. 2-Locations and relative size of existing longleaf acreages of Significant landscapes for Longleaf Conservation. Source: The Conservation Fund.

3.1.2 Fragmentation and Urbanization

The maintenance of habitat connectivity is important for gopher tortoise viability.

Human development of the landscape fragments and replaces natural areas with artificial structures, impervious surfaces, and manicured lawns and gardens containing non-native plant species (Sutherland 2009, p. 35), threatening wildlife communities, including gopher tortoise populations, that rely on a mosaic of interconnected uplands. In addition to the direct loss of habitat, development and urbanization may also threaten gopher tortoise populations on conservation lands by disrupting habitat connectivity across the landscape (decreasing immigration and emigration between local populations) and through the disruption of habitat management activities on conservation lands, particularly through the constraining of prescribed fire activities. In Florida, urban growth and development is identified as one of the primary threats to gopher tortoises (Auffenberg and Franz 1982, p. 112; Diemer 1986, p. 128; Diemer 1987, p. 74-75; Enge et al. 2006, p. 4). Georgia is also anticipated to see dramatic human population increases (Georgia Census 2021, unpaginated), leading to subsequent development and potential loss of gopher tortoise habitat.

Gopher tortoises can occur in residential areas despite the fact that these areas are typically of lower habitat quality. Urbanization impacts many wildlife species from direct loss of habitat, fragmentation of habitat, increased road mortality, increased human persecution, and by the increase in domestic predators, such as cats and/or dogs. Current research is lacking to quantify urbanized landscape impacts on survival, recruitment, health, and long-term persistence. However, urban tortoises may help bridge connectivity between natural habitats, though level of connectivity would vary significantly by how these areas are designed (e.g., presence of fencing, road density, habitat quality).

In addition to habitat loss, a direct impact from development could include mortality of gopher tortoises from entombment in their burrows (for more information regarding entombment, see Section 3.8). In the western portion of the range where the species is federally listed, individual gopher tortoises are translocated from development sites to avoid mortality for land development activities during consultation with the Service under sections 7 and 10 of the Act. Prior to 2007, gopher tortoise relocation was not mandated in Florida, but developers were required to mitigate for the loss of tortoises and habitat associated with the development site through an Incidental Take Permit. This mitigation was provided in the form of a monetary contribution or donation of protected habitat (i.e., conservation easement), with the goal of offsetting the effects of development projects on gopher tortoise populations in Florida. Although FWC no longer issues ITPs, they are perpetual, with many still active. Presently, Incidental Take permittees have the option to relocate gopher tortoises on-site or amend their permit to relocate tortoises to an approved recipient site for no additional mitigation. Since 2007 (76 FR 45130), in Florida, the state wildlife agency requires developers to relocate tortoises out of harm’s way (FWC 2007, p. 10). Other states (Georgia, Alabama and South Carolina) have some measure of legal protection for gopher tortoises, though gopher tortoise burrows are not protected uniformly across the range. When notified, these states work with developers when they identify tortoises on development sites. Conservation activities that assist in mitigating these direct impacts are discussed in detail in Section 3.9.3 (Relocation, Translocation, Recipient Sites, and Headstarting).

A primary driver of urbanization and subsequent habitat fragmentation impacting gopher tortoises is human population growth. Since 2010, with the exception of Mississippi, which shows a 6 percent decrease in human population, all other states within the limits of the historical range of the gopher tortoise have experienced growth in human populations with increases as of 2020 ranging from 3% in Louisiana to 15% in Florida (Table 3.1). Census projections over the next decade indicate similar percent increases from 2019 population numbers (Table 3.1). Additionally, census information available for Florida indicates an estimated 27% increase by 2045 from 2019 estimates (FEDR 2018, unpaginated).

State	2010	2020 (% change from 2010)	2030 Projections (projected % change from 2020)
Alabama	4,780,125	5,024,279 (increase 5%)	5,124,380 (increase 2%)
Florida	18,801,332	21,538,187 (increase 15%)	24,426,178 (increase13.4%)
Georgia	9,688,729	10,711,908 (increase 11%)	11,709,700 (increase 9%)
Louisiana	4,533,487	4,657,757 (increase 3%)	4,813,420 (increase 3%)
Mississippi	2,968,130	2,961,279 (decrease 6%)	3,092,410 (increase 4%)
South Carolina	4,625,366	5,118,425 (increase 11%)	5,488,460 (increase 7%)

Table 3. 1-Human population estimates and future projections (including percentage increases and decreases) for six states within historical range of the gopher tortoise (Blanchard 2007, p. 7; Culver College of Business 2021, unpaginated; FEDR 2018, unpaginated; Georgia Census

2021, unpaginated; Population Projections 2021, unpaginated; SCBCB 2009, p. 2; U.S. Census Bureau 2021, unpaginated).

3.1.3. Solar Farms

As interest in renewable energy increases, the development of solar farms across the landscape is also increasing (Figure 3.3). By 2019, Florida ranked fifth in the nation in total solar power generating capacity and utility (EIA 2018, unpaginated). In South Carolina, the state's net solar power production increased 70% between 2018 and 2019, with two dozen new solar farms becoming operational (EIA 2018, unpaginated). In Georgia, solar energy accounted for 2% of the in-state electricity in 2019 with half of the six largest facilities (capacities greater than 100 megawatts) coming on-line in 2019 (EIA 2018, unpaginated). While total solar generation is small in Alabama, it accounts for 4% of renewable energy in the state with the strongest solar resources located Southeast along the Gulf Coast (EIA 2018, unpaginated). Though the state's first facility came on-line in 2017, in Mississippi, utility-scale solar energy production is small, accounting for 0.5% of the state's total generation (EIA 2018, unpaginated). Solar power generated about one-tenth of Louisiana's renewable generation in 2020. Louisiana's utility-scale (facilities 1 megawatt or larger) solar generation was 40 times greater in 2020 than in 2019 (EIA 2018, unpaginated). A number of solar sites are known to have impacted gopher tortoise habitat. Some solar utility developers and companies recognize the potential impact that this type of development may have on rare species and their habitat and have begun working with conservation organizations to avoid and minimize impacts via strategic siting assessments (NASA Develop 2018, unpaginated). A primary concern regarding large-scale deployment of solar energy is the potentially significant land use requirements (Ong et al. 2013, p. iv), habitat fragmentation and possible exclusion of wildlife including gopher tortoises as a result of fencing, and the need to relocate tortoises from solar farm sites prior to construction. As solar farm development increases, particularly on rural lands, concerns over the protection of sensitive species such as the gopher tortoise are heightened (SELC 2017, p. 3).

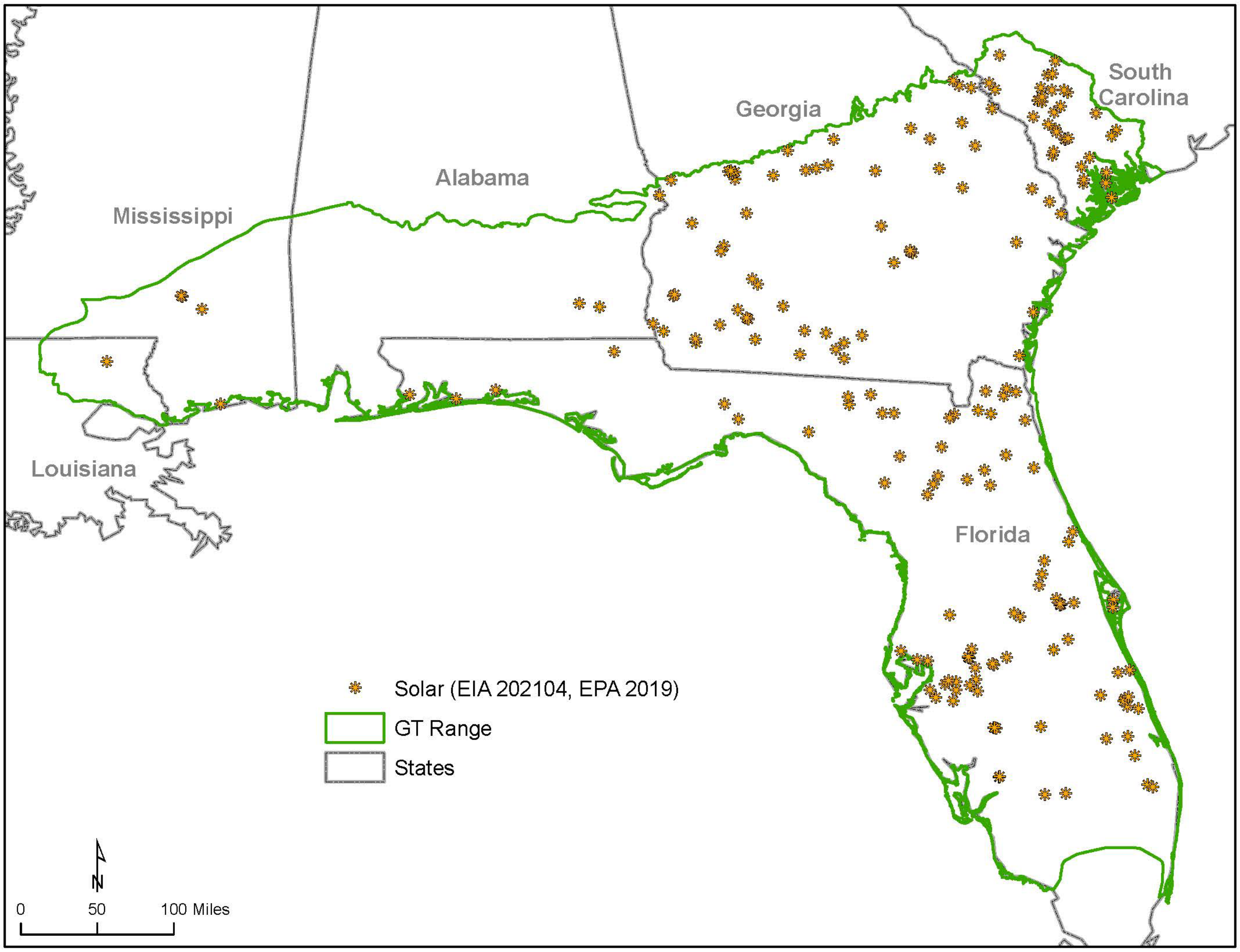


Figure 3. 3-Location of solar power plants within the range of the gopher tortoise.

3.1.4. Agricultural Lands

Over 80 percent of potential tortoise habitat is in private ownership, and much of this falls under agricultural uses. Surveys have shown that sites on suitable soils that had agriculture as the primary land use, were about 6 times less likely to have burrows and contained 20 times fewer gopher tortoise burrows than open pine sites (Hermann et al. 2002, pp. 294-295). Annually tilled agricultural fields are not inhabited by tortoises (Auffenberg and Franz 1982, p. 105). However, after several years of crop abandonment, succession of former agricultural fields into areas that are dominated by perennial herbaceous species may begin to attract gopher tortoises (Auffenberg and Franz 1982, p. 105). It may take many years for the preferred herbaceous species to be established on these fields, but if fire (or other vegetation management) is excluded from the site, the canopy will ultimately close and any gopher tortoises that may have re-colonized will evacuate the site (Auffenberg and Franz 1982, pp. 107-108). While the area of cropland in the South is forecasted to decline as much as 17 million acres (6.9 million hectares) by 2060 (from a base of 84 million acres (34 million hectares) in 1997) (Wear and Greis 2013, p. 45), it is unknown the extent to which abandoned agricultural fields will be restored to a level of suitability necessary to support viable gopher tortoise populations. However, restoration of abandoned agricultural fields into potential gopher tortoise habitat can be accomplished, provided soils are appropriate for gopher tortoises, as seen in the successes of the Conservation Reserve Program converting thousands of acres of agricultural land to forests.

3.2. Road Effects and Mortality

Roads create habitat fragmentation, isolate habitat, pose a barrier to movement, and increase direct mortality for many species of reptiles, including gopher tortoises (Andrews and Gibbons 2005, p. 772; Hughson and Darby 2013, pp. 227-228). Roads that bisect habitat pose hazards to gopher tortoises throughout the range (Figure 3.4), forcing individual gopher tortoises into unsuitable areas and onto highways (Diemer 1987, p. 75; Mushinsky et al. 2006, p. 38). Roads occurring within or adjacent to tortoise habitat are of particular concern because tortoises are attracted to road shoulders where open canopy, grassy areas are maintained (Steen and Gibbs 2004, entire; Steen at al. 2006, p. 271). In a recent study to determine if gopher tortoises use roadsides as movement pathways between larger habitat patches or as residential habitat, gopher tortoises appear to use roadsides independently of larger habitat patches, treating them as areas for residency as opposed to travel corridors among other habitat patches (Rautsaw et al. 2018, p. 141). Gopher tortoises residing along roadsides may be more susceptible to predation. Predators such as raccoons frequently use ecological edges and may occur in high densities in fragmented, suburban landscapes (Hoffman and Gottschang 1977, p. 633; Wilcove 1985, pp. 1213-1214).

While road mortality occurs in gopher tortoise populations, the extent to which it affects populations, or the species, is not well documented. Risk of road mortality on tortoises is likely related to the type of road and its traffic pattern (e.g., an unpaved rural road compared to a major highway), but this relationship has not been quantified. Increases in observed road mortality (episodic or consistent) may be a by-product of new construction, road expansion, or relocation of tortoises; however, there is no information directly linking road mortality to population declines and the magnitude of this influencing factor is uncertain. Information collected through FWC's citizen science application indicates that between 2014 and 2018, 470 tortoises were reported as sick, injured or dead, of which, 41% were tortoises injured or dead on roads (10th Annual GT CCA Report 2019, p. 95) (Figure 3.5).

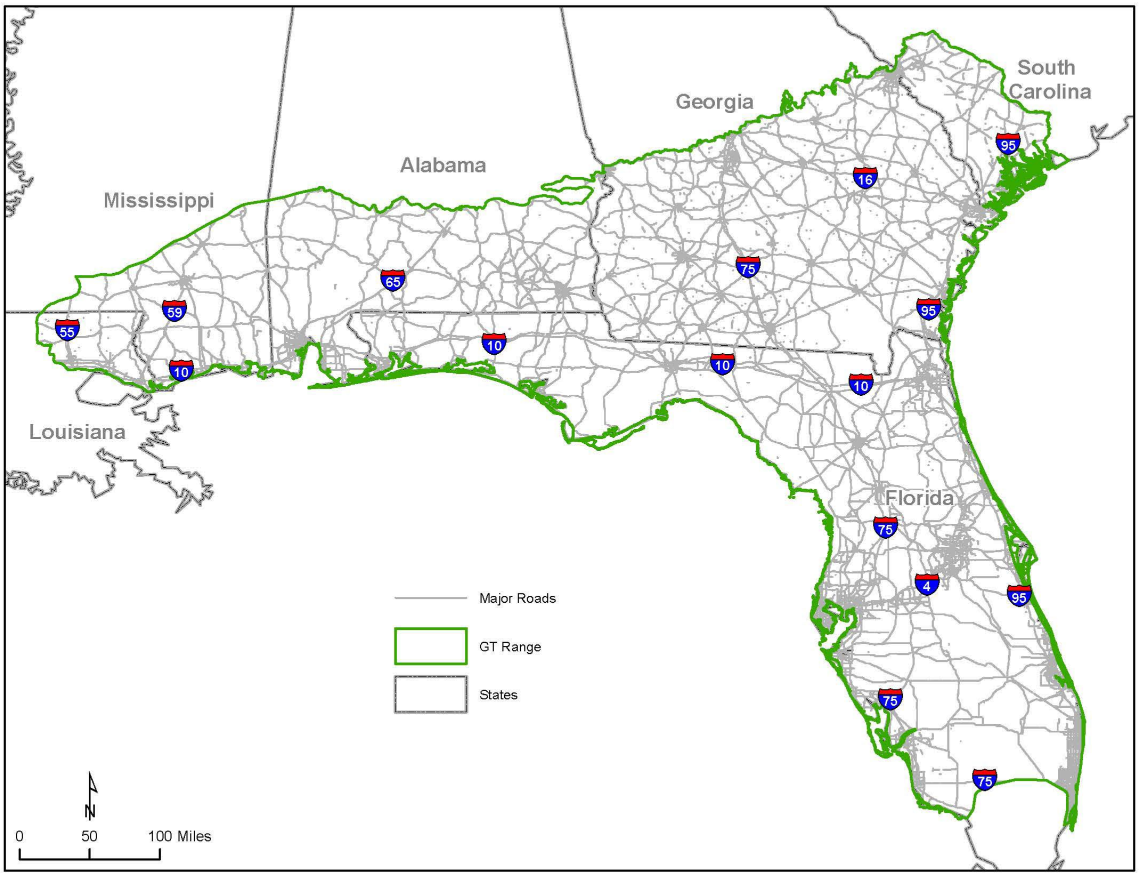


Figure 3. 4-Interstates and major freeways and highways occurring across the range of the gopher tortoise in Florida, Georgia, Louisiana, Mississippi, Alabama, and South Carolina.

Figure 3. 5-Images showing gopher tortoise burrow on road right-of-way (left) and road killed gopher tortoise (right). Image credit: Randy Browning (left) and Jeffrey M. Goessling, Ph.D. (right).

As development and subsequent habitat loss and fragmentation occurs, it is expected that gopher tortoises will continue to disperse to find better quality habitat, putting individual gopher tortoises at risk of road mortality. This threat is likely to increase as road densities and traffic volumes increase and habitat patches become more isolated and more difficult to manage (Enge et al. 2006, p. 10). Highway mortality of gopher tortoises will be highest where there are improved roads adjacent to gopher tortoise populations. Gopher tortoises in the vicinity of urban areas will be particularly vulnerable (Mushinsky et al. 2006, p. 362), especially in areas with heavy traffic patterns and/or high-speed limits. This threat is ongoing and will continue to occur in the future in peninsular Florida and urban centers in coastal portions of Georgia, Alabama and Mississippi where human populations are likely to increase as seen in urban modeling projections using SLEUTH (Terando et al. 2014, entire). Quantification of the effects of road mortality on gopher tortoise populations is difficult because there is no current rangewide monitoring effort for gopher tortoise road mortality.

The installation of wildlife barrier fences along roadways has the potential to minimize gopher tortoise road mortality. In Alabama, two road projects cumulatively resulted in the installation of approximately 16 kilometers (10 miles) of gopher tortoise fencing. The Mississippi Department of Transportation also used fencing to mitigate gopher tortoise road mortality and installed approximately 24 kilometers (15 miles) of fencing, which decreased road mortality in gopher tortoises from between 1 and 2 annually to none. The projects reduced or eliminated road mortality and contributed to sustainability of local gopher tortoise populations. However, they are small in scale and do not substantively reduce the threat of gopher tortoise road mortality throughout its range and they do not eliminate the habitat fragmentation caused by the roads. Additionally, while barrier fencing along roads may reduce road mortality, fencing may also further limit the movement of gopher tortoises.

3.3. Climate Conditions

In the Southeastern United States, the impacts of climate change are already occurring in the form of sea level rise and extreme rain events (Carter et al., 2018, p. 749). Changes in temperatures may result in more frequent drought, more extreme heat (resulting in increases in air and water temperatures), increased heavy precipitation events (e.g., flooding), more intense storms (e.g., frequency of major hurricanes increases), and rising sea level and accompanying storm surge (IPCC, 2014, entire). Higher temperatures and an increase in the duration and frequency of droughts will also increase the occurrence of wildfires and reduce the effectiveness of prescribed fires (Carter et al. 2018, pp. 773-774). Changes in climate may alter the abiotic conditions experienced by species assemblages, resulting in effects on community composition and individual species interactions (DeWan et al. 2010, p. 7; Carter et al. 2018, pp. 768-787).

Despite the recognition of climate effects on ecosystem processes, there is uncertainty about the exact climate future for the Southeastern United States and how the ecosystems and species in this region will respond. The Southeast is part of the transition zone between tropical and temperate climates where salt marshes, pine-dominated forests and hardwood forests meet mangrove forests, pine savannas and tropical freshwater wetlands in the Everglades. It should be recognized that the greatest threat to many species from climate change may come from synergistic effects. That is, factors associated with a changing climate may act as risk multipliers by increasing the risk and severity of more imminent threats. The effects of changing climate conditions are likely to influence gopher tortoises and gopher tortoise habitat.

Gopher tortoises exhibit temperature dependent sex determination, with pivotal temperature for a 1:1 sex ratio being observed at 29.3°C (84.7°F) (DeMuth 2001, pp. 1612-1613). Incubation temperature has also been shown to affect post-hatchling growth in gopher tortoises; eggs incubated at higher temperatures produced hatchlings that grew more than those incubated at lower temperatures, though growth rate was not determined to be significantly different until nearly 9-months post-hatching (Demuth 2001, p. 1614). Mean clutch sizes are also larger in warmer more productive environments (Ashton et al. 2007, pp. 355-362). Because of predicted increases in temperature across the Southeastern U.S. due to climate change, there are potential changes with skewed sex ratios, clutch sizes, hatchling success, and possibly hatchling condition. While temperatures are anticipated to increase in the future due to climate change, the extent to which this may influence gopher tortoise demography is uncertain as the gopher tortoise may modify nest site selection in at least two ways to buffer against potential impacts related to temperature dependent sex determination: selection of cooler nest sites (Czaja et al. 2020, entire), and altering timing of nesting to earlier in the season, and there is evidence that gopher tortoises may already exhibit both of these behaviors (Ashton and Ashton 2008, entire; Moore et al. 2009, entire; Craft 2021, pp. 42-45).

Frequency of severe hurricanes is predicted to increase in the future (IPCC 2014, entire; Carter et al. 2018, entire), and there is some potential for negative direct impacts to gopher tortoises. Gopher tortoise burrows may be impacted by flooding after a hurricane, causing abandonment, though the burrow may become useable again. Gopher tortoise movement was shown to significantly increase in areas that had a higher water table and frequent burrow flooding, though there does not appear to be large-scale shifts in movement to drier habitats for nesting during peak rains (Castellon et al. 2018, pp. 11-14). A study in Cape Sable, Florida, found a 76% decline in active burrows at the site during an 11-year period between 1990 and 2001, attributed largely to mortality as a result of declines in habitat quality and the effects of tropical storms (Waddle et al. 2006, pp. 281-283). Subsequently, in surveys done post hurricane Irma in 2018, evidence of activity in burrows was found but no tortoises were observed (Falk 2018, entire). In addition, over wash of coastal dunes may result in "salt burn" and loss of coastal vegetation, temporarily reducing forage availability in coastal natural communities used by gopher tortoises.

While other habitat management techniques may mitigate the reduced ability to implement prescribed fire, challenges associated with managing gopher tortoise habitat with prescribed fire are a substantial risk factor associated with climate change for this species. Predicted changes in temperature and precipitation due to climate change will limit the number of days with suitable conditions for prescribed burns (Kupfer et al. 2020, entire). This reduction in prescribed fire, combined with the effects of urbanization, will further restrict the ability to manage habitat with prescribed fire. As the ability to implement prescribed fire is increasingly constrained, the ability to reduce woody vegetation and maintain an open under- and mid-story will be limited, and gopher tortoise habitat will likely degrade. In addition to the constrained ability to implement prescribed fire in the future, modelling for the Southeastern United States suggests increased wildfire risk and a longer fire season, with at least a 30% increase from 2011 in lightning-ignited wildfire by 2060 (Vose et al. 2018, p. 239).

There is risk to coastal populations of gopher tortoises due to sea level rise and subsequent inundation and loss of habitat in coastal areas. Global mean sea level has risen 7-8 inches (16-21 cm) since 1900, with about half of that rise occurring since 1993 (Hayhoe et al. 2018, p. 85). In areas of the Southeast, tide gauge analysis reveals as much as 1 to 3 feet (0.30 to 0.91 m) of local relative SLR in the past 100 years (Carter et al. 2018, p. 757). The future estimated amount that sea level will rise depends on the response of the climate system to warming, and on the future scenarios of human-caused emissions (Hayhoe et al. 2018, p. 85). Additionally, the amount of gopher tortoise habitat predicted to be lost within a given population due to SLR varies considerably depending on the location of the population. Loss of habitat within a population will result in a decreased probability of population persistence.

Indirect impacts to gopher tortoises and their habitat may occur due to the relocation of people from flood-prone coastal areas to inland areas (Ruppert et al. 2008, p. 127), including the relocation of millions of people to currently undeveloped interior natural areas (Stanton and Ackerman 2007, p. 15). Alabama, Florida, Louisiana, and Mississippi's interior natural ecological communities will likely be impacted with the increasing need of urban infrastructure to support retreating coastal inhabitants. Increases in gopher tortoise habitat loss related to climate change would be in addition to the 20 percent loss projected to occur by 2060 due solely to people immigrating into Florida (FWC 2008, p. 2). Increasing threats of habitat loss due to coastal retreat is likely to also affect tortoise habitat inland from the Georgia, Alabama, and Mississippi coastal counties. The timing of these impacts will be dependent on the rate at which the sea level rises, and a gradual coastal retreat and concurrent impacts to gopher tortoises are likely during this time.

3.4. Disease

A number of diseases have been documented in gopher tortoises, including fungal keratitis (Myers et al. 2009, p. 582); iridovirus; ranavirus (Johnson et al. 2008, entire); herpesvirus; bacterial diseases related to *Salmonella* spp., *Mycoplasma* spp., *Helicobacter* sp. (Desiderio et al. 2021, entire), and *Dermatophilus*; and numerous internal and external parasites (Ashton and Ashton 2008, pp. 39-41). Upper Respiratory Tract Disease (URTD) resulting from two *Mycoplasma* species (*M. agassizii* and *M. testudineum*) has received the most attention recently (Figure 3.6). URTD has been documented throughout much of the tortoise's range (Berish et al. 2010, p. 696; McGuire et al. 2014a, pp. 737-739; Goessling et al. 2019, pp. 5-6), but the magnitude of threat URTD poses to gopher tortoise populations and tortoise demographics is uncertain (Karlin 2008, p. 1).

URTD has been linked to several large die-offs, the first of which occurred in 1989 on Sanibel Island, Lee County, Florida, and resulted in the estimated loss of 25-50 percent of the adult population (McLaughlin 1997, p. 6). Other large-scale mortality events implicating URTD as a causal factor have also occurred in Florida (Gates et al. 2002, entire; Rabatsky and Blihovde 2002, entire; Dziadzio et al. 2018, entire). Multiple dead individuals have also been found on sites where seroprevalence of *M. agassizii* was documented among living tortoises (Berish et al.

2000, p. 10). Other sites in the candidate range have documented instances of high seroprevalence of URTD (McGuire et al. 2014a, p. 738; Goessling et al. 2019, p. 5), but population-level effects of this disease were unknown. Additionally, there have been few symptomatic tortoises and no recorded deaths determined to be from URTD in the western range.

Figure 3. 6-Image of an adult gopher tortoise with nasal discharge associated with active Upper Respiratory Tract Disease (URTD). Image credit: Jessica McGuire.

Current hypotheses suggest that differences in virulence of various strains of Mycoplasma (Sandmeier et al. 2009, p. 1261) and increased susceptibility to infection due to environmental stressors (e.g., poor habitat quality) may increase risk of URTD outbreaks and associated mortality. However, tortoises have natural antibodies to *Mycoplasma* spp. (Hunter et al. 2008, p. 464) and these natural immune mechanisms may explain why die-offs are not more prevalent throughout the gopher tortoise's range (Gonynor and Yabsley 2009, pp. 1-2; Sandmeier et al. 2009, pp. 1261-1262). In contrast, research suggests that susceptible tortoises in high-seroprevalence (number of individuals exposed to disease) populations have decreased apparent survival and may experience a low level of increased mortality in the initial stages of disease

(Ozgul et al. 2009, p. 796). *Mycoplasma* spp. are spread through horizontal transmission via direct contact during courtship and mating activities (Jacobson et al. 2014, p. 260); thus, juvenile tortoises are less likely to be exposed to these pathogens. These juveniles may provide a pool of tortoises to aid in recruitment after a disease event (Wendland et al. 2010, p. 1257 and 1261); however, these size classes usually represent a small proportion of the overall population. Studies have documented low density populations with high proportions of immature tortoises (up to 71%) recovering from episodes of low apparent adult survival (Goessling et al. 2021, p. 140; Folt et al. 2021, p. 11).

URTD may also result in altered movement and behavior among gopher tortoises. Tortoises expressing severe clinical signs of URTD appear to alter their thermoregulatory behavior, basking outside the burrow more often at lower temperatures than asymptomatic tortoises (McGuire et al. 2014b, pp. 750-754). Tortoises have also been found to elevate their body temperatures behaviorally in response to acute infection (Goessling et al. 2017, p. 488). In addition, tortoises with severe clinical sign moved long distances over relatively short periods of time, potentially increasing dispersal rate of pathogens (McGuire et al. 2014b, pp. 750-754). Tortoises dispersing long distances increase their likelihood of encountering a road (i.e., a barrier), potentially limiting spread of disease but increasing risk of road mortality. However, other studies have found higher apparent survival of seropositive gopher tortoises than for seronegative individuals and suggested 1) this was due to seropositive tortoises representing those that survived the initial infection, and 2) that seropositive tortoises were less likely to emigrate from the site than seronegative individuals (Ozgul et al. 2009, p. 794).

The degree to which exposure to the pathogen correlates to clinical signs of URTD or die-offs is unclear, as is the degree of transfer between animals, and the potential for decreased resistance to the disease based on stresses from habitat modification or relocation. Nasal scarring has been found to be the only positive link between clinical sign and URTD diagnostic tests for *M. agassizii,* and there appears to be no connection between active clinical sign and antibody presence of *Mycoplasma* spp. (Goessling et al. 2019, p. 5). While large-scale die-offs due to URTD appear to be rare, correlations between exposure to *Mycoplasma* spp. and population declines are variable among geographic locations (McCoy et al. 2007, p. 173). Identifying effects of this disease on tortoise populations will require continuous long-term monitoring (Berish et al. 2010, p. 704).

3.5. Human Harvesting and Other Activities

3.5.1. Human Harvest

Human harvest of gopher tortoises for consumption has historically influenced gopher tortoise populations, particularly in portions of the Florida panhandle. Tortoises were harvested in large numbers during the Great Depression, a practice which continued for decades following the Depression (Tuma and Sanford 2014, pp. 145-146). Prior to the closure of tortoise harvest in the late 1980s, a community in Okaloosa County held an annual tortoise cookout (Enge et al. 2006, p. 5). Low numbers of tortoises on sites with otherwise adequate habitat were speculated to reflect episodes of human predation in the 1980s and 1990s in Mississippi (Lohoefener and Lohmeier 1984, p. 1-30; Mann 1995, p. 18; Estes and Mann 1996, p. 21). Though this practice is not as common as it was prior to the 1980's, localized harvest still occurs in some rural areas across the Southeast (Rostal et al. 2014, p. 146) but is likely not a significant threat to current populations.

3.5.2. Rattlesnake Roundups

Rattlesnake roundups are locally organized events that offer prizes for the largest and most rattlesnakes caught. Historically, there were multiple roundups throughout the Southeast. With the recent conversion of two roundups to wildlife festivals (Claxton, GA in 2012; Whigham, GA in 2021), only one roundup remains in the Southeast, in Opp, Alabama.

The technique of blowing fumes of noxious liquids (otherwise known as “gassing”) down tortoise burrows was used primarily to collect snakes for these rattlesnake roundups (Means 2009, p. 139). It is thought this practice of gassing burrows harms or harasses the resident tortoise, though research that quantifies negative direct impacts (i.e., mortality) is limited. For example, one study found that no tortoises died or showed ill-effects after being gassed in their burrows; however, this study did not examine potential long-term impacts or repeated gassing (Speake and Mount 1973, p. 273). Tortoise burrows have also been excavated to retrieve snakes, sometimes in conjunction with burrow gassing (Means 2009, p. 139), rendering the burrows unusable.

Use of gasoline or other chemical or gaseous substances to drive wildlife from burrows, dens, or retreats is now prohibited across Southeastern states (for example, see Alabama Regulation 220–2–.11, Georgia codes § 27–1–130 and 27–3–130, Florida Administrative Code 68A-4.001(2), and Mississippi Code R 5-2.2 B). Effective enforcement of existing regulations would likely be enhanced with development of a regulated harvest or a prohibition on rattlesnake harvest. The conversion of the one remaining roundup to a wildlife festival would reduce incidental mortality of tortoises during rattlesnake collection. While gopher tortoise mortality due to rattlesnake collection has not been quantified, this threat is primarily historical and is not likely a significant influence on populations as only one roundup in the Southeast remains.

3.6. Predation

Gopher tortoise nest predation (Figure 3.7) varies annually and across sites, ranging from ~45-90 percent in a given year (Landers et al. 1980, p. 358; Wright 1982, p. 59; Marshall 1987, pp. 29-32; see section 2.4 Life History above). Gopher tortoises are most susceptible to predation within their first year of life, though most predation appears to occur within 30 days of hatching (Pike and Seigel 2006, p. 128; Smith et al. 2013, pp. 4-5). For example, a 65 percent predation rate has been documented within 30 days of hatching at Camp Shelby, Mississippi; no tortoises within this sample survived to adulthood (Epperson and Heise 2003, p. 310 and 322). Overall annual hatchling survival has been estimated to be approximately 13% (Perez-Heydrich et al. 2012, p. 342). In some instances, predation-related mortality may reach 100% within one-year post-hatching (Pike and Seigel 2006, p. 128).

Raccoons are the most frequently reported predator of nests and juvenile gopher tortoises (Landers et al. 1980, p. 358; Butler and Sowell 1996, p. 456); other predators of nests and/or juvenile tortoises include gray fox (*Urocyon cinereoargenteus*), striped skunk (*Mephitis mephitis*), Virginia opossum*,* coyote (*Canis latrans*), nine-banded armadillo, several snake species (e.g. *Agkistrodon piscivorus*, *Drymarchon corais*, *Masticophis flagellum*), fire ants (*Conomyrma* spp., *Solenopsis invicta*)., and red-tailed hawks (*Buteo jamaicensis*) (Douglass and Winegarner 1977, p. 237; Fitzpatrick and Woolfenden 1978, p. 49; Landers et al. 1980, p. 358; Wilson 1991, p. 378; Mann 1995, pp. 24–25; Butler and Sowell 1996, pp. 456-457; Wetterer and Moore 2005, p. 353; Pike and Seigel 2006, p. 128). Twenty-five species—12 mammals, 5 birds, 6 reptiles and 2 invertebrates—are known to be predators of eggs, emerging neonates, hatchlings, and older tortoises (Ashton and Ashton 2008, p. 27). Adult gopher tortoises are less likely to experience predation except by canines (e.g., domestic dogs, coyotes, foxes) and humans (Causey and Cude 1978, pp. 94-95; Taylor 1982, p. 79; Hawkins and Burke 1989, p. 99, Mann 1995, p. 24). Some predators are subsidized by human activities such as habitat fragmentation and edge effect (e.g., red imported fire ants) (Wetterer and Moore 2005, pp. 352-353), roads and infrastructure (e.g., red imported fire ants) (Stiles and Jones 1998, p. 343), increased availability of food (e.g., raccoons), reduction or elimination of top carnivores (e.g., coyotes, red foxes) (Crooks and Soule 1999, entire), ecological perturbations allowing range expansion (e.g., coyotes), and simply because some are domestic and associated with humans (e.g., cats and dogs).

The gopher tortoise is a long-lived species, which naturally experiences high levels of mortality in early life stages. However, it is unknown what predation rate populations can sustain without impacting population resiliency. Studies on the long-term survival of juveniles across multiple populations are needed to determine the survival rates needed within this life stage to sustain viable populations.

Figure 3. 7-Image of predated gopher tortoise nest (left) and hatchling gopher tortoise predated by raccoon (right). Image credit: Michelina Dziadzio.

3.7. Non-native and Invasive Species

3.7.1. Invasive Flora

The spread of exotic plants species has the potential to alter and degrade gopher tortoise habitat and ultimately influence gopher tortoise viability on a site. Some species postulated to impact tortoise habitat include kudzu (*Pueraria montana*), Chinese privet (*Ligustrum sinense*), Callery pear (*Pyrus calleryana*), natal grass (*Melinis repens*), and Japanese climbing fern (*Lygodium japonicum*), though quantified impacts of these species on tortoises are unknown. One species known to impact gopher tortoise use of habitat is cogongrass (*Imperata cylindrica*), a prolific invasive which occurs throughout much of the gopher tortoise's range. Unlike other invasive plant species in upland communities, cogongrass can rapidly spread following disturbances including prescribed fire (Yager et al. 2010, entire; Holzmueller and Jose 2011, p. 436-437). It can quickly form a tall, dense ground cover with a dense rhizome layer and can outcompete native vegetation (Dozier et al. 1998, pp. 737-740; Mushinsky et al. 2006, p. 360; Minogue et al. 2018, p.1-4). Widespread areas of dense cogongrass (Figure 3.8) could result in habitat loss as gopher tortoises do not use these areas, nor do they consume cogongrass (Basiotis 2007, p. 21). Cogongrass can also decrease gopher tortoise habitat quality by reducing forage quality and quantity, and the availability of burrowing and nesting locations (Lippincott 1997, pp. 48-65; Basiotis 2007, p. 24). Additional research is needed to quantify the impacts of invasive vegetation spread on gopher tortoises and the quality of their habitat.

Figure 3. 8-Image of a heavy infestation of cogongrass (*Imperata cylindrica*). Image credit: Mississippi Forestry Commission

3.7.2. Invasive Fauna

The red imported fire ant was first introduced to the Southeastern U.S. in the early 1900s and now occurs throughout the gopher tortoise's range (United States Department of Agriculture, 2017, unpaginated). Fire ants frequent disturbed sites, particularly areas with disturbed soil, and are common in upland areas used by gopher tortoises (Shearin 2011, p. 22, 30). Gopher tortoises often nest in the soft disturbed soil of their burrow aprons. In one study, red imported fire ants were present at most gopher tortoise burrows, though present more often in disturbed areas (Wetterer and Moore 2005, p. 352) including recently burned sites, indicating risk of fire ant-related mortality of tortoise may be high. Fire ants are not able to breach hard smooth-shelled intact eggs (Diffie et al. 2010, p.295), such as gopher tortoise eggs, but will attack tortoises in the nest prior to emergence (Butler and Hull 1996, p. 17; Dziadzio et al. 2016b, p. 531); fire ants will also depredate hatchlings after they have left the nest (Mann 1995, p. 24)(27 percent post-hatchling mortality by fire ants; Epperson and Heise 2003, p. 320). Fire ants are aggressive, and their stings can result in direct mortality and reduced survival by limiting growth, altering behavior, and changing foraging patterns (Wilcox and Giuliano 2014, pp. 3-4; Dziadzio et al. 2016b, pp. 532-533). There is concern that fire ants could be contributing to the decline of the gopher tortoise if predation on hatchlings by fire ants is an additive source of mortality (Mann 1995, p. 24; Dziadzio et al. 2016b, p. 536). In the western range, gopher tortoise conservation banks and other related sites must include fire ant monitoring and control as part of their management plan to reduce the effects of predation on tortoise eggs and hatchlings (74 FR 46401).

The nine-banded armadillo arrived in the Southeast through a combination of natural range expansion in the mid-19th century and accidental releases of individuals (Taulman and Robbins 1996, pp. 644-645). They use a wide range of natural community types including pine forests, areas frequently occupied by gopher tortoises. They dig their own burrows, but also use the burrows of other species such as the gopher tortoise (Mengak 2004, p. 2) and are known predators of tortoise eggs (Douglass and Winegarner 1977, p. 237; Degroote et al. 2013, pp. 77-79). The relative importance of armadillos as a nest predator appears to vary by site. One study (Dziadzio et al. 2016a, p. 1318) compared predation of natural and artificial tortoise nests at burrows to nests at other open sites and found that 69 percent of natural and artificial nests were depredated by armadillos. Armadillos have the potential to negatively impact gopher tortoise populations if they are an additive source of nest predation, but additional information is needed to evaluate the potential impact of this species on gopher tortoise populations across their range.

Other invasive species that may negatively impact tortoises include the Argentine black and white tegu (*Salvator merianae*), Burmese python (*Python bivittatus*), and black spiny-tailed iguana (*Ctenosaura similis*). Breeding populations of these species are currently restricted to parts of southern and peninsular Florida (Engeman et al. 2011, p. 602, 605, 607), though tegus have recently established a new population in Southeastern Georgia (Haro et al. 2020, entire). Tegus and Burmese pythons have been occasionally found farther north, including recent sightings of numerous tegus in South Carolina (Andrew Grosse, South Carolina DNR, personal communication); Burmese pythons have been found as north as South Georgia (EDDMapS.com) though this individual was likely an escaped or released pet and not part of a breeding population. All three species have been observed using tortoise burrows (Engeman et al. 2009, p. 84; Engeman et al. 2011, p. 607; Bartoszek et al. 2018, pp. 353-354); Burmese pythons have also been observed in breeding aggregations and laying eggs within burrows (Bartoszek et al. 2018, pp. 353-354), though pythons were not documented depredating gopher tortoises in this study. Tegus and spiny-tailed iguanas are documented predators of tortoise eggs and/or juvenile tortoises (Avery et al. 2009, p. 435; Johnson and McGarrity 2017, p. 1; Offner 2017, pp. 56-57). Because of the limited current range of these species and inconsistent results predicting the potential for range expansion (Engeman et al. 2011, p. 602; Goetz et al. 2021, entire), it is unknown the extent of impact these species may have on gopher tortoise populations. New regulations in Florida (F.A.C. 68-5), Alabama (Regulation 220-2-.26), and South Carolina (Regulation123-152(A)) are being implemented to limit possession of black and white tegus to prevent the establishment of tegus in the wild. Therefore, the current threat of these species on gopher tortoise appears low in comparison to other threats.

There are additional non-native faunal species that may depredate tortoises, damage burrows, and/or degrade tortoise habitat, such as the wild pig (*Sus scrofa*), domestic dog (*Canis lupus familiaris*), and possibly domestic cat (*Felis catus*). Frequent damage to burrows could result in increased stress and eventual burrow abandonment by the tortoise. All three of these non-natives are found across the Southeast, but limited data are available to quantify their impacts on tortoise populations. Additional research is needed to determine if these non-native fauna are negatively impacting tortoise populations, and if so, to quantify the extent of this impact.

3.8. Habitat Management

During a workshop on gopher tortoise conservation at the Joseph W. Jones Ecological Research Center in Georgia in 2003, 30 invitees from 6 states ranked habitat destruction and lack of habitat management (e.g., no prescribed fire program) as the top two major threats to the gopher tortoise (Smith et al. 2006, pp. 326-327). Gopher tortoise habitat is maintained via periodic fire. High quality gopher tortoise habitat will only require prescribed fire at regular intervals for natural community maintenance. Areas of degraded gopher tortoise habitat (e.g., areas with little or no fire) require active habitat management, frequently requiring multiple habitat management tools (mechanical and chemical treatments) in conjunction with the reintroduction of prescribed fire to restore natural conditions. However, not all habitat management activities are uniformly beneficial to the species. In general, management actions that minimize soil disturbance, protect burrows, and maintain a diversity of groundcover plants by ensuring that sufficient sunlight reaches the ground are beneficial. Conversely, actions that cause significant soil disturbances or result in the loss of diverse groundcover are detrimental. Additionally, the lack of habitat management or infrequent management is also detrimental. Prescribed fire, selective use of herbicide, mechanical vegetation management (e.g., roller chopping and mowing), and timber harvesting are valuable management techniques in the restoration, management, and maintenance of gopher tortoise habitat and are frequently used in combination.

Heavy equipment is routinely used to manage gopher tortoise habitat occurring on public and private lands throughout the species range. Heavy equipment is utilized in activities such as site preparation, reforestation, restoration, prescribed fire, herbicide applications, and harvest operations (timber, pine straw, etc.). In addition to direct impacts to adult and juvenile tortoises and eggs as a result of crushing, heavy equipment can occlude burrows or cause burrow collapse. Several occasions of direct mortality from heavy equipment have been reported (Landers and Buckner 1981, pp. 1-7). Entombment from burrow collapse or occlusion was historically perceived as a threat, however numerous studies have documented survival and self-excavation by tortoises in collapsed burrows (Landers and Buckner 1981, pp. 1-7; Diemer and Moler 1982, pp. 634-637; Diemer 1992b, p. 163; Mendonca et al. 2007, pp. 3-4; Wester and Kolb 2008, pp. 505-507). No significant differences in home range sizes, number of burrows used, or movement patterns between pre and post burrow collapse were found in one study (Mendonca et al. 2007, pp. 19–21). However, they did suggest potential negative effects of burrow collapse depending upon time of collapse which may include decrease in mating opportunities and potential for gravid females to be unable to deposit eggs in suitable locations. While more information is needed, heavy machinery likely presents risks to gopher tortoise eggs and juveniles, as they are more difficult to detect and therefore more difficult to avoid (Greene et al. 2020, p. 54). A study to experimentally address the distance at which heavy equipment might collapse burrows found that on average, machinery could be operated within approximately 3 m without causing damage. This is important because forest management, including application of prescribed fire, requires operation of a variety of vehicles and heavy equipment. Increasingly, land managers are incorporating best practices into their management plans, including a buffer distance around burrows to minimize disturbance and hazards (Smith et al. 2015, pp. 459-460).

The habitat management methods discussed below are implemented to varying degrees across a variety of different land ownership and use types (e.g., conservation land, commercial forestry, family-owned lands, etc.).

3.8.1. Prescribed Fire

Historically, upland areas commonly associated with gopher tortoises were maintained by frequent, lightning-generated fires, with peak lightning ignition occurring during the growing season, spring to early summer (Knapp et al. 2009, p. 3). Additionally, Native Americans and later, early colonial settlers often burned areas in the winter, fall or late summer for specific purposes or desired effects (Fowler and Konopik 2007, pp. 165-166). While there is uncertainty regarding natural burn regimes among various cover types and along environmental gradients, fire return frequencies throughout the gopher tortoise range are estimated to range between two and six years (Guyette et al. 2012, p. 330). Anthropogenic use of fire has likely been occurring for at least 10,000 years in the Southeastern United States through the early 1900s, when the practice of fire suppression became prevalent on the landscape. Fire suppression resulted in fire being mostly absent on public lands until the 1980s, however some private working lands (farming, grazing, logging) remained managed with fire (Fowler and Konopik 2007, p. 171).

Loss and alteration of gopher tortoise habitat from fire exclusion or fire suppression has a significant effect on survival of gopher tortoises (Boglioli et al. 2000, p. 704). Although burning has generally been accepted as a primary management tool, increased urbanization limits its use in many locations (Ashton and Ashton 2008, p. 78) due to concerns for safety, particularly as it relates to smoke management. Urban sprawl can fragment habitat that supports tortoise populations, and in many areas, complicates the logistics of performing adequate and seasonally appropriate burns, further straining staff and budget resources. Human health and safety issues increasingly complicate fire management as human population grows in an area, resulting in narrow windows of opportunity to implement prescribed fire due to the required parameters (for example: weather, site specifics) for a safe burn. Because of this, many areas of habitat remain unburned each year and without other habitat management, further succeed into unsuitable conditions, hindering the viability of gopher tortoise populations (Kupfer at al. 2020, p. 765).

Many Southeastern pine forests have dense canopies, a high prevalence of mid-canopy shrubs, and suppressed or absent herbaceous ground cover due to fire exclusion (Yager et al. 2007, p. 428). Several studies have reported the direct effect to gopher tortoise populations from fire suppression. Gopher tortoise population life expectancy declined in fire-suppressed savanna communities (Auffenberg and Iverson 1979, p. 562). Gopher tortoise population reduction has been observed to be directly correlated with the degree and rate of successional habitat modification (Auffenberg and Iverson 1979, p. 562). Fire exclusion was observed to reduce a gopher tortoise population by 100 percent in 16 years (Auffenberg and Franz 1982, p. 108). In south-central Florida, sandhill and scrubby flatwoods were abandoned by gopher tortoises after about 20 years of fire exclusion (Ashton et al. 2008, p. 528). However, other types of management actions (e.g., mechanical and chemical treatments) may offset, or slow habitat degradation caused by fire suppression.

The regular application of prescribed fire is critical for the maintenance of habitat conditions required by the gopher tortoise. When applied at appropriate intervals, prescribed fire reduces shrub and hardwood encroachment, and stimulates growth of forage plants such as grasses, forbs, and legumes (Thaxton and Platt 2006, p. 1336). The physical result of fire to tree and shrub species in most cases, reduces canopy cover and creates more light gaps allowing greater sunlight penetration to the ground (Iglay et al. 2014, pp. 39–40). This promotes establishment and maintenance of understory herbaceous forage and is also important for basking and proper gopher tortoise egg incubation. Prescribed fire during the growing season often produces a more beneficial response in the herbaceous layer than dormant season fire (Fill et al. 2017, pp. 156–157). Growing season fire stimulates flowering in many grasses, increases species diversity among understory plants, and result in higher understory biomass production (FWC 2007, p. 32). Although the growing season was historically the primary season for natural lightning-strike fires, variability in fire season, intensity, and frequency may be important to maintaining herbaceous species diversity (FNAI 2010, p. 43).

Periodic burning or shrub removal can increase gopher tortoise carrying capacity (Stewart et al. 1993, p. 79). Mixed stands of longleaf pine, turkey oak, and other scrub oaks that were burned every 2 to 4 years have been found to produce high densities of gopher tortoises (Landers 1980, p. 7). In south-central Florida, tortoises moved into areas that were frequently burned and abandoned areas that were unburned or burned less frequently (Ashton et al. 2008, p. 527). Burned areas have been found to have more herbaceous ground cover and gopher tortoises than in unburned oak-palmetto (Breininger et al. 1994, p. 63). Burned pine stands and longleaf pine scrub oak ridges had nest densities four times higher than in unburned pine stands and ridges in one study (Landers and Buckner 1981, p. 5). Herbaceous ground cover was found to be 2.3 times higher and gopher tortoise density was 3.1 times higher in a frequently burned slash pine plantation compared to an adjacent unburned natural sandhill area (Landers and Speake 1980, p. 518).

On sites with advanced hardwood encroachment, prescribed fire alone may be insufficient in reducing the coverage of undesirable vegetation. Mechanical or chemical treatments are frequently utilized to reduce hardwood competition to levels where prescribed fire can be effective (Greene et al. 2020, p. 50). In addition to use in augmenting a prescribed fire program, these management techniques are increasingly important for areas where prescribed fire use is not a viable option, such as habitat in urbanized areas (Ashton and Ashton 2008, p. 78).

3.8.2. Herbicide Applications

The application of herbicide is a vegetation management tool utilized by some land managers to control unwanted/undesired vegetation, often in combination with mechanical or prescribed fire or when prescribed fire cannot be used. Herbicide may also be required in conjunction with fire, to effectively eradicate infestations of highly invasive species such as cogongrass (Sellers et al. 2018, p. 3) or mid-story overgrowth of drought resistant woody vegetation.

In gopher tortoise habitat, the type of herbicide and rate and method of application should be selected to target shrub and hardwood species with minimal impacts to nontarget plant species, especially herbaceous groundcover vegetation utilized by gopher tortoises. In managed forests, herbicide is used to suppress shrub and hardwood mid-story growth to reduce competition to planted trees or stimulate desired growth of planted trees at critical periods. Fire is often used in conjunction with herbicide treatment on private working forest lands (Miller and Chamberlain 2008, pp. 776-777; Jones et al. 2009, p. 1168, Iglay et al. 2013, p. 40; Platt et al. 2015, p. 913), especially for site preparation purposes. According to a survey of 30 private landowners, herbicide is the most common management tool in the Southeast on production timber forests (Lang et al. 2016, p. 21). Herbicide is also consistently used in public land management and to maintain utility rights-of-way, often in combination with mowing or brush-hogging, which can provide suitable conditions or dispersal corridors for gopher tortoises.

Targeted herbicide application likely has less of a direct impact to gopher tortoises than broadcast spraying, where overspray is a risk. However, no information is available on the direct adverse effects to gopher tortoises, and herbicides used for gopher tortoise habitat management are generally not toxic to wildlife when applied in accordance with label specifications. The main threat from broadcast spraying is over-application using a broad-spectrum chemical, which can kill a significant amount of gopher tortoise forage where populations occur. Cut-and-squirt methods or direct injection into unwanted shrubs or trees is also an effective and less invasive, though more labor-intensive method, of herbicide application. When used carefully, herbicide is another tool for use in the management of gopher tortoise habitat.

Rates and concentrations of herbicide application vary considerably throughout the range of the gopher tortoise and outcomes are often dependent on environmental factors. The primary purpose of herbicide application varies as well, as it is used in many industries such as production forests, agriculture, restoration, and property maintenance. Research has shown that herbaceous groundcover can be maintained and enhanced through targeted and selective herbicide treatment, especially when used in conjunction with prescribed fire (Miller and Chamberlain 2008, pp. 776-777; Jones et al. 2009, p. 1168, Iglay et al. 2013, p. 40; Platt et al. 2015, p. 913). Herbicide can reduce mid-story vegetation growth resulting in more sunlight reaching the ground. In addition, a more open canopy and mid-story allows for proper incubation of eggs and thermal regulation (basking) of tortoises. More research is needed concerning herbicides' direct and indirect effects (short and long term) on gopher tortoise populations.

3.8.3. Mechanical Vegetation Management

Habitat management using mechanical means can be effective in reducing shrub and tree density to promote conditions favorable to herbaceous vegetation. Mechanical treatments are used in habitat restoration, site preparation to promote pine seedling survival and growth, maintenance, and in other agricultural and forestry endeavors. Mechanical vegetation management examples include mulching/chipping, subsoiling, shearing, stumping, root raking into piles or windrows, roller chopping, discing, and bedding. Depending on management objectives and treatment type, mechanical site preparation may result in substantial soil disturbance, affecting soil structure and chemistry and may increase invasive species on a site (Hobbs and Huenneke 1992, pp. 324–325, Jack and McIntyre 2017, p. 189). Careful and systematic cleaning of all mechanical equipment before and after use at every site can reduce the likelihood of spreading seeds of invasive plant species and are often incorporated into best management practices employed by managers (Miller et al. 2010, pp. 10–11). Some of the more intensive mechanical soil-disturbing practices utilized on some silvicultural sites include discing and bedding. While these activities do occur in gopher tortoise habitat, they tend to occur more so on wetter sites that are less suitable for gopher tortoises. Shearing and roller chopping are more common mechanical treatments used in restoration and for site preparation in areas likely to be used by gopher tortoises (Jack and McIntyre 2017, p. 200).

Because sandy and sandy-loam soils are much more erodible and mechanical site prep costs are increasing, herbicides are increasingly replacing mechanical site preparation on working forest lands in some areas. Mechanical vegetation management may be short-term option to maintain habitat in areas where fire use is restricted. Although mechanical vegetation management is effective in reducing the vertical structure and overgrowth in the mid and overstories, it is not an exact surrogate to fire in that mechanical treatments alone do not replicate the stimulation of plant growth, flowering and seed release, and soil nutrient cycling (Dean et al. 2015, pp. 55-56) provided by fire. In addition, mechanical treatments that are not followed up with herbicide applications and/or prescribed fire often result in more dense regrowth of hardwood or shrub species originally targeted for control. While empirical data on effects of mechanical vegetation management practices on gopher tortoise populations is largely lacking, best conservation practices (FDACS 2012, entire; FWC 2013, entire; USFWS 2013, entire; GDNR 2014, entire; FDACS 20115, entire) are available and are increasingly utilized by landowners and managers when using mechanical treatments (Jack and McIntyre 2017, p. 200).

Care should be taken in certain cover types where the gopher tortoise is known to occur. For example, in scrub, mechanical vegetation management is the only way to reset late successional conditions without burning under extreme wildfire conditions. However, scrub habitat is sensitive to soil disturbance and excessive soil disturbance may permanently alter it. Low ground pressure mulching equipment can be used to reduce above ground vegetation; however, care needs to be taken to leave the vegetation in a state where it can be consumed during prescribed burning. If vegetative material is mulched too fine or too much time elapses between mulching and burning, the material may not burn and may alter the soil and enhance conditions for invasive plant species (Hobbs and Huenneke 1992, pp. 324–325, Jack and McIntyre 2017, p. 189). While soil disturbance in scrub may permanently alter conditions, in the case of fire suppressed scrub, strategically creating sandy openings through mechanical soil disturbance may be necessary to create a matrix of open areas when coppicing fire adapted plants create a dense low overstory (S. Howarter, Service Biologist, comment submitted during review, 2021).

3.8.4. Timber Management

Not all forested lands provide appropriate conditions for gopher tortoises. However, on land with suitable soils and depending on forest management objectives, forests may provide the open canopy and the dense herbaceous groundcover conditions needed for gopher tortoise viability. . Several management goals are shared between timber and gopher tortoise habitat management. For example, reduction of hardwood competition is advantageous for the management of pine production and gopher tortoises because it favors pine survival and growth while allowing increased opportunity for sunlight to reach the ground, promoting herbaceous forage proliferation and suitable conditions for gopher tortoise basking and egg incubation (NRCS 2020, entire). Several management practices associated with working forests such as planting densities, age of stand, time until first and subsequent thinning(s), have a direct influence on whether these lands provide and maintain habitat for the species.

In slash pine plantations in Alabama, tortoise burrows were found in areas with the most open canopy. Burrow abandonment averaged 22 percent annually and abandoned burrows were associated with canopy closure, higher hardwood midstory, higher tree density and higher basal area (Aresco and Guyer 1999b, p. 32). Gopher tortoises more frequently abandoned burrows and emigrated from poor habitat conditions associated with closed canopy pines plantations (Diemer 1992a, p. 288; Aresco and Guyer 1999b, p. 32). Gopher tortoises often persist in pine plantations (slash and loblolly) at lower densities than reported in other cover types, and densities may be below the threshold necessary to sustain a viable population (Wigley et al. 2012, p. 42). Closed canopy conditions do not sustain gopher tortoises. A wide range of silvicultural practices influence canopy. Even-aged regeneration harvests often used in pine management provide abundant sunlight to stimulate groundcover vegetation establishment and growth. However, benefits are ephemeral as reforested areas grow and develop closed canopy conditions that shade groundcover (Greene et al. 2019, p. 203).

Most modern production forests incorporate management strategies to maintain open canopy conditions for the majority of a commercial stand's life. Reforestation at lower seedling densities can extend the interval to canopy closure. Pre-commercial and commercial thinning operations reduce canopy coverage and favors conditions that can support increased groundcover development. Recognizing that stand growth and development include periods of higher than preferred canopy cover, yet minimizing the duration of closed canopy conditions, is important not only to gopher tortoises but also commercial forests. Additionally, landscape considerations that provide for a matrix of structural conditions and connectivity or corridors linking gopher tortoise habitat are important to sustain populations in areas with production pine objectives. A National Council for Air and Stream Improvement (NCASI Inc.) survey of Member Companies revealed that open pine conditions are maintained over 47.2 percent of the life of a stand rotation (Weatherford et al. 2020, p. 4). Open pine in the above survey were limited to upland, xeric or mesic, pine dominated sites as coded by the USDA's Forest Inventory and Analysis program, further, open canopy was based on descriptions in Nordman et al. (2016, pp. 57–58), and Greene et al. (2019, p. 204).

Privately owned production pine forests are a dominant land use within the range of the gopher tortoise. Gopher tortoise persistence has been documented when suitable conditions occur on production pine forests (Diemer-Berish et al. 2012, pp. 51-52; Greene et al. 2019, p. 51). One study demonstrated positive responses in life history parameters four years following a clearcut on a pine plantation in northern Florida (Diemer-Berish and Moore 1993, p. 426). Most commercial timber operations grow loblolly or slash pine, rather than longleaf pine. Gopher tortoises may exploit appropriate stand conditions and other habitat characteristics, such as, stand structure conditions (e.g., basal area; overstory and midstory canopy closure) or suitable soil (Greene et al. 2020, pp. 52-53; Wigley et al 2012, p. 43), rather than a particular tree species. Common practices used in operational forestry such as stand establishment, thinning, and mid-rotation management can create similar structural conditions to fire-maintained conditions (NRCS 2020, p. 20). However, more information is needed, as there is no uniform method for tracking gopher tortoise activity on private lands. Additional research is needed to understand how management can further improve conditions, especially given the large area of private, working forests within gopher tortoise range. While some information regarding gopher tortoises is available (discussed in section 3.9.9), systematic surveys in managed forests across the range of the gopher tortoise are needed to properly assess populations on these lands and to allow for a more holistic assessment of the species range wide.

Contemporary management practices on private working lands have evolved in response to market demands that require conservation of biological diversity. Furthermore, development of diversified markets for forest products has increased forest management practices that benefit gopher tortoises (Greene et al. 2020, p. 55). Many corporate and non-corporate private landowners manage to high conservation standards to meet their objectives and in some cases to maintain important forest certifications such as Sustainable Forestry Initiative (SFI) or Forest Stewardship Council certification. Thinning and planting at lower densities, using herbicides to reduce midstory vegetation, and harvesting at an older stand age are more commonly used and provide vegetation conditions that gopher tortoises can occur and persist (Greene et al. 2019, p. 201; Greene et al. 2020, p. 55).

However, not all lands, public or private, are managed to these standards, and detrimental practices and lack of management continue to affect gopher tortoise habitat. Nearly complete groundcover weed control during site preparation or release treatments degrade habitat by removing forage plants. High seedling stocking rates quickly shade groundcover. Short timber rotations with a minimal proportion of the rotation being open canopied is problematic in that this practice may result in excessive shading, suppressed groundcover vegetation, and generally unsuitable conditions for gopher tortoises. Exclusion of prescribed fire and dense hardwood midstory encroachment within open canopied forests degrade habitat through suppression of groundcover and loss of open areas for burrowing and movement.

While we cannot quantify the extent to which detrimental practices occur and while these may not be practices utilized on certified forests, there is likely some percentage of habitat that has been impacted by these practices and therefore has influenced gopher tortoise viability. While we cannot account for all land management practices, there has been significant progress made between private landowners and conservation agencies, such as best conservation practices for gopher tortoises developed by states, and conservation incentive programs and partnerships that promote compatibility between timber and gopher tortoise management.

3.9. Conservation Measures

3.9.1. Federal and State Protections and Conservation

This section includes discussions of key protections and conservation efforts provided by various federal and state entities.

Federal

Natural Resources Conservation Service (NRCS)

The NRCS offers technical and financial assistance to help agricultural producers voluntarily conserve gopher tortoise habitat on private lands. This assistance helps producers plan and implement conservation activities and practices that provide benefits to several species, including the gopher tortoise while balancing conservation practices with natural resource and production goals.

The gopher tortoise is a nationally identified target species of the Working Lands for Wildlife (WLFW) partnership, which is a collaborative approach to conserving habitat on working lands. The NRCS works to restore longleaf pine across its historical range through the Longleaf Pine Initiative (LLPI). Additionally, NRCS conservation practices that benefit gopher tortoises include prescribed fire, forest stand improvements, herbicide applications, and brush management (NRCS 2020, pp. 22-23). Since 2012, NRCS has certified 943,740 acres (378,276 ha) in which private landowners have received assistance to implement management practices that benefit gopher tortoises and gopher tortoise habitat (Table 3.2). The WLFW program focused on promoting increased use of prescribed fire, improving vegetation management, re-establishing longleaf forests, supporting prescribed grazing management, and protecting existing quality habitat to benefit gopher tortoises across the range of the species (NRCS 2018, p. 1).

Table 3. 2-Gopher Tortoise Project Boundary: WLFW and LLPI Totals by Practice and Year. Data submitted by NRCS.

	Sum of Certified Acres by Year								
Practice and Priority	**Sum of 2012**	**Sum of 2013**	**Sum of 2014**	**Sum of 2015**	**Sum of 2016**	**Sum of 2017**	**Sum of 2018**	**Sum of 2019**	**PRACTICE SUMS**
Core Practices	**8,371.0**	**52,245.8**	**79,935.7**	**34,466.3**	**20,767.8**	**5,062.4**	**6,897.4**	**5,490.8**	**213,237.2**
Gopher Tortoise	**3,507.0**	**49,873.0**	**79,749.7**	**34,269.5**	**20,552.4**	**3,896.7**	**6,742.8**	**3,975.2**	**202,566.3**
Early Successional Habitat Development-Mgt	110.0	1,459.7	1,605.4	1,924.6	3,084.0	100.4	390.7	36.0	8,710.8
Restoration of Rare or Declining Natural Communities	1,781.3	7,396.9	11,057.0	4,936.3	5,368.9	1,178.3	672.3	37.0	32,428.0
Upland Wildlife Habitat Management	1,615.7	41,016.4	67,087.3	27,408.6	12,099.5	2,618.0	5,679.8	3,902.2	161,427.5
Longleaf Pine	**4,864.0**	**2,372.8**	**186.0**	**196.8**	**215.4**	**1,165.7**	**154.6**	**1,515.6**	10,670.9
Early Successional Habitat Development-Mgt	12.2	43.5	115.5	70.8	165.4	1,165.7	101.1	736.0	2,410.2
Restoration of Rare or Declining Natural Communities	4,788.4	2,312.3	37.0	59.0	0.0	0.0	40.0	0.0	7,236.7
Upland Wildlife Habitat Management	63.4	17.0	33.5	67.0	50.0	0.0	13.5	779.6	1,024.0
Supporting Practices	**35,548.6**	**86,491.5**	**98,111.2**	**84,904.3**	**76,495.7**	**95,342.5**	**119,531.7**	**134,077.5**	**730,503.0**
Gopher Tortoise	**12,009.9**	**68,810.3**	**74,879.2**	**48,179.6**	**47,051.8**	**55,407.8**	**72,806.5**	**81,932.1**	**461,077.2**
Brush Management	866.3	2,041.2	3,963.0	3,064.8	2,333.3	2,071.8	870.9	2,652.8	17,864.1
Forest Stand Improvement	5,653.7	7,356.4	4,567.4	4,751.0	5,436.8	5,010.7	3,823.6	6,815.9	43,415.5
Herbaceous Weed Treatment	1,224.2	2,410.2	3,875.9	3,518.1	921.2	2,465.1	3,320.8	3,417.8	21,153.3
Prescribed Burning	3,171.9	47,779.2	50,089.4	29,629.3	32,532.4	38,325.9	53,349.1	53,235.7	308,112.9
Prescribed Grazing	0.0	0.0	0.0	636.3	1,219.4	3,859.5	5,428.3	11,327.7	22,471.2
Tree/Shrub Establishment	1,093.8	9,223.3	12,383.5	6,580.1	4,608.7	3,674.8	6,013.8	4,482.2	48,060.2
Longleaf Pine	**23,538.7**	**17,681.2**	**23,232.0**	**36,724.7**	**29,443.9**	**39,934.7**	**46,725.2**	**52,145.4**	**269,425.8**
Brush Management	155.5	455.4	671.2	2,309.9	231.9	348.1	207.6	270.0	4,649.6
Forest Stand Improvement	447.5	29.0	267.9	1,019.1	830.6	406.1	1,022.3	1,414.4	5,436.9
Herbaceous Weed Treatment	240.8	487.7	1,366.6	1,226.3	1,717.1	1,968.1	3,283.6	4,682.2	14,972.4
Prescribed Burning	12,194.6	11,066.2	11,765.1	17,514.7	17,932.4	22,097.7	24,542.6	26,221.2	143,334.5
Tree/Shrub Establishment	10,500.3	5,642.9	9,161.2	14,654.7	8,731.9	15,114.7	17,669.1	19,557.6	101,032.4
Grand Total	**43,919.6**	**138,737.3**	**178,046.9**	**119,370.6**	**97,263.5**	**100,404.9**	**126,429.1**	**139,568.3**	**943,740.2**

U.S. Fish and Wildlife Service

The gopher tortoise population located west of the Tombigbee and Mobile Rivers in Alabama was federally listed as Threatened by the Service in 1987. Subsequently, the Service finalized a Recovery Plan (Service 1990, entire) which delineated actions required to recover and/or protect the species. The two primary objectives of the recovery plan were to prevent the listed population from becoming endangered and a long-term objective of delisting.

Sections 7 and 10 of the Act establish processes that allow the Service to review federal and non-federal actions that will affect species listed as endangered or threatened under the Act, and to provide exemptions to prohibitions outlined in section 9(a) of the Act. Section 7(a)(1) requires the Service to review programs administered and to utilize such programs in furtherance of the purposes of the Act. Section 7(a)(1) also requires all other federal agencies to implement programs for the conservation of listed species. Section 7(a)(2) requires that federal agencies consult with the Service to ensure that their actions are not likely to jeopardize the continued existence of listed species and are not likely to result in the destruction or adverse modification of designated critical habitat for listed species.

Section 10 of the Act allows a non-federal party to apply for and obtain a permit that authorizes the incidental take of federally listed wildlife or fish, subject to the development of a conservation plan. The Act defines incidental take as "[take that] is incidental to, and not the purpose of, the carrying out of an otherwise lawful activity." Section 10(a)(1)(A) of the Act authorizes the Service to develop a Safe Harbor Agreement with an interested party and issue a permit to enhance the propagation or survival of a listed species. The Service must determine that the conservation measures to be implemented throughout the agreement will contribute to recovering the species by providing a net conservation benefit. Section 10(a)(1)(B) of the Act allows an applicant to apply for and obtain an incidental take permit for a listed species. Preparing a conservation plan, generally referred to as a Habitat Conservation Plan, is required for all Section 10(a)(1)(B) permits. Conservation plans developed for all section 10 incidental take permits must meet Service issuance criteria (50 CFR 17.22 and 50 CFR 17.32).

Recognizing that many species may spend at least part of their life cycle on non-federal lands, the Service implements conservation delivery tools and programs that aid in the conservation of listed and at-risk species, such as the gopher tortoise, on non-federal lands. The Cooperative Endangered Species Conservation Fund (Section 6) is a tool that provides grants to states to participate in a wide array of voluntary conservation projects for candidate, proposed, and listed species. Additionally, cooperative conservation programs such as the Safe Harbor Program and the Partners for Fish and Wildlife Program provide technical and financial assistance to private landowners and others for the conservation of wildlife and associated habitat. Partners for Fish and Wildlife Program projects implemented on private lands include landowner agreements terms ranging from 10 to 30 years depending on state and project specifics. Between 2010 and 2019, under the Partners for Fish and Wildlife Program, approximately 65,000 acres (26,305 ha) of restoration and enhancement activities were implemented in gopher tortoise habitat occurring on private lands in Alabama, Florida, Georgia, and Mississippi (Service 2020, unpaginated).

State Listing Protections

Each state within the historical range of the gopher tortoise provides some measure of protection for the species. The gopher tortoise is protected by regulation as a non-game species in Alabama, is state listed as threatened in Florida, Georgia, and Louisiana and is state listed as endangered in Mississippi and South Carolina. Gopher tortoise protections vary by state, however, laws within most states focus on prohibitions against the take, possession, export/sale, and killing of gopher tortoises. Alabama, Florida, Georgia, and Mississippi include specific prohibitions against gassing of wildlife burrows, including those of the gopher tortoise. South Carolina has prohibitions on the take of gopher tortoises and gopher tortoise burrows.

In Florida, through the Landowner Assistance Program, the FWC assists private landowners with plans to improve their wildlife habitat. In fiscal year 2017-2018, a typical planning year, this program planned beneficial management activities on 44,158 acres (17,870 ha) of gopher tortoise habitat in 34 Florida counties (FWC 2020a, p. 6). This program prepares 10-year plans for private land management activities and updates these plans on a 10-year interval. Over the next ten years, the FWC estimates that more than 440,000 acres (178,061 ha) of gopher tortoise habitat will have been managed with assistance from Landowner Assistance Program planning efforts(FWC 2020a, p.6).

3.9.2. Florida Gopher Tortoise Management Plan and Permitting Guidelines

Florida has developed a management plan and permitting guidelines to guide gopher tortoise recovery efforts. The primary goal of the Gopher Tortoise Management Plan (FWC 2007, revised 2012, entire) is to identify and conserve gopher tortoise populations through the implementation of conservation actions that include minimizing loss of tortoises, gopher tortoise population restoration and enhancement, and increasing and improving gopher tortoise habitat. While relocation activities (discussed below) are conducted in other states, Florida has also developed Gopher Tortoise Permitting Guidelines (FWC 2008, revised July 2020; entire) that direct regulatory actions, including mitigation, habitat management, and habitat acquisition objectives. Florida's regulations require that take of tortoises be authorized by a FWC permit and that the impacts be considered and mitigated.

3.9.3. Relocation, Translocation, Recipient Sites, and Headstarting

Relocation is the intentional movement of individuals to another location within its home range, or more frequently described as within the same site. Translocation describes the intentional capture and transfer of individuals (or groups of individuals) from one location to another. Gopher tortoises have been considered one of the most translocated species in the Southeast U.S. (Dodd and Seigel 1991, p. 340) and translocation is commonly used as a conservation strategy to mitigate the loss of tortoises from land slated for development. These displaced tortoises are often translocated to reestablish extirpated populations or augment existing populations (Griffith et al. 1989; p. 477). Due to its use for conservation, numerous studies have sought to evaluate the success of gopher tortoise translocation and improve its efficacy. However, tortoises are long lived, slow-growing, and are slow to reach maturity, making it difficult to determine if translocations result in viable tortoise populations without long-term monitoring.

Measures of translocation success in scientific literature include high site fidelity and survival rates as retention of tortoises on-site is imperative to establishment of stable populations. A population viability model for translocated tortoises concluded 90 percent annual retention of tortoises would be necessary to stabilize a translocated population (Siegel and Dodd 2000, p. 222). However, this model assumed retention rates were constant over time, which conflicts with findings in research studies. Emigration from recipient areas is high within the first-year post-translocation (Lohoefener and Lohmeier 1986, pp. 37-40; Burke 1989, p. 299; Diemer 1989, p. 2; Mushinsky et al. 2006, p. 366), but appears to decline over time (73 percent retention in first year following translocation; 92-100 percent retention 2-17 years post-translocation; Ashton and Burke 2007, p. 785). Apparent survival was found to be reduced the first 1-2 years post-translocation, but high in subsequent years; reduced apparent survival immediately post-translocation was primarily attributed to dispersal rather than mortality (Tuberville et al. 2008, pp. 2694-2695). High dispersal rates may be due to larger home ranges and greater long-distance movements post-translocation (Tuberville et al. 2005, p. 353; Bauder et al. 2014, p. 1449); these movements could relate to disorientation, attempts to return to their original home range, or exploration of their new environment (Bauder et al. 2014, p. 1450). Soft-release, or the temporary penning of gopher tortoises within a recipient area, is highly effective at limiting dispersal post-translocation. One study found a 76.9 percent dispersal rate when tortoises were not penned, a 38.5 percent dispersal rate when tortoises were penned for 9 months, and only an 8.3 percent dispersal rate when tortoises were penned for 12 months (Tuberville et al. 2005, p. 354).

Several considerations have been suggested to improve translocation success, such as: know and accommodate the biological constraints of the species, understand genetic factors, and minimize the risk of disease transmission (Dodd and Seigel 1991, pp. 344-346). Tortoise density and habitat condition should also be considered to ensure recipient sites provide sufficient space for foraging, reproduction, cover, and social interaction (Dodd and Seigel 1991, pp. 344-346). It has been recommended that relocations be conducted when: they are economically and logistically justified, have a high probability of success, include at least 100 individual tortoises, occur in areas of high-quality habitat, and take place where habitat management will occur after translocation (Ashton and Burke 2007, p. 786). Concerning disease transmission, it is recommended to not relocate tortoises showing clinical signs of disease and ensuring protection and management of recipient sites (Mushinsky et al. 2006, p. 369).

Studies have also sought to evaluate the impacts of translocation on body weight and habitat selection (Riedl et al. 2008, entire; Bauder et al. 2014, entire), disease risk and transmission (Hernandez et al. 2010, entire; Cozad et al. 2020, entire), translocation of tortoises to different latitudinal ranges (DeGregorio et al. 2012, entire; McKee et al. 2021, entire), mating systems (Tuberville et al. 2011, entire), social structure (Schulte 2020, entire), and interactions with resident populations (Riedl et al. 2008, entire).

While translocation is successful at removing tortoises from immediate danger due to development, there are still uncertainties about its efficacy. Additional research is needed to inform improvements to translocation methodology and may include: evaluating the efficacy and improvements to release methodology, the effect of habitat quality and size of resident populations on site fidelity of translocated animals, the relationship between cover type and quality on suitable site stocking densities, initial mortality rates post-translocation, disease risk, and long-term population demography of translocated populations (Tuberville et al. 2005, p. 356; Tuberville et al. 2008, p. 2695).

Gopher tortoise relocation and translocation practices are being implemented and included as regulatory agency guidance (Ginger 2010, personal communication; Service 2019 (84 FR 54732 54757)) in both the western and eastern portions of the range. The primary goals for recipient sites are to help prevent the loss of tortoises and retain the local or regional tortoise resource; and while habitat is lost on the development site, recipient sites can contribute to habitat conservation if sites receive long-term protection and subsequent habitat management. These sites can provide high conservation value by restocking tortoises to appropriately suitable lands where populations have previously been depleted. However, this practice could result in an overall net loss of habitat if not implemented in conjunction with acquisition and additional protection of habitat.

Florida's gopher tortoise permitting program includes the largest scale use of relocation and translocation practices in the range. When possible, FWC permits on-site relocation of tortoises to areas within the property boundaries of development sites, if an appropriate quantity and quality of habitat will be retained within the site boundary; this is part of an effort to retain the local populations of gopher tortoise in these areas. When habitat will not be retained on-site, tortoises are translocated to FWC-approved recipient sites. As of December 9, 2019, the FWC has permitted 39 long-term protected recipient sites (these sites are encumbered under a perpetual conservation easement that requires active management to ensure tortoise habitat suitability) comprising greater than 41,700 acres (16,875 ha), over 23,000 acres (9,308 ha) of which are permitted as gopher tortoise habitat. As of April 23, 2021, there is space for approximately 14,400 gopher tortoises available across long-term and short-term protected permitted recipient sites in Florida. This number fluctuates as reservations are made or released and is subject to change as new sites are permitted, recipient sites reach capacity, or when action is taken in the event that a permitted site falls out of compliance. For example, there are currently (as of April 23, 2021) greater than 20 sites in the pre-application stage or pending review by the FWC for consideration as potential recipient sites. In addition to long-term and short-term protected recipient sites, Florida also has several incidental take permitted recipient sites, such as Eglin Air Force Base (AFB) and Nokuse Plantation. To date, Eglin AFB has received over 1,200 gopher tortoises. Eglin AFB has established a goal of relocating 6,000 tortoises to the base. To continue efforts of re-establishing tortoises in the Florida Panhandle and alleviate constraints on recipient site capacity for other gopher tortoise translocation needs in Florida, Eglin AFB will accept tortoises from solar development sites under a Memorandum of Agreement (MOA) with FWC executed in 2020. Other recipient site options in Florida include restocking of public conservation lands, waif (tortoises of unknown origin) recipient sites, and research recipient sites.

Several other states are currently considering projects or have ongoing efforts to translocate tortoises, providing benefit to the species. For example, there is an ongoing effort to restock gopher tortoises on public lands where they are currently depleted in South Carolina using waif gopher tortoises (McKee et al. 2021, entire). More than 180 adult gopher tortoises from across the species' range have been translocated to the Aiken Gopher Tortoise Heritage Preserve in South Carolina; the total gopher tortoise population is approximately 300 tortoises. A 600 acre (243 ha) parcel in Mobile County, AL was purchased to conserve tortoises and serve as a recipient site for tortoises displaced by Alabama Department of Transportation sponsored projects. With implementation of appropriate management, this site has the capacity to support an estimated population of 346 tortoises (Federal Highways Administration 2010, p. 1). In Alabama, a plan will be developed for translocation and population augmentation with recommendations and protocol pertaining to donor and recipient sites.

In the western portion of the gopher tortoise's range, individual animals are typically translocated either to avoid mortality during land development activities or because they are considered waif tortoises by the state agencies and the Service (76 FR 45130). Tortoises suitable for these translocations include those brought in by the public, those that are reproductively isolated, or individuals determined to be in danger (e.g., crossing roads, burrows near road edges, etc.). At the time of capture, all waif tortoises and, for development projects, all tortoises at both the impact and relocation sites are evaluated to determine whether they have clinical signs of URTD through a physical examination and laboratory blood tests may also be completed. Tortoises that test positive for URTD antibodies are evaluated on a case-by case basis, but generally are not relocated to a URTD-negative tortoise population. Since some individual tortoises have tested seropositive and then tested seronegative upon re-testing months later (Wendland 2007, pp. 88-89), there are uncertainties about the utility of the testing protocol and whether impacts of translocation stress or seasonality play a role in affecting test results.

Headstarting, or the process of hatching and/or rearing juvenile turtles in captivity through their most vulnerable period (Spencer et al. 2017, p.1341) has shown success as a technique that could be used to boost depleted gopher tortoise populations (Holbrook et al. 2015, pp. 542-543; Tuberville et al. 2015, pp. 467-468; Quinn et al. 2018, p. 1552; Tuberville et al. 2021, p. 92). Headstarting turtles allows hatchlings to reach larger body size classes more quickly compared to their counterparts living under natural conditions, presumably making them less susceptible to predation (Heppell et al. 1996, p. 556; O'Brien et al. 2005, entire; Tuberville et al. 2021, p. 88). Natural predation rates of eggs and hatchling gopher tortoises are high (See section 3.6) and increasing survival of these life stages through headstarting or other measures could serve as a useful conservation tool. Eggs or hatchlings obtained from nests, when collected from robust populations, minimizes negative effects on donor populations (Quinn et al. 2018, p. 1554). The headstarting technique has historically garnered considerable controversy (Frazer 1992, entire; Seigel and Dodd 2000, entire; Burke 2015, entire), but there is increasing recognition of its potential role, particularly when used in concert with other management actions (Turtle Conservation Fund 2002, entire; Spencer et al. 2017, entire). Headstarting may be most beneficial to areas where gopher tortoise populations are severely depleted. However, headstarting is resource-intensive and can potentially pull limited resources away from land management activities or other conservation actions if implemented in areas with established populations or robust translocation and repatriation programs. Headstarting should be carefully considered, with specific conservation targets identified, prior to implementation.

Headstarting has only recently been explored as a management tool for the gopher tortoise. The gopher tortoise headstarting program at Camp Shelby in Forrest County, Mississippi (funded by the MS Army National Guard) has been ongoing since 2013 and is still active. It began as an experimental study to determine if tortoises could successfully be reared indoors for several years, and at what age they would reach a size that, when released, would have a high likelihood of survival (Holbrook et al. 2015, entire). These initial objectives have been met, as tortoises have successfully been reared indoors for several years with a very high (greater than 95 percent) survival rate; initial releases of 2- to 3-year old tortoises into the wild indicate that these juveniles have a much higher survival rate as well (70–80 percent versus some accounts of approximately 30 percent for wild 2- to 3-year old tortoises). Headstarted juveniles are often 2 to 3 times larger than wild cohorts. Plans for tortoises currently in the headstarting program will continue to be released into other areas within the installation where habitat has been restored and is either no longer occupied by tortoises or the tortoise population is lacking a juvenile size class. Due to the ongoing success of the Camp Shelby headstarting program, plans are now in development to expand the program into adjacent habitat located in DeSoto National Forest (M. Hinderliter 2021, Service, personal communication).

In Georgia and South Carolina, post release monitoring of head started yearling gopher tortoises opportunistically released at two protected sites has been reported (Tuberville et al. 2015, entire). Several years of the mark–recapture study revealed that head started gopher tortoises have the potential to experience post-release annual survival as high as 80 percent. A subsequent study used radiotelemetry to estimate survival and reported that 8- to 9-month head-started gopher tortoises exhibited 70 percent annual survival when predation risk during soft-release penning was mitigated (Quinn et al. 2018, entire). However, annual tortoise survivorship was observed to vary among release groups and across even small spatial scales because of variation in predation risk (Tuberville et al. 2005, p. 353; Quinn et al. 2018, p. 1548), which may confound perceived benefits of headstarting without a direct comparison to hatchlings. To account for spatial and temporal variability in survivorship and more explicitly quantify the benefits of headstarting, Tuberville et al. (2021, p. 89) released hatchling and head started yearling gopher tortoises as pairs directly into adult burrows and compared their post release movement and survival until winter dormancy. The study results indicated that yearling head started gopher tortoises experienced significantly higher survival to dormancy but exhibited similar movement patterns when compared to hatchlings released simultaneously (Tuberville et al. 2021, p. 90). Additional investigation is needed into the optimal duration of headstarting and whether longer headstarting periods confer an additional survival advantage (Tuberville et al. 2021, p. 92).

3.9.4. The Gopher Tortoise Conservation and Crediting Strategy

The Gopher Tortoise Conservation and Crediting Strategy is a conservation initiative designed to balance military mission activities and gopher tortoise conservation in Southeast installations (Service 2017, entire). The Crediting Strategy establishes the framework for determining credit for Department of Defense (DoD) conservation actions. The Crediting Strategy is an important instrument in providing for the conservation of the gopher tortoise across the candidate range and is intended to achieve a net conservation benefit to the species. The Crediting Strategy focuses on identification, prioritization, management, and protection of viable gopher tortoise populations and best remaining habitat, as well as increasing the size and/or carrying capacity of those viable populations while promoting the establishment of new, viable populations through increased connectivity or translocation and repatriation efforts (Service 2017, entire).

3.9.5. Conservation Agreements

A Candidate Conservation Agreement (revised 2018) for gopher tortoise conservation was developed as a cooperative effort among state, federal, non-governmental, and private organizations (e.g., The Longleaf Alliance, Joseph W. Jones Ecological Research Center, American Forest Foundation, etc.). The primary function of this agreement is to implement proactive gopher tortoise conservation measures across the candidate range.

In 2017, a Candidate Conservation Agreement with Assurances (CCAA) was established with the Camp Blanding Joint Training Center providing protections for approximately 17,000 acres (6,879 ha) of sandhill to be managed for the benefit of multiple at-risk species, including the gopher tortoise (Service et al. 2017a, entire).

In 2012 in Florida, FWC entered into a 30-year MOA with Mosaic Fertilizer, LLC (Mosaic) to facilitate the conservation of gopher tortoises and establish a long-term structure for tortoise relocations (implemented under the September 2012 Gopher Tortoise Permitting Guidelines). Mosaic land encompasses approximately 300,000 acres (121,405 ha) in Florida, approximately 1 percent of which are utilized in mining and reclamation operations but also includes forested, shrub, herbaceous, wetlands, upland communities; the area occupied by tortoises on Mosaic lands is unknown (FWC 2020a, p. 2). As part of this MOA, prior to mining operations, Mosaic relocates all gopher tortoises from the mine site to a certified recipient site, consistent with FWC Gopher Tortoise Permitting Guidelines (FWC 2020a, p. 2). Additionally, through this MOA, Mosaic promotes management of gopher tortoise habitat through payments to state agencies and non-governmental organizations to carry out controlled burns or other habitat management activities that benefit tortoises (FWC 2020a, p.2).

3.9.6. Conservation Strategies, Best Management Practices, and Other Conservation Initiatives and Guidelines

The Rangewide Conservation Strategy for the Gopher Tortoise was developed in 2013 by the Service to guide conservation of the gopher tortoise. Specifically, this Strategy is designed for partners, including the states within gopher tortoise range, the Service, and other public and private entities to collect and share information on gopher tortoise threats, outline highest priority conservation actions, and identify organizations best suited to undertake those conservation actions (Service 2013, entire).

In Florida, Forestry Wildlife Best Management Practices for State Imperiled Species were developed in 2014 to enhance silviculture's contribution to the conservation of wildlife and to provide guidance to landowners who chose to implement these voluntary practices (FDACS 2015, entire). As of 2020, the Florida Forest Service had received a Notice of Intent to implement conservation practices from 198 landowners on more than 3.7 million acres (1.5 million ha), ranging from small private non-industrial landowners to large working forest ownerships (FWC 2020, unpaginated). Subsequent to the Forestry Wildlife Best Management Practices, in 2015, Florida Department of Agriculture and Consumer Services and FWC collaboratively developed the Agriculture Wildlife Best Management Practices for State

Imperiled Species for other commodity groups to promote sound, agricultural land use, natural resource conservation, and reduce the potential for incidental take of State Imperiled Species (FDACS 2015, p. ii), including burrowing animals such as the gopher tortoise. As of 2021, Notice of Intent to implement conservation practices was provided by 28 landowners for approximately 425,031 acres (172,004 ha) of privately owned land (FWC 2021, p. 1). The FWC also provides recommendations to landowners annually. In fiscal year 2017-2018, the FWC recommended beneficial management and/or mitigation activities on 98 projects encompassing 29,495 acres (11,936 ha) of tortoise habitat across 40 counties (FWC 2021, p.1).

There are numerous other gopher tortoise conservation tools and guides, including the 2018 Best Conservation Practices for Gopher Tortoise Habitat on Working Forest Landscapes, that was collaboratively developed by partners including the Georgia Department of Natural Resources (GDNR) and the Service to assist in making recommendations for best conservation practices for creating and maintaining gopher tortoise habitat in the candidate portion of the range (GDNR et al. 2018, entire). GDNR developed the Forest Management Practices to Enhance Habitat for the Gopher Tortoise, which details the essentials of managing habitat for gopher tortoises including prescribed fire, timber harvest, and selective herbicide use (GDNR 2014, unpaginated) . The Georgia Gopher Tortoise Initiative is an extension of the GDNR's long-standing effort in conserving longleaf pine systems. The initiative is a collaborative effort between several public and private entities and is geared towards the protection, restoration, and long-term management of gopher tortoise habitat.

3.9.7. Conservation Lands

The conservation of multiple large, contiguous tracts of habitat is essential to the persistence of gopher tortoises. Gopher tortoise habitat occurs across a wide range of public ownerships with varying levels of management. An estimated 1.7 million acres (688,000 ha) of potential gopher tortoise habitat occurs on protected lands across a wide range of ownerships including federal, state, local government, non-governmental organizations (NGOs), and private lands (e.g., conservation easements) throughout the species' range (see Figure 4.11).

Land Acquisition and Management Planning

Land acquisition for conservation is a primary tactic in preventing habitat loss, fragmentation, and degradation. Each state within the historical range of the gopher tortoise has statutory authority to acquire land for conservation purposes. With the publishing of the 12-month finding (76 FR 45130) in 2011, all states within the historical range have made concerted efforts to protect gopher tortoise habitat via strategic land acquisition. Between 2011 and 2019, Alabama, Florida, Georgia, and South Carolina have reported fee-simple acquisition of approximately 42,000 acres (16,996 ha) of potential gopher tortoise habitat with an additional approximate 78,000 acres (31,565 ha) acquired in conservation easements (CCA 2019, pp. 52-73). Federal entities including the U.S. Air Force, the Forest Service, and the Service recorded an additional 2,740 acres (1,109 ha) of potential gopher tortoise habitat acquired and approximately 24,000 acres (9,712 ha) of conservation easements acquired (CA 2019, pp. 52-73).

Habitat improvement and management are vital factors in restoring and maintaining the structure and composition of vegetation within gopher tortoise habitat. As described in Chapter 2, over most of its range, the gopher tortoise inhabits open canopy pine ecosystems, scrub oak uplands, and flatwoods maintained by frequent growing season fire. Habitat management activities may include ecosystem restoration and enhancement, non-native and invasive plant and animal control, prescribed fire, chemical and mechanical vegetation management activities, and timber management. Habitat management occurring on public conservation lands is often accomplished via natural resource planning instruments (e.g., land management plans, comprehensive conservation plans, resource management plans, etc.).

Department of Defense

As part of the implementation of the Sikes Improvement Act (1997; 16 U.S.C. 670 et seq), the Secretaries of the military departments are required to prepare and implement Integrated Natural Resource Management Plans (INRMP) for each military installation in the United States. The INRMP must be prepared in cooperation with the Service and State fish and wildlife agencies and must reflect the mutual agreement of these parties concerning conservation, protection, and management of wildlife resources (16 U.S.C. 670a). The DoD must conserve and maintain native ecosystems, viable wildlife populations, Federal and State listed species, and habitats as vital elements of its natural resource management programs on military installations, to the extent that these requirements are consistent with the military mission (DoD Instruction 4715.3). Several installations (e.g., Eglin AFB) occur within the historical range of the gopher tortoise, providing important habitat for the species. Many of these installations specifically include gopher tortoise habitat and population management prescriptions and goals within their individual INRMPs. Most INRMPS also include species specific management for other upland species, likely benefiting gopher tortoises as well. Additionally, as part of their INRMPS, military installations across the Southeast complement state and federal laws by maintaining regulations on training restrictions in areas where rare species are found. According to an ArcGIS estimate, there is approximately 830,000 acres of gopher tortoise habitat occurring on military installations throughout the range. The condition of this habitat and the extent to which these areas are occupied by gopher tortoises is not fully understood.

U.S. Forest Service

The Forest and Rangeland Renewable Resources Planning Act (16 U.S.C. 36), as amended by the National Forest Management Act of 1976 (16 U.S.C. 1600-1614), requires that each National Forest (NF) be managed under a forest plan which is revised every 10 years. Forest plans provide an integrated framework for analyzing and approving projects and programs, including conservation of listed species. Several National Forests (e.g., Ocala NF, Desoto NF, Conecuh NF, Apalachicola NF, etc.) occur within the historical range of the gopher tortoise, providing important habitat conservation for the species. Identification and implementation of land management and conservation measures to benefit gopher tortoises vary among National Forests, but generally include habitat restoration and management objectives and maintaining buffers around gopher tortoise burrows during various forest management activities.

The Desoto NF recently completed 10 years of implementing a Collaborative Forest Landscape Restoration Program, in which they implemented longleaf pine restoration goals on approximately 374,000 acres of National Forest Land. Restoration goals included: pine thinning (30,716 acres), longleaf reestablishment (13,132 acres), prescribed burning (995,000 acres), hazardous fuel reduction and wildlife habitat improvement with herbicide (8,600 acres), non-native invasive species control (975 acres), pitcher plant bog restoration (775 acres), and road decommissioning (300 miles). Almost all of these conservation goals support gopher tortoise populations on Mississippi National Forest lands and have the potential to not only enhance but increase suitable habitat. With successful results and high support among partners, this Program was recently extended. In addition, the Desoto NF has prioritized any management treatment that contributes to improvement of habitat for federally listed species, including the gopher tortoise, as set forth in their Mission, Vision, and Operational Strategy (USFS 2020, entire).

U.S. Fish and Wildlife Service

The National Wildlife Refuge System Improvement Act of 1997 (16 U.S.C. 668dd) requires that each Refuge be managed under a Comprehensive Conservation Plan which is revised every 15 years. Additionally, this Act states that each Refuge shall be managed to, among other things, consider the needs of fish and wildlife first and to maintain the biological integrity, diversity, and environmental health of the Refuge System. Several National Wildlife Refuges (NWR) (e.g., Merritt Island NWR, Lake Wales Ridge, NWR, Lower Suwannee NWR, St. Marks NWR, etc.) occur within the historical range of the gopher tortoise, providing important habitat conservation for the species. Management activities included in NWR Comprehensive Conservation Plans that influence gopher tortoises include habitat restoration activities such as pine thinning and other mechanical vegetation management for restoring desired vegetative conditions in pine and scrub systems, and tortoise management and monitoring actions based on priorities of the refuge and available resources.

States

Through statute, the state of Florida requires that managers of lands that contain imperiled species consider the habitat needs of these species during preparation of management plans and that all land management plans include short-term and long-term goals to serve as the basis for land management activities; these goals include measurable objectives for imperiled species habitat maintenance, enhancement, restoration, or population restoration (253.034(5)). In Georgia, land management planning on state property is directed by policies contained within the Georgia Planning Act of 1989 (O.C.G.A. 12-2-28) and the Georgia Environmental Policy Act (O.C.G.A. 12-16-1). In South Carolina, the Heritage Trust Act (S.C. Code Section 51-17-80 and –90) requires a management plan, but does not require regular reviews or updates and while ongoing planning is not prescribed by state law, some timber harvest planning does occur under S.C. Code Section 50-3-510 et. seq. In Mississippi, while there are no statutes requiring resource management plans, MS Code Section 49-5-103 allows for annual appropriations for the General Fund for the management of nongame and endangered species.

3.9.9. Private Lands Conservation Efforts

Most forested land within the gopher tortoise range is privately owned. Privately owned lands account for approximately 80 percent of potential gopher tortoise habitat, of which approximately half are managed for forest production. (Greene et al. 2019, p. 201). As the human population continues to grow in the Southeast, development and related socioeconomic pressures will increasingly threaten forest resources, with effects such as forest conversion to non-forest uses and increasing fragmentation and degradation of forests. Forest loss may lead to loss of ecological function and connectivity essential for the dispersal of gopher tortoises across the landscape. With >90% of land in private ownership, couple with increasing numbers of urban and absentee landowners, forested lands within the range of the gopher tortoise are particularly susceptible to fragmentation and land-use conversion, It is important to strategically target forest-retention efforts, particularly as landscapes are subject to rapid conversion to development, and volatility in timber markets increase risk in private forestland timber production.

It is important to note, data included in our viability analysis (included in chapters 4 and 5) represents a subset of gopher tortoises likely to occur on the landscape, as the majority of data from private lands were lacking. Thus, population estimates in this SSA do not represent an assessment of all populations of gopher tortoises, but rather represent information that was provided by partners through much of the species' range. Most population estimates came from assessments of populations on lands managed for the conservation of biodiversity or natural resources.

Large Working Forest Lands

Coordinating with large working forest landowners and managers, NCASI provides technical information and scientific research needed to achieve environmental goals and principles, including species conservation. Across the entire range of the gopher tortoise, 12 large working forest ownerships in the listed range and 16 in the candidate portion of the gopher tortoise range account for over 6 million acres (2.4 million ha) (NCASI 2020, p. 3) of forest land, representing a significant land use with the potential to influence gopher tortoise resiliency in a multitude of ways across the range. While not all working forest lands include appropriate habitat conditions for gopher tortoises, approximately 2.78 million acres (1.12 million ha) of suitable soil types and 2.98 million acres (1.21 million ha) of open pine conditions are estimated to occur on private forest ownerships within the NCASI database (NCASI 2021, p. 1). Evidence of gopher tortoise occurrence from informal surveys and observations was reported by NCASI from Member Company lands in 107 counties between 1977 and 2019 (Figure 3.9). While the data reported does not cover all gopher tortoise habitat on Member Company land and does not include all lands under private forest management within range of the gopher tortoise, the information provided does reflect over 10,000 observations recorded between 2013 and 2019 (91 counties rangewide) (NCASI 2020, p. 9-11; Miller, pers. comm., 2021).

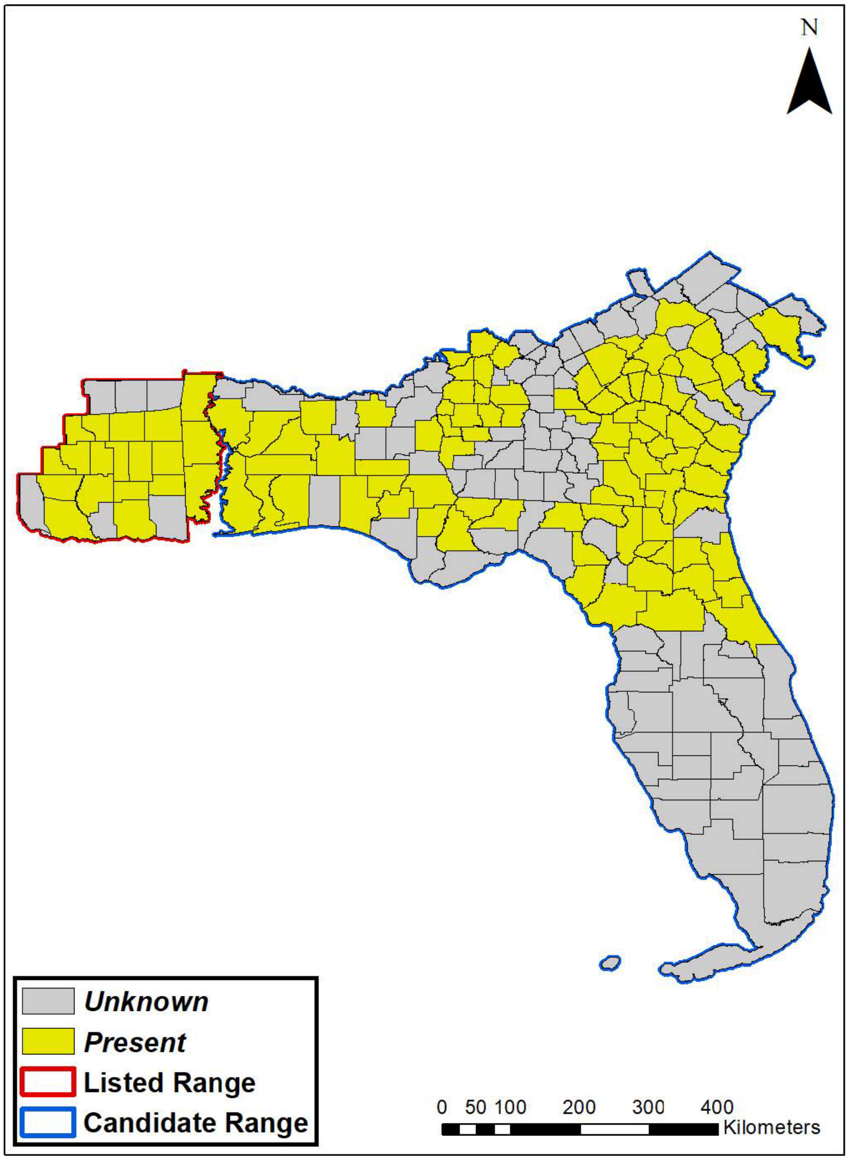


Figure 3. 9-Gopher tortoise known occurrence location (yellow) and unknown (gray) on NCASI Member Company lands. Data compiled here includes informal and formal surveys, burrow observations, presence at a stand level, and tortoise sightings. Unknown counties (gray) do not imply absence on NCASI Member Company lands as some counties do not contain Member Companies, some Member Company land in some counties may not include gopher tortoise habitat, and not all Member Company lands had survey data (NCASI 2020, p. 8).

While working to meet a range of objectives including timber production, many larger private working forests also accomplish conservation within a broad network (Figure 3.10) of collaboration with Federal, State and local government agencies, universities, and environmental non-governmental organizations (ENGOs). Forest certification is one method used to ensure forest lands are managed to provide habitat for wildlife, including gopher tortoises. Participants in forest certification programs such as the Sustainable Forestry Initiative (SFI), and Forest Stewardship Council, adhere to a set of principles that reflect a commitment to providing certain societal benefits, including conservation of biological diversity (NCASI 2020, p. 11). Certification is maintained through third party audits to demonstrate conformance with applicable standards. Standards applicable to gopher tortoise conservation include: 1) having a program to incorporate conservation of native biological diversity, including species, wildlife habitat, and ecological community types at stand and landscape scales; 2) developing criteria and implementing practices to retain stand-scale wildlife habitat elements; and 3) working individually or collaboratively to support diversity of native forest cover types and age or size classes that enhance biological diversity at the landscape scale. An estimated 13.7 million acres (5.5 million ha) within states where gopher tortoises occur are certified through SFI (SFI 2021, unpaginated), though the proportion of certified acres that occur within the range of the gopher tortoise is unknown. Additionally, the proportion of certified acres that include gopher tortoises or gopher tortoise habitat is also unknown.

Across the range of the gopher tortoise, master logger programs are available in each state. These programs include training that meets SFI program standards and in addition to increasing safety and efficiency within the profession, provides professional loggers with environmental training, Environmental training includes BMPs, the ESA, and threatened and endangered species management, including gopher tortoise. Trained master/professional loggers supervise most forest harvesting operations to meet the requirements of the SFI.

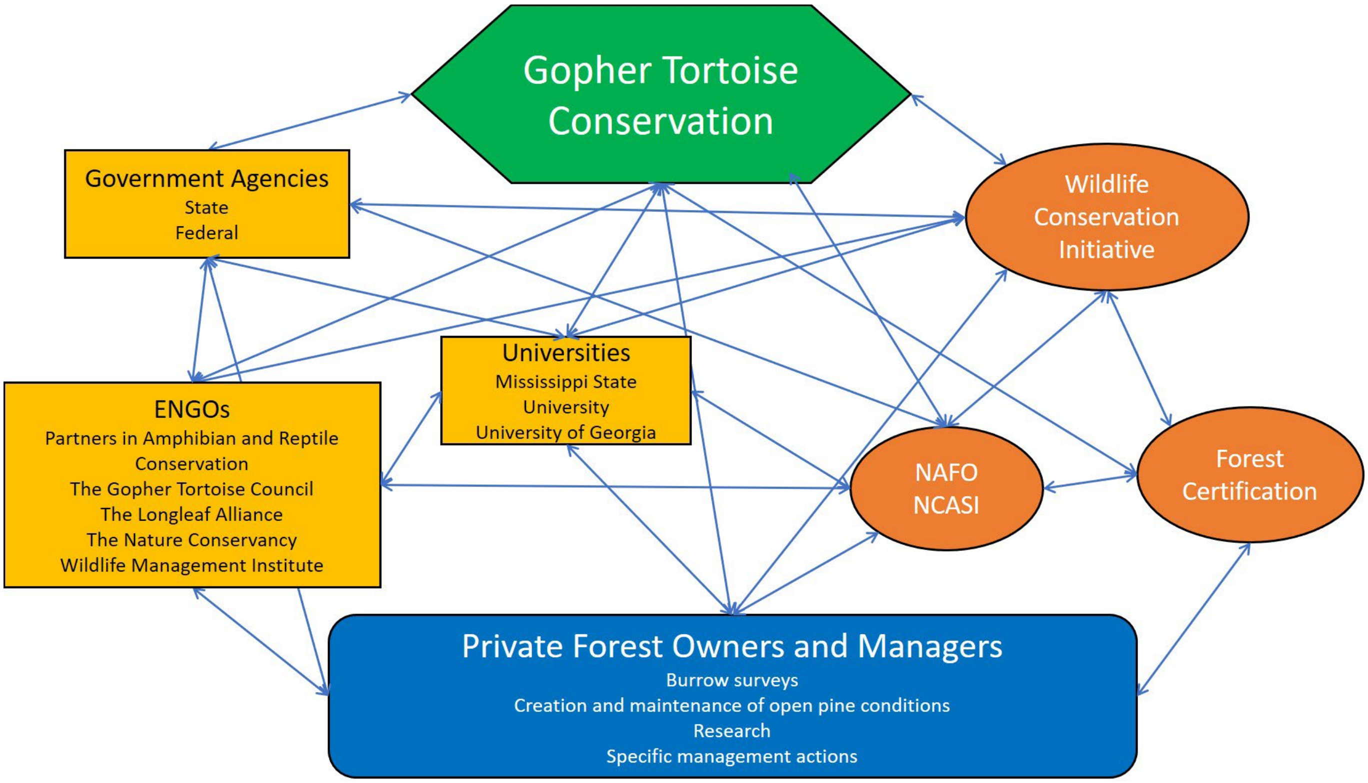


Figure 3. 2-Gopher tortoise conservation occurs through collaboration among several entities. Large private working forest owners and managers (blue) complete gopher tortoise conservation within their own organizations but also collaborate with environmental non-governmental organizations (ENGOs), government agencies, and universities (yellow). Furthermore, private forest owners and managers cooperate with each other via the National Alliance of Forest Owners, NCASI, and the Wildlife Conservation Initiative (orange) to ensure gopher tortoise conservation efforts happen throughout the species' range. Lastly, forest certification programs (orange) provide further assurances that at-risk species conservation (including gopher tortoise conservation) will continue to be a priority on private forests. Entities listed do not represent an exhaustive list of cooperators and partners. Source: NCASI

Family Forests

The largest forest landowner group in the United States is the family forest landowners, controlling 36 percent of forest lands in the country (Butler et al. 2016, p. 641) and in the south, private ownerships account for 87 percent of forest land (Oswalt 2014, p. 6). Similar to large working forest landowners, family forest landowners accomplish conservation through a broad network of conservation partners (Figure 3.11). Conservation values are important and family forest landowners rank beauty, wildlife, nature, and legacy as top reasons for owning land, and timber production as not one of the top ten reasons (Butler et al. 2016, p. 644). Working with smaller, family forest landowners, the American Forest Foundation (AFF) works to increase sustainable wood supplies on family forests while protecting and enhancing habitat for at-risk species, including the gopher tortoise. In accomplishing this objective, in 2017 the AFF has partnered with the Service's Partners for Fish and Wildlife Program to support conservation of at-risk species on private lands within the Southeast. Participating landowners work with Partners biologists to develop habitat improvement plans that meet their long-term objectives for the property, receive cost share for habitat improvement projects and commit to actively managing the project area. Consistent with the Partners program requirements, landowners enter into formal agreements with the Service and AFF for a minimum of 10 years. Since 2017, the partnership has engaged landowners with over 3,500 acres (1,416 ha) under agreement where habitat improvement projects have included approximately 2,000 acres (809 ha) of longleaf pine establishment and the introduction of prescribed fire to more than 1,400 acres (566 ha) of existing pine forests. An additional focus of this partnership is the implementation of wildlife surveys, including gopher tortoise. Since 2017, gopher tortoise surveys on participating forests have identified 762 gopher tortoises, including 2 populations that meet the MVP criteria (AFF 2021, unpaginated). As with the large working forests, family forest landowners may participate in forest certification programs such as the American Tree Farm System (ATFS). The ATFS has certified more than one million acres of private lands in each of the Southeast states and requires landowners and managers to implement BMPs, identify and protect state and federal listed species, and to protect soil and water resources. ATFS certification, as are most forest certifications, is a third-party audited certification system authorized by the Program for the Endorsement of Forest Certification (PEFC). It is unknown how many acres of ATFS certified lands occur within the gopher tortoise range, include gopher tortoise habitat, or support gopher tortoise populations.

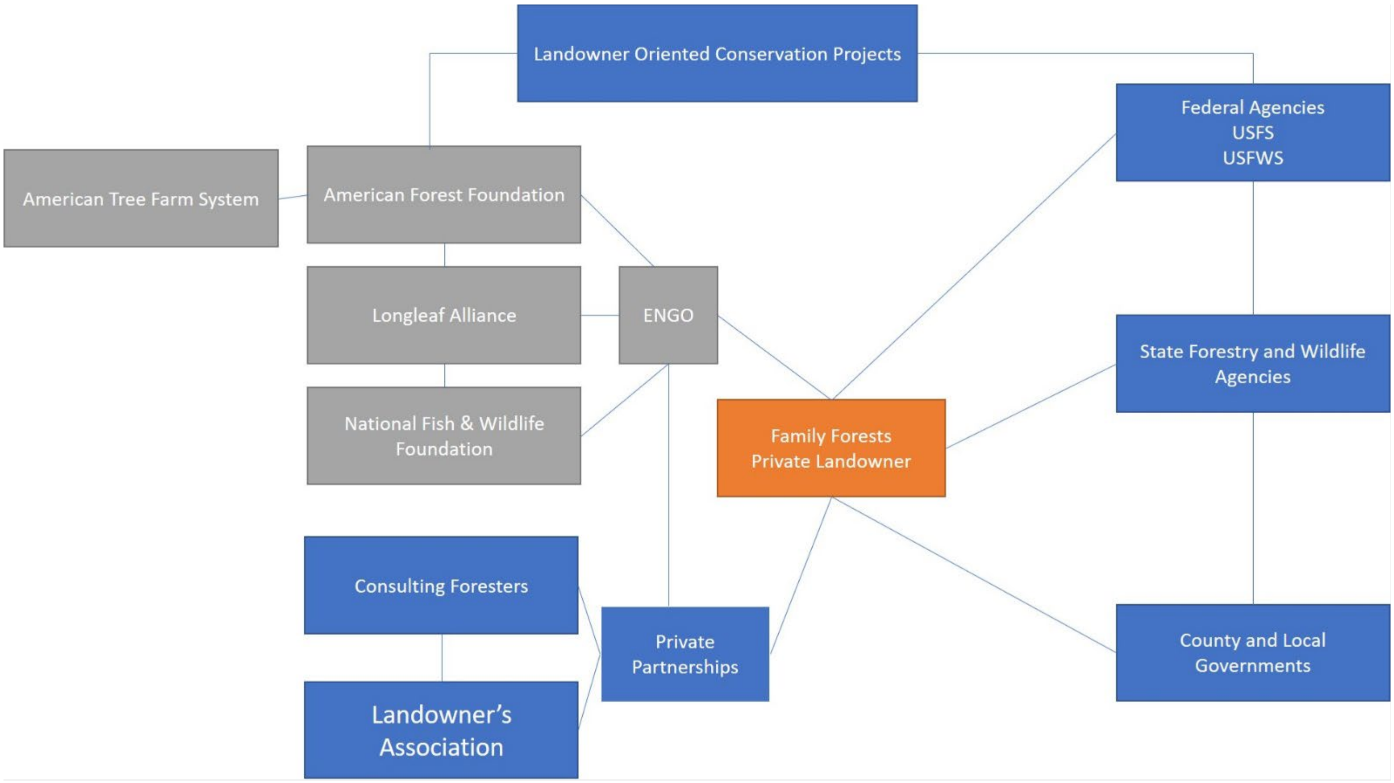


Figure 3. 11-Gopher tortoise conservation delivery network for small family forests. Entities listed are not exhaustive of all potential partners and stakeholders. Source: AFF

Additionally, The Longleaf Alliance works with private landowners and other partners across the range of the gopher tortoise to restore and maintain habitat as an essential part of their larger focus in restoring the longleaf pine ecosystem. In providing technical and financial assistance, the Longleaf Alliance in 2019, assisted landowners with the implementation of over 55,000 acres (22,258 ha) of prescribed fire within gopher tortoise habitat in addition to assistance with longleaf pine plantings, groundcover restoration, and invasive plant management efforts (SERPPAS 2020, p. 17).

Conservation Banks

Several privately-owned tracts of land are managed as mitigation/conservation areas for gopher tortoises in both Mississippi and Alabama, providing suitable habitat, protection, and habitat management. In Greene County, MS, the 1,230-acre Chickasawhay Gopher Tortoise Conservation Bank was established in 2009 to accept tortoises displaced by development within the Bank's service area and to compensate impacts to tortoises. As the only official mitigation bank for the gopher tortoise, the national mitigation banking guidelines are followed for maintaining optimal habitat, including aggressive prescribed fire and longleaf restoration programs.

In Mobile County, AL, four gopher tortoise conservation areas are managed through HCPs with the Service. These areas serve as a relocation site for tortoises impacted by utility and county construction and maintenance and are required to follow habitat plans which include restoration and management of the open-canopied, upland longleaf pine habitat used by gopher tortoises. However, they are all less than 700 acres and primarily surrounded by urban landscapes with incompatible habitat.

3.10. Summary of Factors Influencing Viability

The best available information regarding the gopher tortoise and gopher tortoise habitat indicates that habitat loss, degradation, and fragmentation (due to land use changes from urbanization), climate change, and habitat management are the most significant factors influencing gopher tortoise viability. Urbanization results in a range of impacts that either remove or degrade/fragment remaining habitat, or impact gopher tortoises directly through development. Urbanization brings road construction and expansion, which may cause direct mortality of gopher tortoises. In addition, this type of development may also create conditions beneficial to invasive species, increase predators and inadequate conditions for fire management. Temperature increases associated with long term climate change are likely to further constrain use of prescribed fire through a decrease in the number of suitable burn days. Habitat loss resulting from sea level rise associated with climate change is a risk for coastal populations of gopher tortoise. These factors are considered to have population level effects and were evaluated further in the current condition and future condition analysis.

CHAPTER 4 – POPULATION AND SPECIES NEEDS AND CURRENT CONDITION

4.1. Introduction

In this chapter, we consider the gopher tortoise's current distribution, species needs, and how the species needs influence the 3 Rs. We first define populations of the species. Next, we characterize population and habitat factors for the species in terms of the 3 Rs. Finally, we estimate the current condition of the gopher tortoise using population metrics used to characterize the 3 Rs.

Survey methodologies

We received a variety of data to assess resiliency factors for the gopher tortoise, including information from state and federal agencies, local governments, and private lands. These data represent a subset of gopher tortoises likely to occur on the landscape due to the lack of a comprehensive private lands data set. Data were collected using burrow surveys of various methodologies and included burrow surveys (comprehensive and area-constrained) both with and without burrow scoping incorporated, and line transect distance sampling (LTDS; Buckland et al. 1993, entire; Thomas et al. 2010, entire); some burrow data were submitted with unknown methodology. Comprehensive burrow surveys, sometimes called 100 percent surveys, involve a team of researchers searching a site to count the total number of gopher tortoise burrows present. Area-constrained surveys, also referred to as belt transect surveys, use a similar methodology as comprehensive surveys. However, these surveys are restricted to a transect of pre-delineated length and width, and population estimates are extrapolated site-wide based on the proportion of the site that was surveyed (Auffenberg and Franz 1982, pp. 95-96; Cox et al. 1987, p. 39). As counting burrows alone during these surveys results in unknown occupancy estimates, an occupancy rate (or correction factor), is often used to estimate population size for comprehensive and belt transect surveys (0.614, Auffenberg and Franz 1982, p. 96; 0.5, Ashton and Ashton 2008, p. 158; 0.40, Guyer et al. 2012, p. 132).

Biologists also sometimes use burrow-scope cameras in conjunction with burrow surveys to directly estimate abundance of local populations by counting individuals within burrows; this method assumes that all potentially occupied gopher tortoise burrows were detected at sites and that only a single gopher tortoise is present in a burrow. Line transect distance sampling is a survey method to derive estimates of abundance where a research team walks transects, observes gopher tortoise burrows, searches the burrow for a gopher tortoise with a burrow scope, records the precise spatial location of occupied burrows, and measures the perpendicular distance of each occupied burrow to the transect line (Smith et al. 2009a, entire). Invariably, burrows and individuals are imperfectly sampled because detection probability of burrows is less than one. However, analysis of LTDS data generates functions estimating the decay of the detection rate with increasing distance from the transect line, and this detection function can then be used to account for undetected burrows and therefore estimate the total number of occupied burrows in the search area (i.e., total population size). Because juvenile gopher tortoises have small burrows that are difficult to observe, detection of juveniles during all burrow survey types (comprehensive, belt transect, LTDS) is lower than adults; thus, surveys may underrepresent smaller size classes in the population estimates (Smith et al. 2009a, p. 356; Gaya 2019, pp.13-31).

Because data were provided by a variety of sources, contained disparate levels of data resolution, and were collected in various ways, we could not reliably determine abundance, density, habitat availability, or other metrics for all populations. All population data provided are integral to evaluating the current condition of the gopher tortoise, although different data types come with different assumptions and limitations as described below.

Spatially explicit data

The most useful data, from an analysis perspective, are those data that come from standardized and systematic surveys which result in spatially explicit burrow locations and subsequent population estimates. There are several advantages to spatially explicit data, including the ability to make more reliable estimates of populations size; use of spatial buffering to delineate populations based on species biology (see Delineating Populations section below); ability to tie site-specific factors, such as habitat and management factors, to locations of gopher tortoises; and, ability to estimate future parameters, such as probability of persistence and estimated future abundance of gopher tortoise populations.

Due to discrepancies in historical data collection, surveys have recently been performed using LTDS (Buckland et al. 1993, entire; Thomas et al. 2010, entire) when possible and applicable. This methodology is believed to be the most statistically reliable to assess accurate measurements of gopher tortoise populations (Smith et al. 2009b, p. ii). Surveys using this methodology have been done across the range of the gopher tortoise and have been providing more comprehensive data on the status of the species, at least in conservation lands where it has been mostly used. Some belt transect survey data submitted were incomplete and the proportion of habitat surveyed, and therefore the proportion of burrows or tortoises, was unknown. Also, population estimates derived from the belt transect method tend to be less accurate than LTDS; unlike LTDS, the belt transect method involves an area-constrained survey and assumes that burrows occur uniformly and independent of space. Moreover, LTDS analyses yield estimates of precision and detectability that cannot by calculated using the belt transect methodology. Some burrow data were included with unknown survey methodology. In these instances, it is likely that these data do not represent the true population sizes for these sites.

County level information

Private landowners, large and small, play a vital role in conserving habitat for fish, wildlife, and plants, highlighted by the fact that more than two-thirds of the nation's threatened and endangered species use habitat found on private land. The gopher tortoise is no different, where a large percentage of potential habitat is located on land that is privately owned. This highlights the importance of including data from private lands when assessing species viability. The vast majority of the private lands data obtained for this assessment lack a spatial component because of issues associated with confidentiality of location data; this does not preclude the utility and importance of these data in the species status assessment. To this end, we created a landowner questionnaire and utilized responses to estimate population, habitat, and management factors at a county scale to ensure privacy for respondents (Appendix A). We received 167 responses to the landowner questionnaire, with respondents owning properties covering much of the range of the gopher tortoise (Figure 4.1). Responses likely represent a small percentage of private lands that currently support gopher tortoises, particularly given the reluctance many private landowners have sharing occurrence data for at risk species. In addition to these responses, the Florida Forestry Association (FFA) sent out their own questionnaire to additional landowners in the state of Florida, with an additional 34 respondents. Although the FFA questionnaire was similar to the one found in Appendix A, a key difference was that we were not able to obtain population estimates from the 34 responses, thus are unable to estimate current resiliency for populations on these properties.

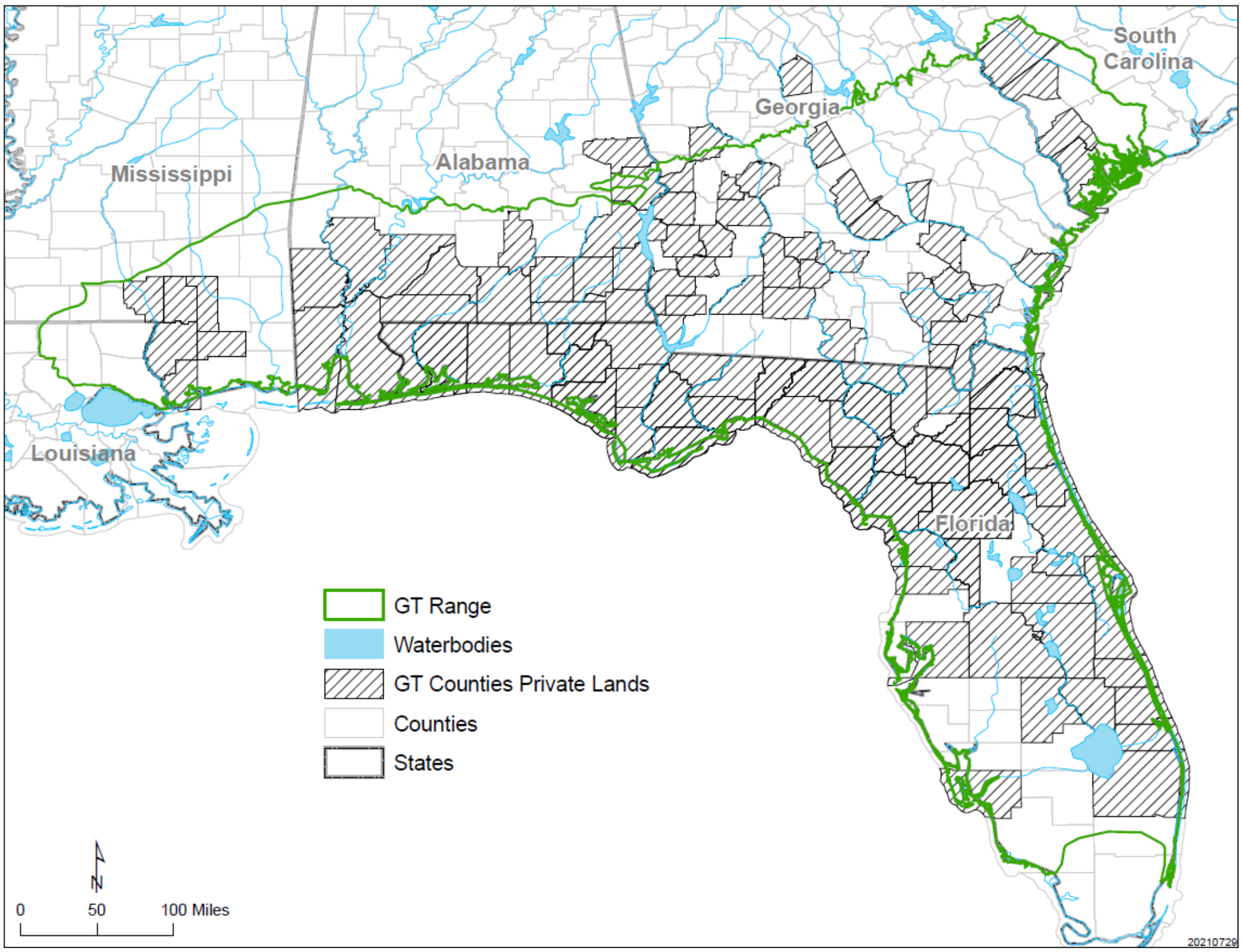


Figure 4. 1-Location of counties with responses to the private landowner questionnaire (with hatching).

Because data received from these questionnaires are not spatially explicit, there are limitations to the applicability of the data as it relates to delineation of populations, assessment of site-specific factors such as habitat quality and quantity, and management regimes, and use of abundance data in projections of future scenarios. Due to these limitations, we present results for current conditions for both types of data (spatially explicit and county level) separately. As will be discussed in Chapter 5 (Future Conditions), we only used spatially explicit data to inform the population model used to forecast future scenarios for the gopher tortoise, which introduces a degree of uncertainty into future projections, given we were only able to use a subset of populations that likely occur on the landscape.

4.2. Delineating populations

As the population is a biologically meaningful unit in an analysis of resiliency, which is then scaled up to redundancy and representation at the species scale, appropriately defining and delineating populations is a crucial step to assess species viability. Below we discuss the challenges of delineating populations for the gopher tortoise and outline our approach.

For this assessment, we defined populations for the species as contiguous areas surrounding known gopher tortoise burrows with habitat conducive to survival, movement, and inter-breeding among individuals within the area. To delineate populations, we compiled and used all records with spatially explicit information, as detailed previously. In addition to naturally occurring gopher tortoise populations, we also included long-term recipient sites in Florida and South Carolina (hereafter, recipient sites) that currently support translocated individuals. A detailed discussion of recipient sites can be found in Chapter 3 (3.9.3 Translocation, Relocation, Recipient Sites and Headstarting). We could not delineate populations for county records that were lacking coordinates, thus we placed these records at the county's centroid and summarized population and habitat factors separately.

Using spatial survey data from across the range of the gopher tortoise, we sought to operationally identify populations at two spatial scales: local populations and landscape populations (Figure 4.2). Local populations can be considered groupings of individuals discovered by demographic or spatial analysis (Smallwood 2001, entire; Goessling et al. 2021, p. 141), whereas landscape populations can refer to the assemblage of individuals found within a property or region of interest (Goessling et al. 2021, p. 141). We defined local populations as geographic aggregations of individuals that interact significantly with one another in social contexts that make reproduction significantly greater between individuals within the aggregation than with individuals outside of the aggregation (sensu Smallwood 1999). We operationally delineated local populations by identifying aggregations of individuals or burrows where individuals were clustered together within a 1,968 feet (600 m) buffer to the exclusion of other adjacent individuals or burrows. Studies of gopher tortoise populations in Alabama (Conecuh NF; C. Guyer, unpublished data), Georgia (Ft. Stewart Army Reserve; E. Hunter and D. Rostal, unpublished data), and Florida (Boyd Hill Nature Preserve; J. Goessling and G. Heinrich, unpublished data) have found that greater than 80 percent of gopher tortoise movements within and among years were less than 1,640 feet (500 m). We recognize that although gopher tortoise interactions may primarily occur within 600 meters of a burrow cluster, the extent to which a tortoise will travel and interact with other tortoises varies by population, and this is likely influenced by many factors, including demographics (sex and size class ratios), population density, whether the population is naturally occurring or a translocated population, habitat type, management, nearby urbanization, and degree of habitat fragmentation.

We selected a 1,968 feet (600 m) distance to buffer populations to encompass typical movement distances and adjacent habitat around surveyed populations that might include gopher tortoises. Because gopher tortoise habitat and demography vary across the range, the 1,968 feet (600 m) buffer represents a compromise across geography and habitat based on a thorough literature search and species expert input. We assumed that areas unsuitable for gopher tortoises were unsuitable for gopher tortoise movement or survival and considered those strict barriers when delimiting local populations. Thus, movement barriers included interstates, freeways, and expressways (HPMS 2019); major rivers and lakes (Sciencebase.org); wetlands, and highly urbanized areas as determined by visual inspection with ESRI imagery.

Local populations can be connected to other, nearby local populations by dispersal; together, connected local populations may form landscape populations. Gopher tortoises infrequently move long distances from established core home range areas, and such movements can result in permanent emigration and immigration into other populations. Local populations that are spatially proximate to other local populations might receive immigrants that bolster population size. While little quantitative information is available describing the frequency or success of immigration, one study found that 2 percent of adults emigrated from local populations each year (Ott-Eubanks et al. 2003, p.319). It is important to note that this emigration estimate was based on only 2 individuals and may underestimate true immigration. We identified instances of two or more local populations that may be connected by dispersal through gopher tortoise habitat as landscape populations.

Although the term landscape population has been used to identify areas where individuals are located within a human defined boundary (Goessling et al. 2021, p. 141), such as a property line, we define a landscape population as a series of local populations that are connected by some form of movement; individuals within a landscape population are significantly more likely to interact with other individuals within the landscape population than individuals outside of the landscape population. Gopher tortoises have been shown to move over 4,921 feet (1,500 m) throughout multiple years, with distances as large as 8,802-15,220 feet (2,683-4,639 m) (McRae et al. 1981, p.172; Diemer-Berish et al. 2012, p. 52; Guyer et al 2012, entire; Castellon et al 2018, p. entire; unpublished data from Goessling and Rostal and Hunter). We operationally delineated landscape populations by identifying local populations connected by habitat within 8,202 feet (2.5 km) buffer around each local population; habitat was considered any areas other than open water, wetlands, paved roads (interstates, freeways, and expressways), and urbanized areas. Landscape populations could comprise multiple local populations or a single local population if no other local populations were within 8,202 feet (2.5 km) buffer, or otherwise separated by a barrier to gopher tortoise movement.

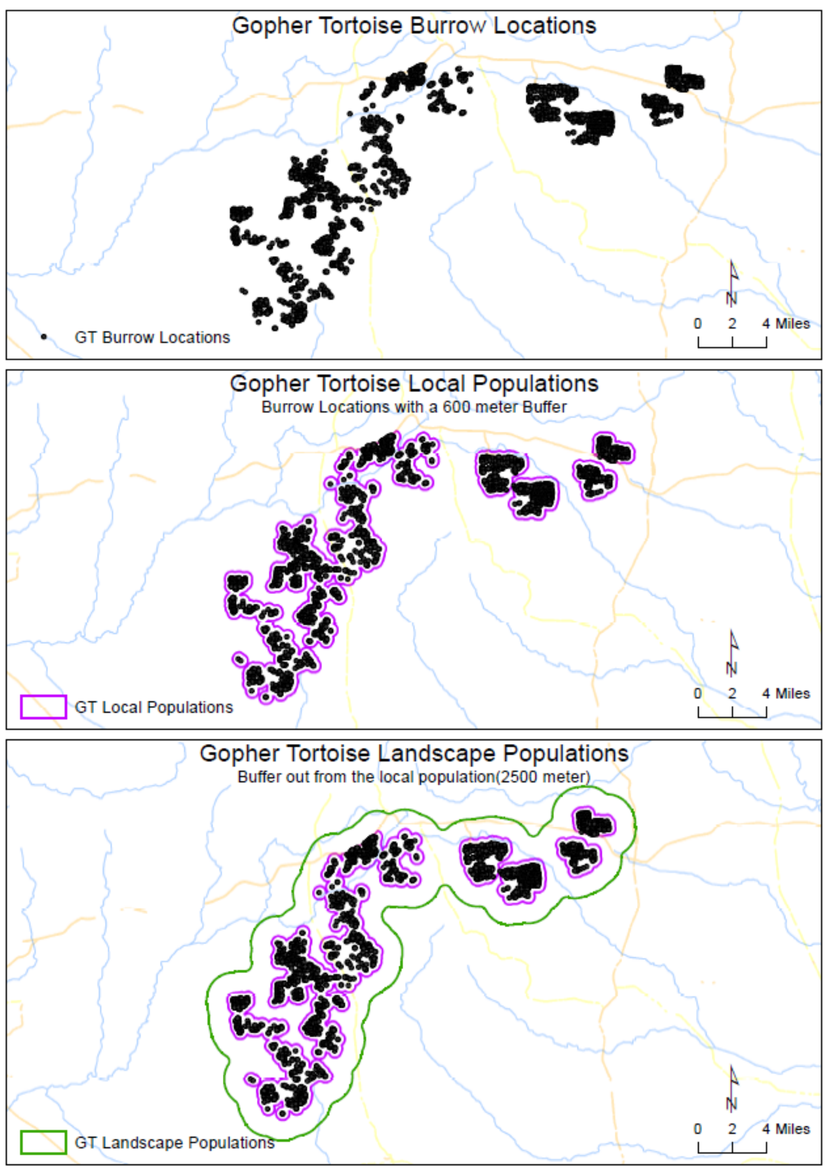


Figure 4. 2-Process for delineating local (0.37 miles/600 m buffer) and landscape populations (1.55 miles/2500 m buffer) using burrow locations for gopher tortoises.

Our process of spatially delineating local populations and landscape populations resulted in a dataset of 656 local populations from 253 landscape populations (Figure 4.3); Florida had the greatest number of local (316) and landscape populations (161), followed by Georgia (151, 63, respectively), Mississippi (99, 7), Alabama (77, 14), Louisiana (7, 5), and South Carolina (6, 4).

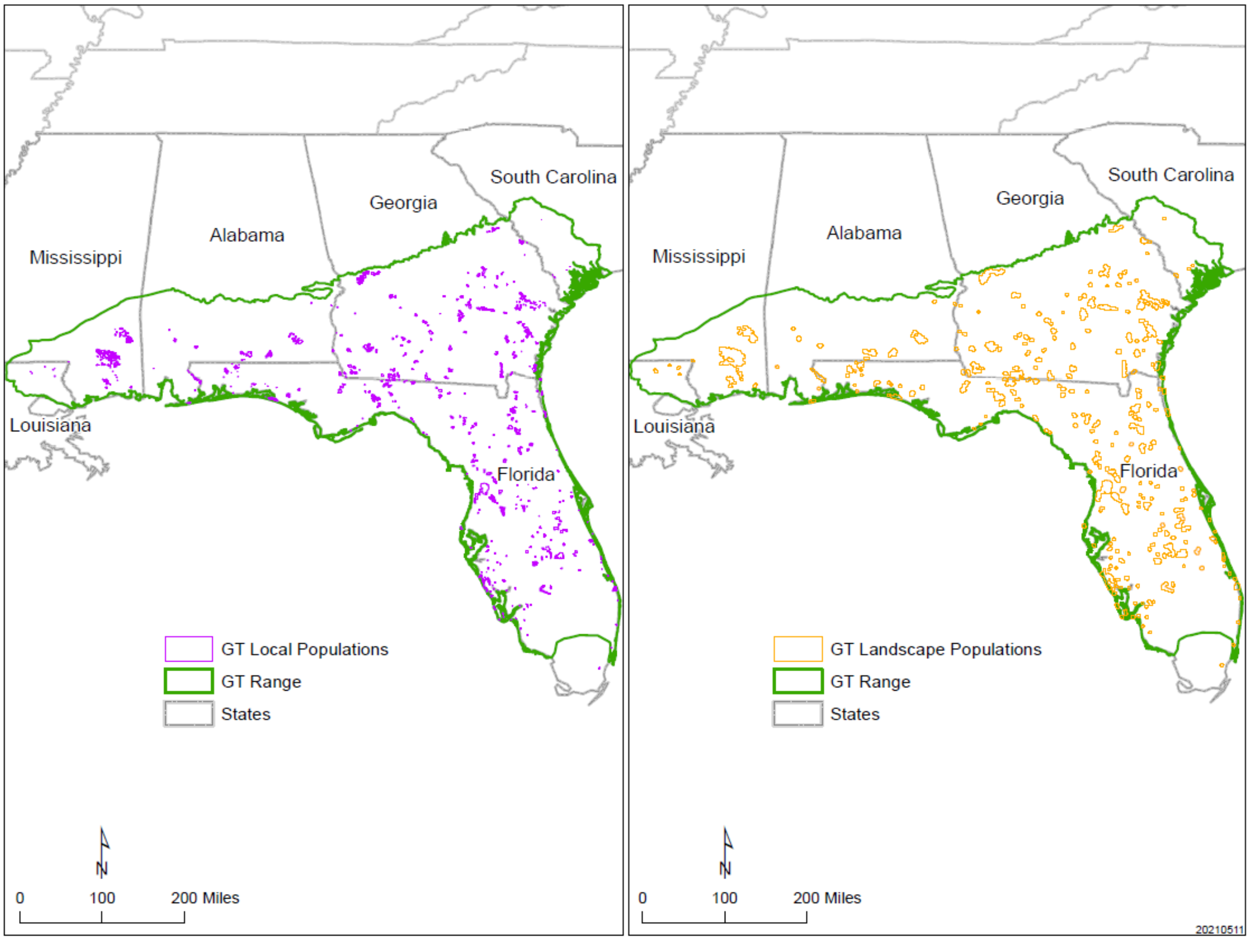


Figure 4. 3-Location of spatially delineated local populations (left panel) and landscape populations (right panel) across the range of the gopher tortoise.

4.3. Delineating representative units

Representation refers to the breadth of genetic and environmental diversity within and among populations, which influences the ability of a species to adapt to changing environmental conditions over time. Differences in life history traits, habitat features, and/or genetics across a species range often aid in the delineation of representative units, which are used to assess species representation. Representation improves with the persistence of populations spread across the range of genetic and/or ecological diversity within the species.

Drawing conclusions about genetic subdivisions and unique genetic assemblages based on available data are difficult because methodologies varied among studies, sample sizes were small in some areas, distances among samples were large in some cases, and areas covered by each study varied. While there is molecular support for recognizing the western portion of the range as genetically distinct, other research has suggested that additional structure exists at both rangewide and regional scales (Ennen et al. 2010, entire; Clostio et al. 2012, entire; Ennen et al. 2012, entire; Galliard et al. 2017, entire). A recent study investigating genetic structure at multiple scales found five genetic regions (Western, Central, West Georgia, East Georgia, and Florida), loosely delineated by biogeographical features including the Tombigbee-Mobile Rivers, Apalachicola-Chattahoochee Rivers, and transitional areas between physiographic provinces of the Coastal Plains (Figure 4.4; Galliard et al. 2017, pp. 503-507). The Tombigbee-Mobile Rivers separate the Western region from the rest of the range, which corresponds to the listed portion of the range of the species. The Apalachicola-Chattahoochee Rivers divide the Central and West Georgia regions, although there is a high degree of admixture at the border of these two regions. The rest of the genetic groups are associated with transitional zones between the Eastern Gulf, Sea Island, and Floridian physiographic province sections of the Coastal Plains, with high amounts of admixture between adjacent genetic groups (Figure 4.4; Galliard et al. 2017, pp. 503-507).

With respect to gene flow, levels of gene flow have been found to be asymmetric from central to peripheral regions, with the highest levels from the Central to Western Regions, and the lowest between the Florida and Western Georgia groups (Galliard et al. 2017, p. 509). Finally, significantly lower genetic diversity is found at the periphery of the range, with low diversity in the Western and East Georgia regions (Ennen et al. 2010; Clostio et al. 2012; Galliard et al. 2017, p. 509).

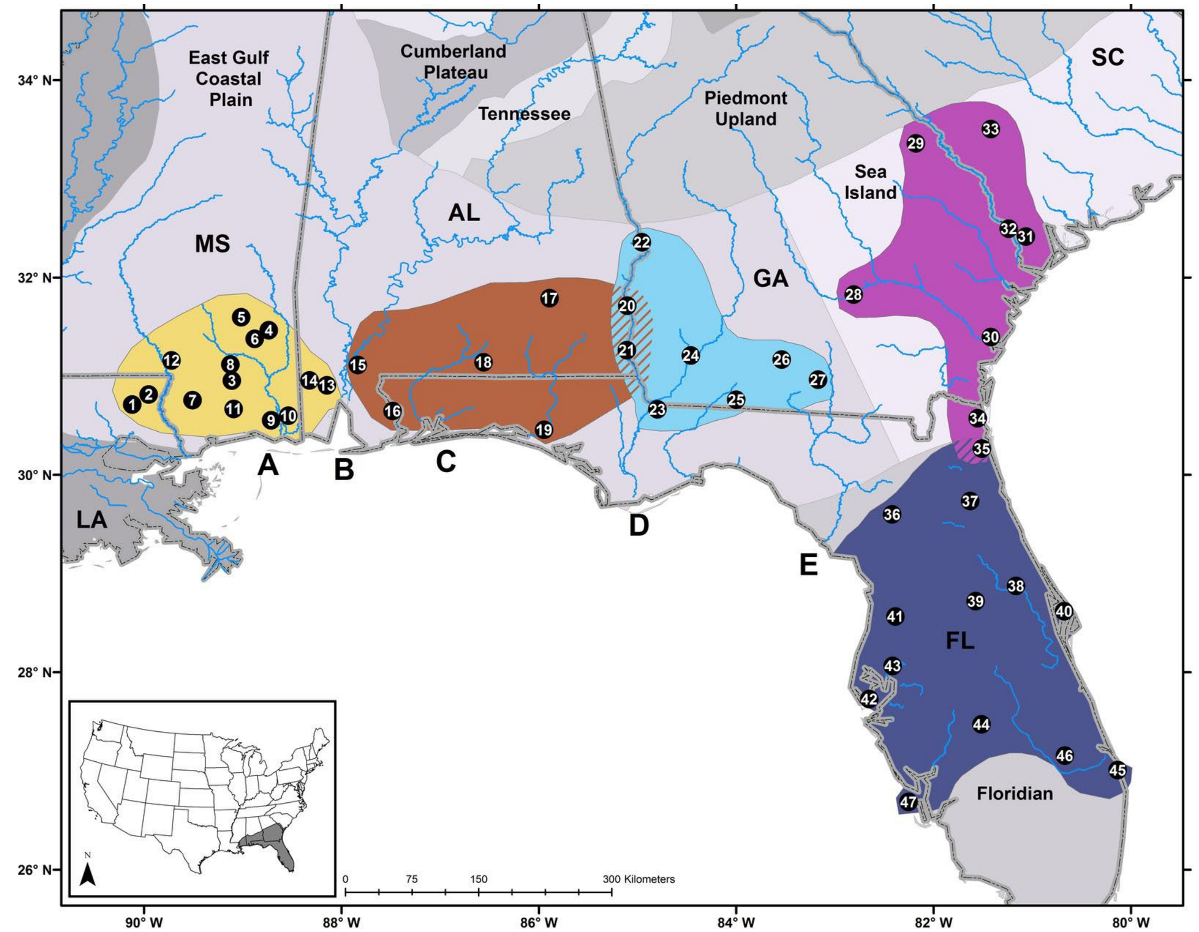


Figure 4. 4-Sampling locations and subsequent genetics units from genetics study by Galliard et al. 2017. The colored shaded areas around sampling sites represent their assignment to one of the five genetic groups (regions) as follows: yellow (Western), brown (Central), light blue (West Georgia), magenta (East Georgia), and dark blue (Florida).

For this assessment, we delineated five representative units (hereafter analysis units) based on the results of Galliard et al. (2017, entire), physiographic regions, and the input of species experts (Figure 4.5). We used the Tombigbee-Mobile Rivers and Apalachicola-Chattahoochee Rivers as boundaries between the Western (Unit 1), Central (Unit 2), and West Georgia (Unit 3) analysis units. Because of the high degree of admixture and lack of well-defined boundaries found within transitional zones of physiographic regions, we used other biogeographic barriers and expert input to delineate boundaries between West Georgia, East Georgia (Unit 4), and Florida (Unit 5) analysis units. We used U.S. Environmental Protection Agency (EPA 2013, unpaginated) Level IV ecoregions to delineate the boundaries between the two Georgia units, and the East Georgia and Florida unit. We used the Suwanee River to separate the West Georgia and Florida units, as this river represents a significant barrier to dispersal, and gene flow between these 2 units is known to be low (Galliard et al. 2017, p. 509).

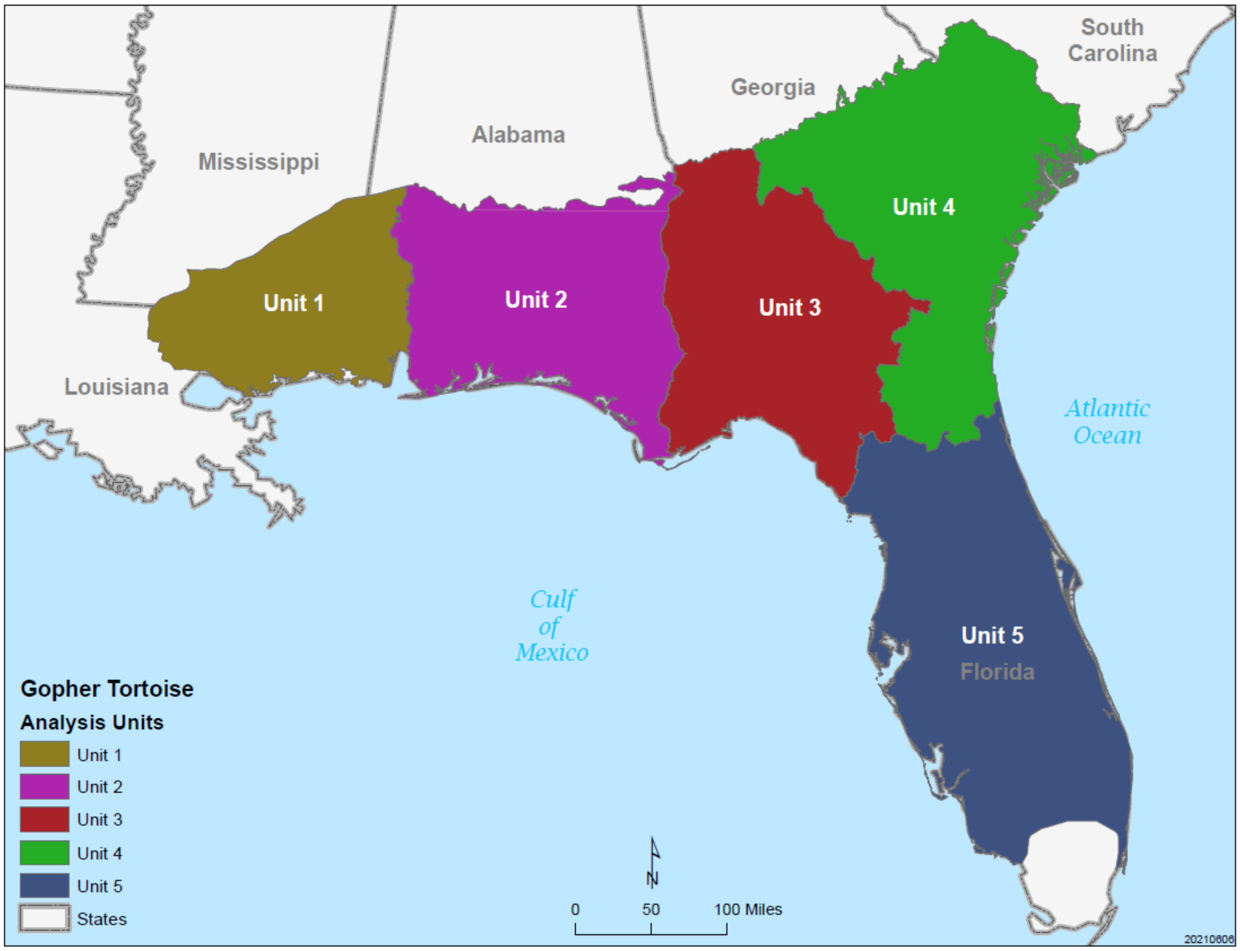


Figure 4. 5-Analysis units used as units of representation for the gopher tortoise in this Species Status Assessment. Analysis units include Western (Unit 1), Central (Unit 2), West Georgia (Unit 3), East Georgia (Unit 4), and Florida (Unit 5).

4.4. Current resiliency

Resiliency describes the ability of a species to withstand low-level stochastic events and is associated with population size, growth rate, and habitat quality. Highly resilient populations are more likely to withstand disturbances such as random fluctuations in fecundity (demographic stochasticity), variation in mean annual temperature (environmental stochasticity), or the effects of anthropogenic activities, such as local development projects. Viability denotes a species' ability to sustain populations over a determined time frame and is closely tied with population resiliency. Below, we describe population, habitat, and management factors that contribute to resiliency of gopher tortoise populations.

4.4.1. Population factors

For gopher tortoise populations to persist for a biologically meaningful timeframe, they must have an adequate number of individuals (population size), be above a particular density (population density), and have sufficient genetic exchange between local populations to maintain genetic diversity (Figure 4.6). There must also be sufficient habitat to support individual and population needs, which we discuss in the next section (Habitat and Management Factors). Population size and density are driven by a variety of underlying demographic parameters, including fecundity, sex ratio, and survival at various life history stages (egg, nest, hatchling, juvenile, and adult survival). Genetic diversity is primarily driven by rates of emigration and immigration between local populations.

It is important to note that populations of gopher tortoises experience great variation in abiotic characteristics across the species' range, and variation in abiotic characteristics influences demographic rates among populations. At southern latitudes, populations experience significantly warmer mean annual temperature, which may afford greater overall opportunity for thermoregulation, energy acquisition, and metabolism when compared to northern populations. As a result, southern populations of gopher tortoises experience faster growth rates, younger ages of sexual maturity (hereafter, maturity age), and increased clutch size (Ashton et al. 2007; Moore et al. 2009, pp. 387-392; Meshaka Jr. et al. 2019, entire).

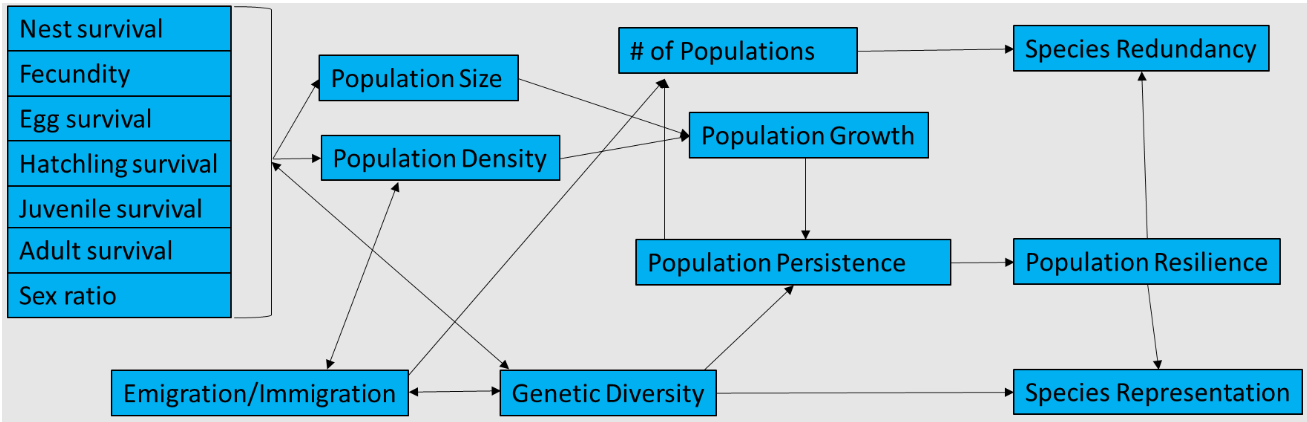


Figure 4. 6-Influence diagram depicting population factors contributing to viability of gopher tortoise.

Minimum viable population (MVP) size is a benchmark used to identify the smallest population size that will reliably persist through a biologically appropriate time frame. The purpose of establishing MVP parameters is to provide acceptable benchmarks for conservation and recovery efforts and is not to determine absolute minimum thresholds that if not met, will result in certain population demise, or that meeting targets implies viability. To reach scientific consensus on appropriate MVP parameters for the gopher tortoise, the GTC convened the Minimum Viable Population and Minimum Reserve Size Working Group in July 2013 and October 2014 (GTC 2013, 2014; entire); this working group determined an MVP includes at least 250 adult gopher tortoises. This abundance criterion was informed by population viability analyses which found populations of 250 or more individuals were most likely to withstand stochastic events and persist for 100 years (Miller et al. 2001, p. 28) or 200 years under favorable habitat conditions (Tuberville et al. 2009, p. 19). The working group also determined an MVP contains a density of no less than 0.4 gopher tortoises per hectare (approximately 0.16 gopher tortoises per acre); this criterion was based on Guyer et al. (2012, pp. 130-131) which found populations with densities below this threshold exhibited altered movement patterns that could negatively impact gene flow and viability. The working group also concluded that at least 247 acres (100 hectares) of high quality, managed habitat was required for a population to persist (McCoy and Mushinsky 2007, p. 1404; GTC 2013, pp. 2-3). Additional MVP criteria included an approximate 1:1 ratio of males to females, evidence of recruitment into the population, variability in size and age classes, and no major constraints to gopher tortoise movement (GTC 2013, pp. 2-3).

The MVP working group recognized populations of less than 250 adults as support populations with two categories, primary and secondary support. Primary support populations contain between 50-249 adult individuals, and secondary support populations are those with less than 50 adults (GTC 2014, p. 4). These support populations may persist for a long period of time under high-quality habitat conditions (Folt et al. 2021, p. 13), but are likely more vulnerable to stochastic events than MVPs (Miller et al. 2001, p. 28; GTC 2014, p. 4). Thus, viability can be evaluated as a measure of the likelihood that a species will sustain populations over time, rather than as a specific state of viable or not viable.

Because we lack consistent and reliable estimates of density, sex ratios, recruitment, dispersal, habitat, and management effort for all sites with available spatial occurrence data, we qualitatively assessed resiliency at the population level by evaluating the estimated current abundance of local populations and creating ordinal resiliency categories. Population estimates for this assessment include data on State, Federal, local government, and private lands, collected in various ways, ranging from standardized survey techniques including belt transect surveys and LTDS (Spatially Explicit), to private lands population information provided at the county level (County Level), to long-term recipient sites (Spatially Explicit). Data were provided by a variety of sources and contain disparate levels of data resolution; thus, we could not reliably determine abundance, density, or other metrics used to identify MVPs (see above) for all populations. All population data provided are integral to evaluating the current condition of the gopher tortoise. Therefore, we used a burrow conversion factor for properties that provided burrow counts and locations but did not have a corresponding abundance estimate from a LTDS survey. Although there is no single burrow conversion factor that would be appropriate for all population across the range of the species, we used a conventional burrow conversion factor of 0.4 individuals/burrow (Guyer et al. 2012, pp. 130-131) to calculate an estimated current population size based on the literature and expert input.

We used estimated abundance of adult gopher tortoises as a metric for categorical levels of resiliency: high (greater than or equal to 250), moderate (51-249), and low (less than 50). These resiliency levels align with the MVP working group's categories for minimum viable (high resiliency), primary support (moderate resiliency), and secondary support (low resiliency) populations (GTC 2014, p. 4). Landscape populations likely provide a higher level of resiliency than local populations, assuming gopher tortoises are able to disperse at a landscape scale, although we do not quantify this explicitly in our resilience assessment. Resiliency categories for local populations are defined as follows:

- High-local population highly likely to persist through a biologically appropriate time frame.
- Moderate-local population likely to persist for a long period of time under high-quality habitat conditions, although more vulnerable to stochastic disturbances compared to highly resilient populations.
- Low-local population may persist for a long period of time under high quality habitat conditions and high levels of management, but highly vulnerable to stochastic disturbances.

Population Factors: Results

Table 4.1 and Figure 4.7 summarize the results of the resiliency analysis for spatially delineated populations of gopher tortoises. It is important to note that abundance estimates are only from spatially delineated populations (i.e., do not contain county level data or gopher tortoises that are present, but not reported), and that these estimates likely significantly underestimate the true number of gopher tortoises present across the species' range. Based on available data, there are an estimated 149,152 gopher tortoises from 656 spatially delineated local populations across the range of the species, with local abundance categories as follow: 360 low, 169 moderate, and 127 high. Most gopher tortoises are found in the eastern portion of the range with Unit 5 supporting 47 percent of the estimated rangewide population total, and Units 3 and 4 supporting 26 percent and 19 percent, respectively. Units 1 and 2 support much smaller numbers of gopher tortoises, with 2 percent and 6 percent of the estimated rangewide population total, respectively, likely driven by differences in soils, as discussed earlier in Chapter 2: Species Biology.

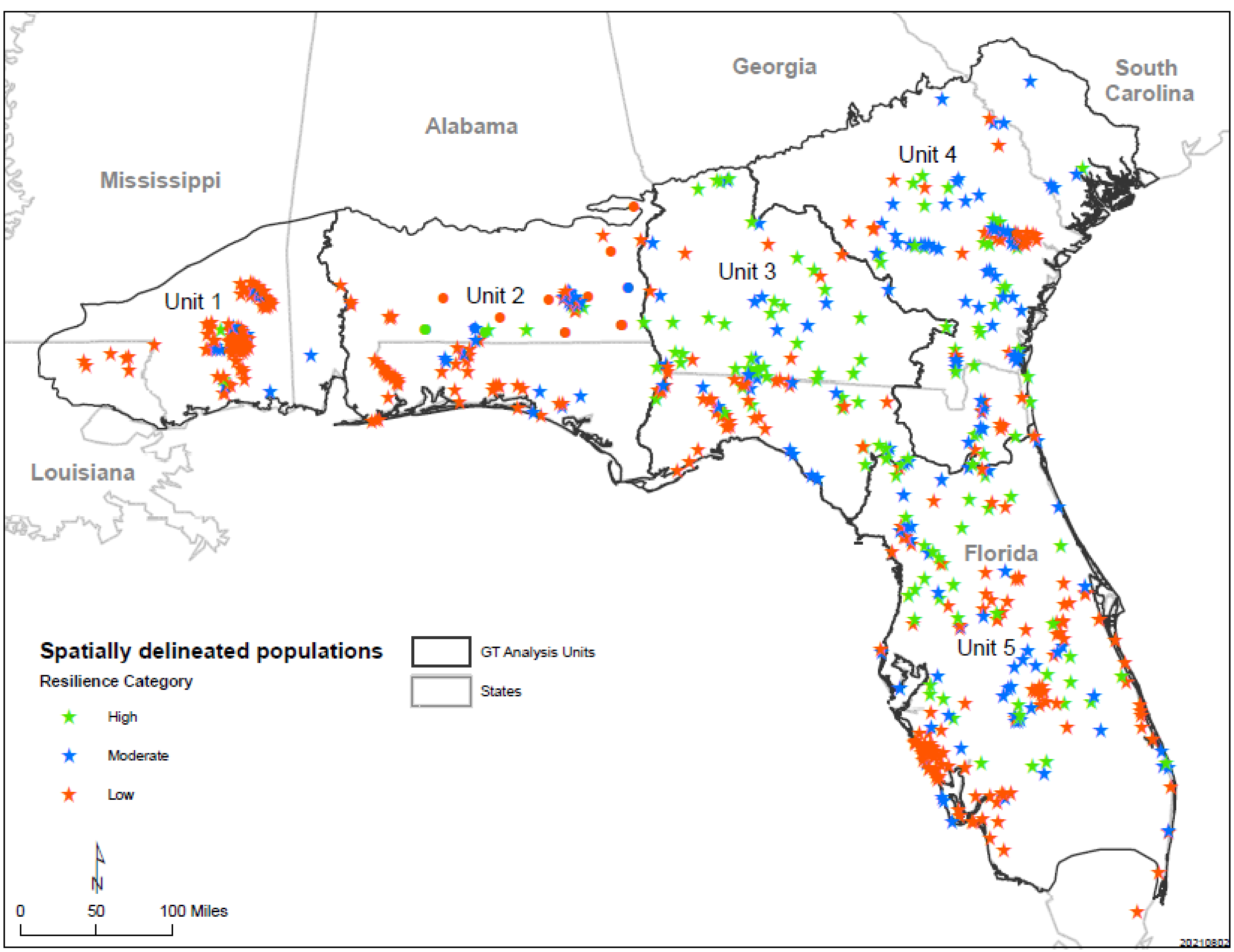


Figure 4.7-Location and associated resiliency (red = low; blue = moderate; green = high) for spatially delineated local populations of gopher tortoise.

Table 4.1-Site specific data population factors and current resiliency for spatially delineated local populations of gopher tortoise.

Analysis unit	# of burrows	# of landscape pops	# of local pops	Abundance	Current Resiliency
1	8,815	13	106	3,100	Low (94)
					Moderate (10)

					High (2)
2	5,809	30	106	8,642	Low (71) Moderate (27) High (8)
3	17,867	55	109	38,947	Low (42) Moderate (24) High (43)
4	20,216	46	124	28,408	Low (35) Moderate (58) High (31)
5	24,783	109	211	70,055	Low (118) Moderate (50) High (43)
Rangewide	**77,490**	**253**	**656**	**149,152**	**Low (360)** **Moderate (169)** **High (127)**

Table 4.2 summarizes the county location and results of the population factors we were able to obtain from the landowner questionnaire. We received responses from 167 properties across all analysis units, which represents approximately 25 percent of all data available for this report. Ninety-one (91) of these properties reported juveniles present, meaning approximately 55 percent of properties show evidence of reproduction. Although respondents only provided categories of abundance on the questionnaire, as opposed to precise abundance estimates, we provide estimates of low, moderate, and high condition classes for abundance as with the spatially delineated populations as follows: 63 low, 11 moderate, and 11 high. As with the spatially delineated populations, most of the properties classified as moderate or high abundance are in the eastern portion of the range, with the western portion supporting many populations

with low abundance. The results reported here for the landowner questionnaire do not include over 10,000 observations recorded between 2013 and 2019 (91 counties rangewide) by an informal NCASI survey (NCASI 2020, p. 9-11; Miller, pers. comm., 2021). Thus, results are assuredly an underestimate of gopher tortoise occurrences on private forests as they are derived from mostly informal surveys, do not cover all possible locations of gopher tortoises across the properties, and only includes a subset of acres under private forest management within gopher tortoise range.

Table 4. 2-County level data population factors (presence of juveniles, estimated number of burrows, and estimated abundance) derived from landowner questionnaire, organized by analysis unit.

Analysis unit	# of properties	Juveniles present?	Estimated # of burrows	Estimated abundance
1	17	Yes (7) No (10) Unknown (0)	Unknown (4)	Unknown (4)
			1-50 (13)	1-50 (13)
			50-250 (0)	50-250 (0)
			>250 (0)	>250 (0)
2	32	Yes (17) No (6) Unknown (9)	Unknown (27)	Unknown (29)
			1-50 (5)	1-50 (3)
			50-250 (0)	50-250 (0)
			>250 (0)	>250 (0)
3	48	Yes (21) No (8) Unknown (19)	Unknown (31)	Unknown (31)
			1-50 (12)	1-50 (12)
			50-250 (1)	50-250 (2)
			>250 (4)	>250 (3)
4	22	Yes (11) No (8) Unknown (3)	Unknown (2)	Unknown- (6)
			1-50 (9)	1-50 (10)
			50-250 (8)	50-250 (5)
			>250 (3)	>250 (1)
5	48	Yes (35) No (6) Unknown (7)	Unknown (12)	Unknown (12)
			1-50 (18)	1-50 (25)
			50-250 (11)	50-250 (4)
			>250 (7)	>250 (7)

4.4.2. Habitat and management factors

The Minimum Viable Population and Minimum Reserve Size Working Group discussed the influence of habitat size, quality, and management on the viability of gopher tortoise populations and concluded that the minimum reserve size to support a viable gopher tortoise population was 247 acres (100 ha), if that site is of superior quality and will be maintained at that quality (GTC 2013, p. 2). Persistence is believed to increase with habitat quality, and previous efforts involving expert workshops and habitat suitability modeling has shown that habitat suitability for gopher tortoises increases with the amount of well-drained soil, compatible land cover (e.g., evergreen forests, shrub), and fire frequency (Figure 4.8 and 4.9; Crawford et al. 2020, pp. 134-136).

Gopher tortoises may be found in a variety of vegetative community types, including upland pine systems such as sandhill and mesic flatwoods, scrub, xeric hammock, dry prairie, coastal grasslands and dunes, mixed hardwood-pine communities, and ruderal communities, with the primary determinants of gopher tortoise habitat suitability being well-drained sandy soils and the presence of an open savanna-like vegetation community. Given the gopher tortoise's affinity for open savanna conditions, maintenance of an open canopy and mid-story is the primary focus of management. Historically, frequent surface fires on the order of every 1-5 years were the primary driver that maintains savanna-like vegetation communities on most sites occupied by the gopher tortoise, although some extremely xeric sites may be maintained largely by moisture limitation. Today, this fire regime is best maintained through prescribed fire, as fragmentation of the landscape by roads and other fire barriers, and social/societal constraints (i.e., suppression efforts) prevents the spread of fire from natural lightning ignitions. Loss and alteration of gopher tortoise habitat from fire exclusion or fire suppression has a significant effect on survival of the gopher tortoise (Boglioli et al. 2000, p. 704), and increased urbanization has limited its use in many locations (Ashton and Ashton 2008, p. 78). Mechanical and chemical treatments to reduce midstory vegetation can also be effective techniques, particularly in areas with constraints to conducting prescribed fire (e.g., at wildlife urban interfaces where smoke management and liability can severely limit the ability to conduct prescribed fire).

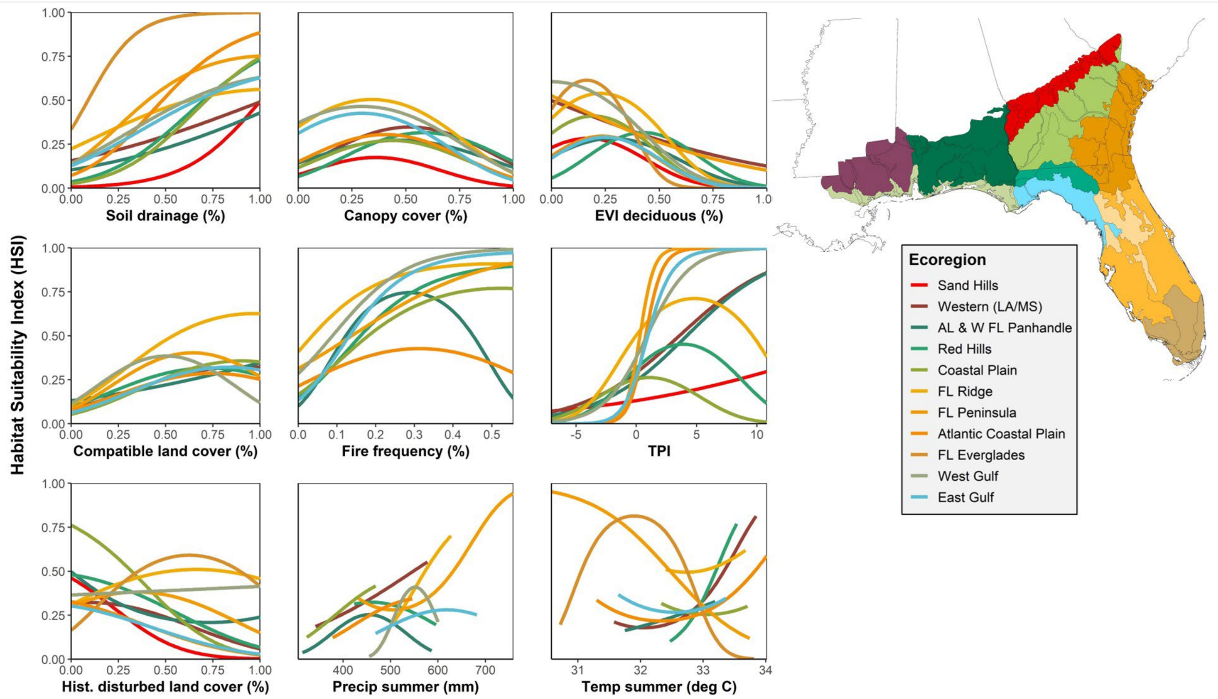


Figure 4. 8-*From Crawford et al. 2020:* Relationships from the best-fitting model between habitat suitability and environmental predictors, by ecoregion group (top right), for the gopher tortoise. Although relationships varied by ecoregion, gopher tortoise habitat suitability tended to increase with the amount of well-drained soil, compatible land cover (e.g., evergreen forests, scrub/shrub), and fire frequency.

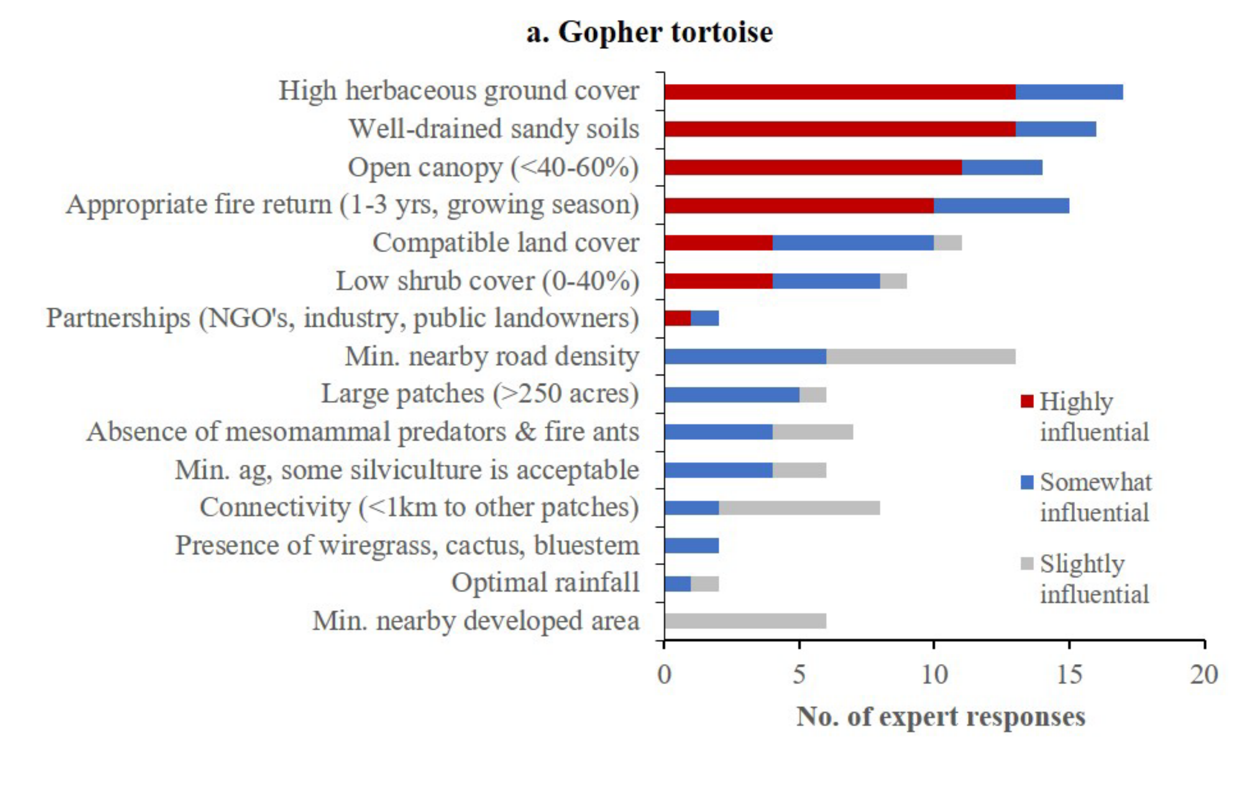


Figure 4. 9-*From Crawford et al. 2020, p. 68:* Influential environmental, landscape, and biophysical attributes for gopher tortoise habitat and presence at a site, as identified in questionnaires of 16 experts. Attributes are generally ordered from highest (top rows) to lowest (bottom rows) influence on habitat suitability and species presence. Definitions for attribute rankings: Highly – attributes must occur at a site for the species to be present; Somewhat – attributes occurring on the landscape greatly increase the likelihood of species being present, but species may occasionally use landscapes without these attributes; Slightly – attributes occurring on the landscape slightly or variably increase the likelihood of species being present, but species may use landscapes without these attributes.

<u>Habitat Factors: Results</u>

Because habitat data were provided by a variety of sources and contain disparate levels of data resolution, we could not reliably determine estimates of habitat within all populations across the range of the gopher tortoise. Thus, we summarize the spatially delineated populations and county level information separately, and estimates of habitat were not used to assess resiliency of gopher tortoise populations; only abundance was used to assess resiliency Estimates of occupied habitat are derived from the Habitat Suitability Index (HSI) model described below (Figure 4.10), and include all suitable habitat found within the 1,968 feet (600 m) buffers used to delineate local populations (Table 4.3). We also calculate estimates of potential habitat by calculating the amount of suitable habitat as predicted by the HSI model, which is located outside of the 1,968 feet (600 m) buffers used to delineate local populations (Table 4.3). Finally, we summarize the amount of low, medium, and high quality habitat as provided by landowners from the questionnaire described earlier (Table 4.4).

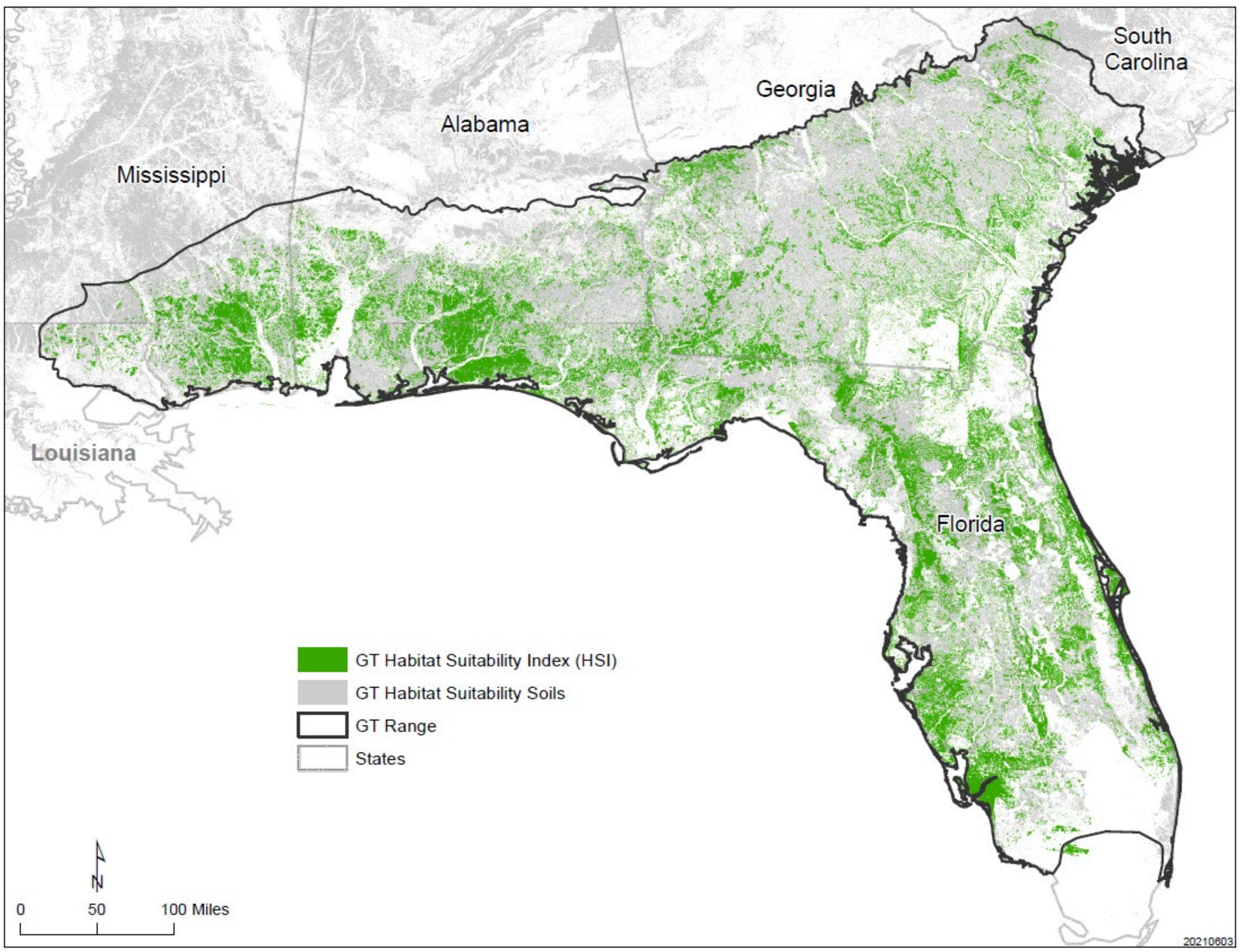


Figure 4. 10-Location of suitable habitat (green) from the HSI model (Crawford et al. 2020) and suitable soils (grey).

Table 4. 3-Estimates of known occupied habitat (habitat included within local population boundaries) and potential habitat (habitat located outside of local population boundaries), by analysis unit, as predicted by the HSI model. Total habitat is the sum of occupied and potential habitat.

Analysis Unit	Occupied Habitat	Potential Habitat	Total Habitat
1	103,582 acres	1,937,559 acres	2,041,141 acres
2	68,430 acres	3,416,877 acres	3,485,307 acres
3	220,127 acres	2,932,265 acres	3,152,392 acres
4	149,146 acres	2,768,120 acres	2,917,266 acres
5	303,627 acres	5,284,111 acres	5,587,738 acres
Rangewide Total	**844,912 acres**	**16,338,932 acres**	**17,183,844 acres**

Table 4. 4-Estimates of low, moderate, and high suitability habitat based on responses to landowner survey. Total habitat is the sum of low, moderate, and high suitability habitat.

Analysis Unit	Low Suitability Habitat	Moderate Suitability Habitat	High Suitability Habitat	Total Habitat
1	4,599 acres	10,943 acres	9,153 acres	24,695 acres
2	18,246 acres	84,004 acres	18,251 acres	120,501 acres
3	18,195 acres	21,356 acres	54,615 acres	94,167 acres
4	30,118 acres	38,131 acres	28,813 acres	97,063 acres
5	37,807 acres	33,208 acres	39,898 acres	110,914 acres
Rangewide	**108,965 acres**	**187,642 acres**	**150,730 acres**	**447,340 acres**

<u>Management Factors: results</u>

To assess gopher tortoise management, we used several data sets available from multiple sources and at multiple spatial scales and these data may include some overlap. First, we used the Tall Timbers Southeast fire history dataset, derived from the U.S. Geological Survey Burned Area (v2) Products (Hawbaker et al. 2020, entire) representing years 1994-2019, which allowed for estimates of acres burned (prescribed fire and wildfire) within gopher tortoise populations across multiple years. The advantages of these data are that they cover the entire range of the species and can be summarized by habitat acreage estimates for the gopher tortoise; however, we are unable to estimate other midstory management techniques such as chemical and mechanical treatments with these data. Acres burned across all units has generally increased over time, with significantly more burning occurring in Unit 5 (Table 4.5). It should be noted that we did not use any management metrics in our resiliency assessment; only abundance was used to assess population resiliency.

Table 4. 5-Acres burned (prescribed fire and wildfire), rangewide, and by analysis unit, for the years 1994-2019. Data obtained from the Tall Timbers Southeast fire history dataset.

Year	Unit 1 fire acres	Unit 2 fire acres	Unit 3 fire acres	Unit 4 fire acres	Unit 5 fire acres	Total acres
1994	17064	29580	22325	28969	41777	139716
1995	17351	23740	32089	29225	56752	159157
1996	14663	33233	68453	67842	103565	287756
1997	23548	28191	39641	47278	65203	203861
1998	22581	35007	60527	72085	99443	289644
1999	42810	76413	107046	94854	174827	495949
2000	70032	88929	134093	92035	163276	548366
2001	51095	68601	123032	102376	174164	519268
2002	45423	60584	71056	71704	104606	353374
2003	28963	43311	44151	45206	80722	242353
2004	40680	64721	85354	77782	145806	414342
2005	29955	59132	52668	61542	130292	333590
2006	89316	111019	102895	90224	249825	643279
2007	73774	90137	152646	161408	192678	670643
2008	53711	73615	104675	104038	140159	476199
2009	50212	79730	108016	93087	167332	498377
2010	38619	67389	85344	68852	129831	390035
2011	54290	101537	188435	292767	210675	847704
2012	16508	54169	68760	135385	117246	392067
2013	50671	106243	164417	106302	135898	563532
2014	69394	113388	162379	183892	218601	747655
2015	68604	105771	112364	102538	177518	566795
2016	89220	156954	193986	112830	188606	741597
2017	88513	197421	340685	331213	415134	1372965
2018	70181	149963	346703	213304	516060	1296210
2019	35795	106202	194682	161009	582368	1080058

We also used summary data for prescribed fire and other midstory maintenance activities available from America's Longleaf Restoration Initiative (ALRI) FY2019 annual report. An advantage of these data is the inclusion of management practices beyond prescribed fire, although the spatial scale of the data is the historical range of longleaf pine, thus estimates of management, include areas outside of gopher tortoise habitat. Also, gopher tortoises use a variety of pine communities, so by limiting reported management actions to longleaf stands, data reported by ALRI excludes some areas within the species range where gopher tortoises are likely present. Florida reported by far the most acres of habitat managed for longleaf by fire and other methods, with nearly 600,000 acres (242,811 ha) treated between October 2018-September 2019. Much of the management implemented by partners under the ALRI umbrella is likely to benefit gopher tortoise.

Table 4. 6-Midstory management, including acres burned and acres managed by other means (e.g., chemical and mechanical) between October 2018-Septemeber 2019, as reported by ALRI (2019).

State	Acres burned	Acres treated (other)	Total acres treated
Alabama	141,054	7,788	148,842
Florida	529,086	58,330	587,416
Georgia	133,019	503	133,522
Mississippi	52,941	3,505	56,446
Louisiana	53,716	9,135	62,851
South Carolina	64,276	5,170	69,446

Next, we summarize management practices as detailed in the gopher tortoise CCA 2021 annual report, which covers management actions implemented during FY2021 (Table 4.7). The goal of the CCA is to organize a cooperative approach to gopher tortoise management and conservation in the eastern portion of its range, and the standardized report generated by partners helps to support this approach and encourages uniform actions and reporting, integrating monitoring and research efforts, and support partner formation. Advantages of the CCA management data are they are specific to sites known to support gopher tortoises and include both prescribed fire and other beneficial practices such as chemical and mechanical treatments, and invasive species control. Unfortunately, the CCA data are limited to the eastern portion of the range, thus does not include information for the western portion.

Table 4. 7-Midstory management, including acres burned and acres managed by other means (e.g., chemical and mechanical), by agency, for FY2021, as reported by the gopher tortoise CCA report (2021). Data cover only the candidate portion of the gopher tortoise range. *Other includes Poarch Band of Creek Indians, Longleaf Alliance, Jones Center, Alabama Forestry Commission, National Park Service, and Georgia Power.

Agency	Acres burned	Acres treated (other)	Total acres restored or maintained
DoD	75,505	13,636	89,141
Forest Service	48,548	3,606	52,154
USFWS	20,362	1,639	22,001
Alabama	6,030	7,229	13,259
Florida	111,891	146,230	258,121
Georgia	33,209	2,530	35,739
South Carolina	431	100	531
Other*	98,513	3,233	101,746

Finally, Table 4.8 summarizes the results provided by respondents to the landowner questionnaire, including total acres burned on the property using prescribed fire, estimated burn frequency in years, and whether other practices beneficial to gopher tortoises are implemented on the property. A total of 228,454 acres (92,452 ha) were burned by private landowners that responded to the questionnaire, with most of this prescribed burning occurring in analysis units 3 and 5. Although there is some variance by analysis unit, many property owners are implementing prescribed fire on a 1-3 year cycle, with few landowners burning on a cycle of greater than 5 years. Finally, many landowners are implementing additional beneficial practices, including chemical and mechanical midstory treatments, invasive species control, and flagging of burrows prior to thinning of forest stands.

Table 4. 8-Results provided by respondents to the landowner questionnaire, by analysis unit, including acres burned, estimated burn frequency in years, and whether other practices beneficial to gopher tortoises are implemented on the property.

<table>
<tr><th>Analysis Unit</th><th>Acres burned</th><th>Burn frequency in years (# of respondents)</th><th>Other beneficial practices Y/N (# of respondents)</th></tr>
<tr><td rowspan="3">1</td><td rowspan="3">11,605</td><td>1-3 (14)</td><td rowspan="3">Y- (17)
N- (0)</td></tr>
<tr><td>3-5 (0)</td></tr>
<tr><td>>5 (1)</td></tr>
<tr><td rowspan="3">2</td><td rowspan="3">33,562</td><td>1-3 (9)</td><td rowspan="3">Y- (23)
N- (9)</td></tr>
<tr><td>3-5 (5)</td></tr>
<tr><td>>5 (1)</td></tr>
<tr><td rowspan="3">3</td><td rowspan="3">66,299</td><td>1-3 (14)</td><td rowspan="3">Y- (21)
N- (27)</td></tr>
<tr><td>3-5 (7)</td></tr>
<tr><td>>5 (0)</td></tr>
<tr><td rowspan="3">4</td><td rowspan="3">12,361</td><td>1-3 (8)</td><td rowspan="3">Y- (17)
N- (5)</td></tr>
<tr><td>3-5 (4)</td></tr>
<tr><td>>5 (3)</td></tr>
<tr><td rowspan="3">5</td><td rowspan="3">104,627</td><td>1-3 (7)</td><td rowspan="3">Y- (40)
N- (8)</td></tr>
<tr><td>3-5 (13)</td></tr>
<tr><td>>5 (11)</td></tr>
</table>

4.5. Current resiliency results

Below, we summarize the results of the current condition analysis for both spatially delineated and county level local populations, by analysis unit (Table 4.9 and Figure 4.11). Current resiliency is derived from the estimated abundance at each local population (except for county level data which did not have an estimated abundance; these were labeled as unknown); although our resiliency assessment was limited to abundance within each population, habitat and management factors are also summarized for each analysis unit.

Table 4. 9-Number of local populations and current resiliency of gopher tortoise, by analysis unit; includes spatially explicit and county level data.

Analysis unit	# of local populations	Current Resiliency
1	123	Low (107)
		Moderate (10)
		High (2)
		Unknown (4)
2	138	Low (74)
		Moderate (27)
		High (8)
		Unknown (29)
3	157	Low (54)
		Moderate (26)
		High (46)
		Unknown (31)
4	146	Low (45)
		Moderate (63)
		High (32)
		Unknown (6)
5	259	Low (143)
		Moderate (54)
		High (50)
		Unknown (12)
Rangewide	**823**	**Low (423)**
		Moderate (180)
		High (138)
		Unknown (82)

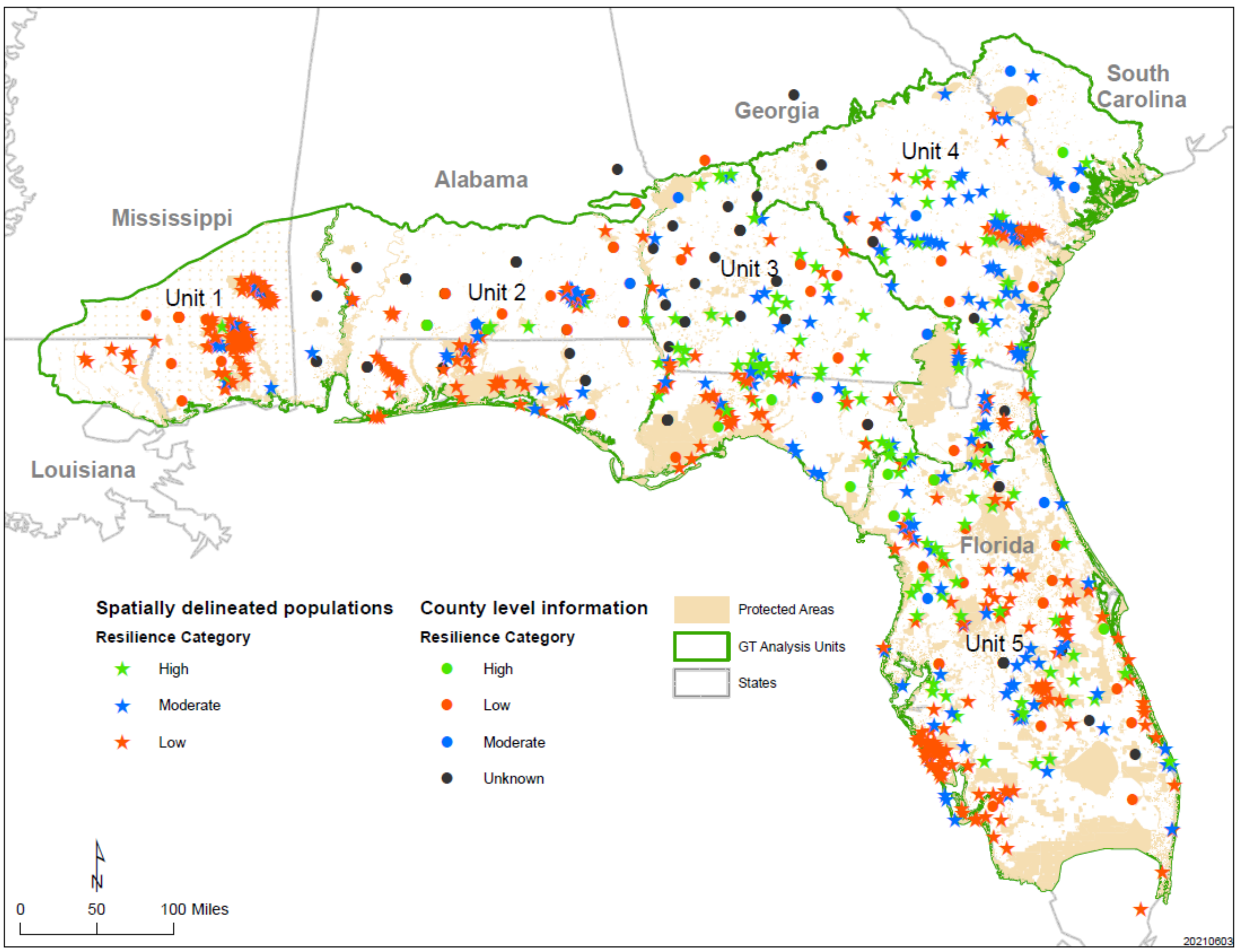


Figure 4. 11-Location of protected areas and local gopher tortoise populations with associated current resiliency, by analysis unit; includes spatially explicit and county level data.

Unit 1

Based on available data, analysis unit 1 is composed of many small, disconnected populations, and very few larger populations (123 local populations; 13 landscape populations), spread across private and public land. Based on current abundance, there are 107 low, 10 moderate, and 2 high resiliency populations within this unit; 4 populations have an unknown resiliency due to no population estimates being available for these properties (Figure 4.12). Camp Shelby, a DoD property, is the stronghold of the unit with a local population having an estimated 1,003 individual gopher tortoises. Seventeen properties on private land in the unit support gopher tortoise populations based on responses to the landowner survey, with 7 properties reporting signs of reproduction.

Although over 103,000 acres (41,682 ha) of habitat are currently known to be occupied by gopher tortoises, there is nearly 2 million acres (809,371 ha) of estimated habitat where gopher tortoise occupancy is unknown and where future surveys may reveal more gopher tortoises to be present on the landscape. The most current estimates for prescribed fire implementation show that over 35,795 acres (14,485 ha) were burned within this unit in 2019, over a 2 times increase over time since 1994. Over 90 percent of landowners who responded to the questionnaire, report implementing prescribed fire on a 1-3 year rotation, with all respondents reporting implementing additional beneficial practices for gopher tortoises.

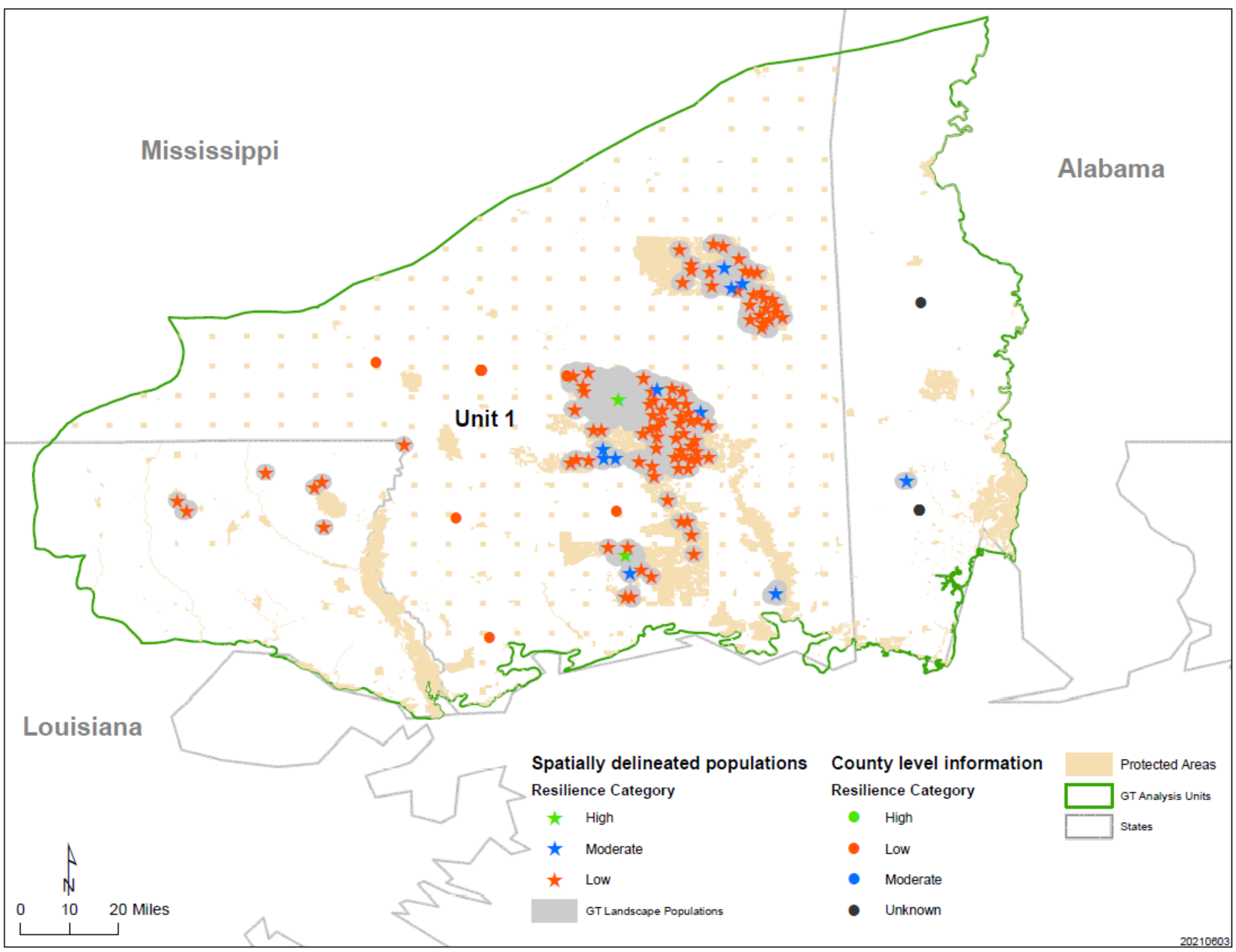


Figure 4. 12-Location and associated resiliency (red = low; blue = moderate; green = high) for local populations of gopher tortoise in analysis unit 1.

Unit 2

Based on available data, analysis unit 2 has 138 local populations and 30 landscape populations. Based on current abundance estimates, this unit is composed of 74 low, 27 moderate, and 8 high resiliency local populations; 29 populations have an unknown resiliency due to no population estimates being available for these properties (Figure 4.13). The 8 highly resilient populations are found on Fort Rucker, Conecuh NF, Apalachee WMA, Perdido WMA, Geneva State Forest, and an unnamed private property. Thirty-two properties on private land in the unit support gopher tortoise populations based on responses to the landowner survey, with 17 properties reporting signs of reproduction.

Although over 68,000 acres (27,518 ha) of habitat are currently known to be occupied by gopher tortoises, there is nearly 3.4 million acres (1.37 million ha) of estimated habitat where gopher tortoise occupancy is unknown and where future surveys may reveal more tortoises to be present on the landscape. The most current estimates for prescribed fire implementation show that approximately 106,000 acres (42,896 ha) were burned in 2019, just over a 3 times increase since 1994. Sixty percent of landowners who responded to the questionnaire, report implementing prescribed fire on a 1-3 year rotation, with 72 percent of respondents reporting implementing additional beneficial practices for gopher tortoises.

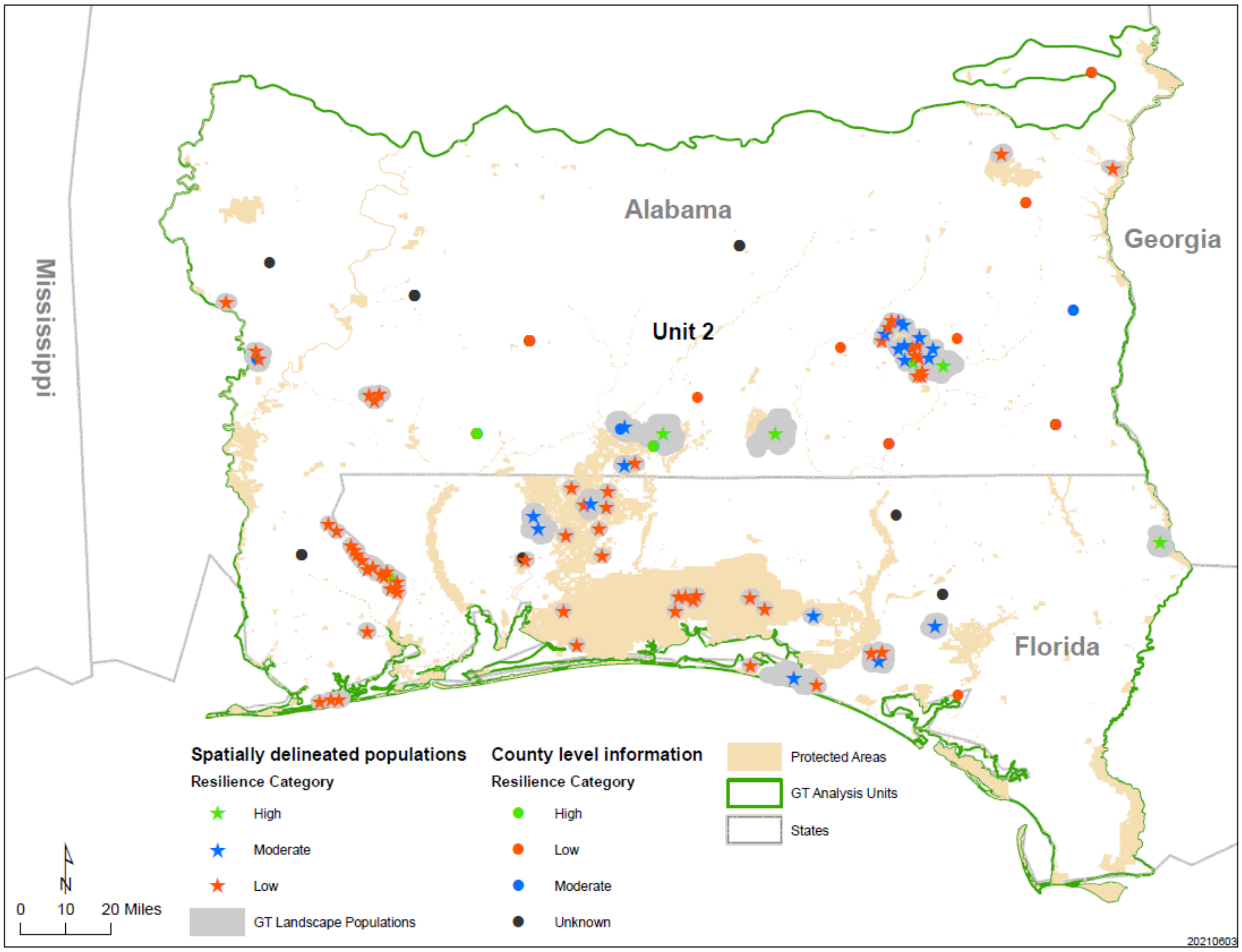


Figure 4. 13-Location and associated resiliency (red = low; blue = moderate; green = high) for local populations of gopher tortoise in analysis unit 2.

<u>Unit 3</u>

Based on available data, analysis unit 3 has 157 local populations and 55 landscape populations. Based on current abundance estimates, analysis unit 3 is composed of 54 low, 26 moderate, and 46 high resiliency populations; 31 populations have an unknown resiliency due to no population estimates being available for these properties (Figure 4.14). Of the 46 highly resilient populations, 7 populations have estimates exceeding 1,000 individuals, including Twin Rivers State Forest, Chattahoochee Fall Line WMA, River Bend, Alapaha River WMA, Apalachicola NF, and the Jones Center at Ichauway. Forty-eight properties on private land in the unit support gopher tortoise populations based on responses to the landowner survey, with 21 properties reporting signs of reproduction.

Although over 220,000 acres (89,030 ha) of habitat are currently known to be occupied by gopher tortoises, there is over 2.9 million acres (1.17 million ha) of estimated habitat where gopher tortoise occupancy is unknown, and where future surveys may reveal more tortoises to be present on the landscape. The most current estimates for prescribed fire implementation show that over 194,000 acres (78,509 ha) were burned in 2019, almost a 10 times increase since 1994. Sixty-seven percent of landowners who responded to the questionnaire, report implementing prescribed fire on a 1-3 year rotation, with 44 percent of respondents reporting implementing additional beneficial practices for gopher tortoises.

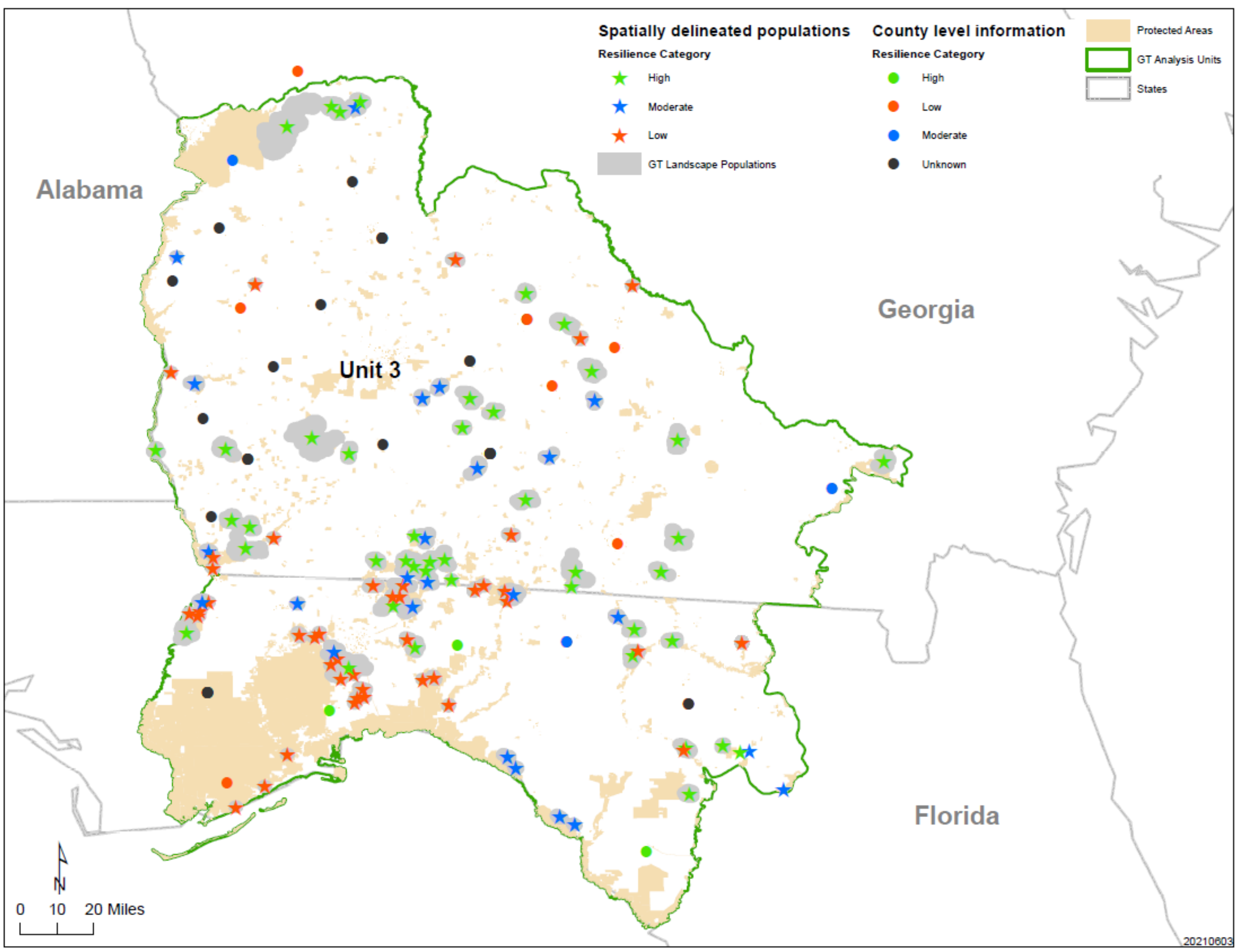


Figure 4. 14-Location and associated resiliency (red = low; blue = moderate; green = high) for local populations of gopher tortoise in analysis unit 3.

Unit 4

Based on available data, analysis unit 4 has 146 local populations and 46 landscape populations. Based on current abundance estimates, analysis unit 4 is composed of 45 low, 63 moderate, and 32 high resiliency populations; 6 populations have an unknown resiliency due to no population estimates being available for these properties (Figure 4.15). Of the 32 highly resilient populations, 5 populations have estimates exceeding 1,000 individuals, including Ohoopee Dunes WMA, Ralph E. Simmons State Forest, Jennings State Forest, and Fort Stewart. Twenty-two properties on private land in the unit support gopher tortoise populations based on responses to the landowner survey, with 11 properties reporting signs of reproduction.

Although over 149,000 acres (60,298 ha) of habitat are currently known to be occupied by gopher tortoises, there is over 2.7 million acres (1.09 million ha) of estimated habitat that is currently not known to be occupied where future surveys may reveal more gopher tortoises to be present on the landscape. The most current estimates for prescribed fire implementation show that over 161,000 acres (65,154 ha) were burned in 2019, over a 7 times increase since 1994. Fifty-three percent of landowners who responded to the questionnaire, report implementing prescribed fire on a 1-3 year rotation, with 77 percent of respondents reporting implementing additional beneficial practices for gopher tortoises.

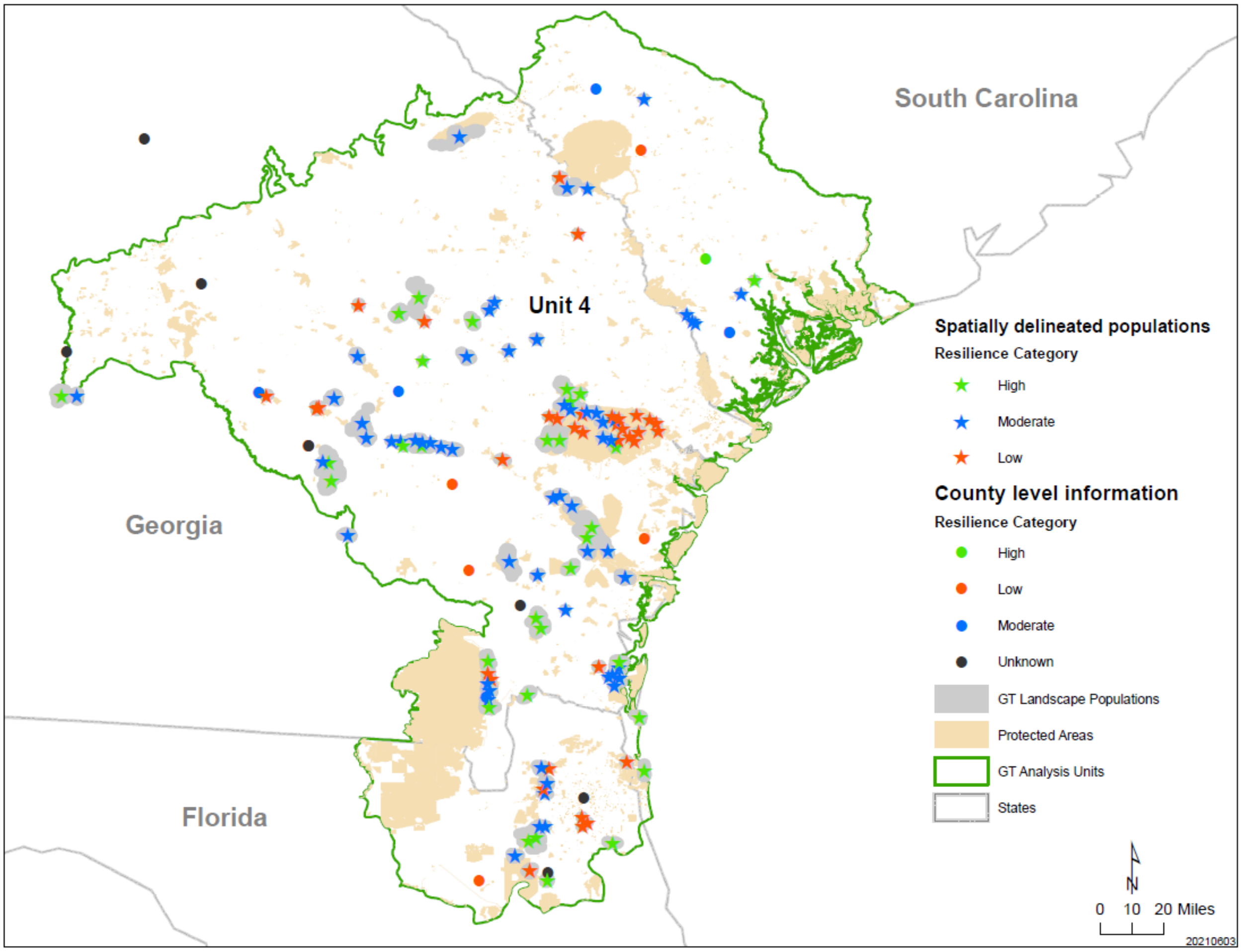


Figure 4. 15-Location and associated resiliency (red = low; blue = moderate; green = high) for local populations of gopher tortoise in analysis unit 4.

Unit 5

Based on available data, analysis unit 5 has 259 local populations and 109 landscape populations. Based on current abundance estimates, analysis unit 5 is composed of 143 low, 54 moderate, and 50 high resiliency populations; 12 populations have an unknown resiliency due to no population estimates being available for these properties (Figure 4.16). Of the 47 highly resilient populations, 12 populations have estimates exceeding 1,000 individuals, including Camp Blanding and Goldhead Branch State Park; Ocala NF; Chassahowitzka WMA; Ichetucknee Springs State Park; Bell Ridge Wildlife and Environmental Area; Etoniah Creek State Forest; Halpata Tastanaki and Cross Florida Greenway; Lake Louisa State Park; Kissimmee Prairie Preserve State Park; Green Swamp West Unit WMA; Withlacoochee State Forest's Citrus Tract;

and Perry Oldenburg Wildlife and Environmental Area and Withlachoochee State Forest's Croom Tract. Forty-eight properties on private land in the unit support gopher tortoise populations based on responses to the landowner survey, with 35 properties reporting signs of reproduction.

Although over 300,000 acres (121,405 ha) of habitat are currently known to be occupied by gopher tortoises, there is nearly 5.3 million acres (2.14 million ha) of estimated habitat where gopher tortoise occupancy is unknown and where future surveys may reveal more gopher tortoises to be present on the landscape. The most current estimates for prescribed fire implementation show that over 582,368 acres (235,675 ha) were burned in 2019, a nearly 14 times increase over time since 1994. Twenty-three percent of landowners who responded to the questionnaire, report implementing prescribed fire on a 1-3 year rotation, with 83 percent of respondents reporting implementing additional beneficial practices for gopher tortoises.

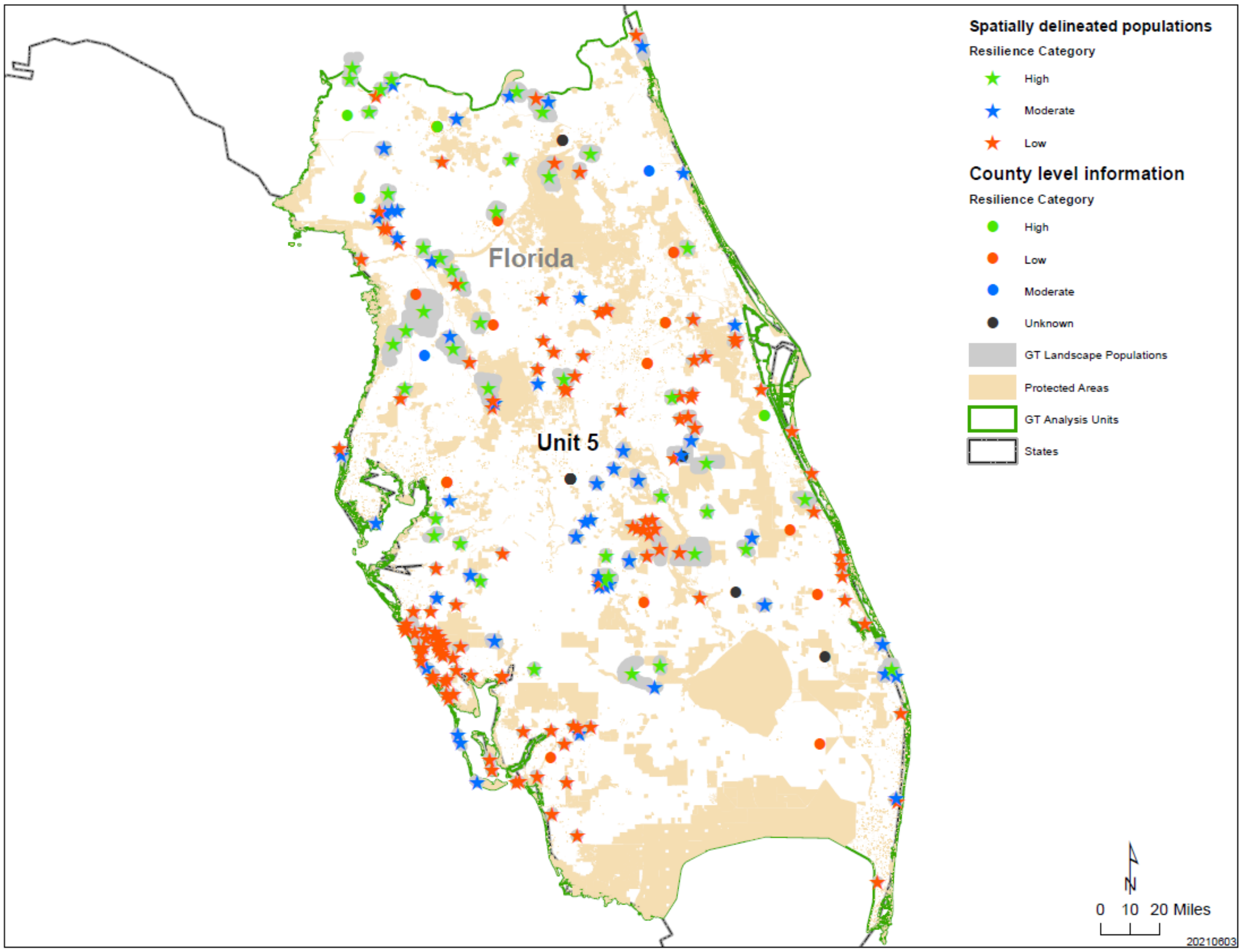


Figure 4. 16-Location and associated resiliency (red = low; blue = moderate; green = high) for local populations of gopher tortoise in analysis unit 5.

4.6. Current representation and redundancy

As described previously in this chapter, representation for this species is assessed primarily based on genetic variation across the range of the species (5 analysis units; Galliard et al. 2017, entire). We evaluated current representation by examining the number of populations and their associated resiliency within the five population analysis units across the species' range (Gaillard et al. 2017, entire). We report redundancy for gopher tortoise as the total number and resiliency of populations and their distribution within and among representative units.

Although gopher tortoises occupy vegetative communities with a variety of pine types, the species was historically associated with longleaf pine systems, which once covered an estimated 92 million acres (37.2 million ha) (Frost 1993, p. 20), but has declined significantly due to forest clearing and conversion for agriculture and development (Landers et al. 1995, p. 39). Due to loss of open pine conditions, gopher tortoise representation and redundancy have likely decreased significantly from historical levels. Currently, all five analysis units are occupied by multiple local populations, although the resiliency of these populations varies across the range (Figure 4.17). Unit 1, in the far western portion of the species range, is comprised of many small, isolated populations (although there is uncertainty in whether currently unknown populations are present on private lands which could ultimately connect these small populations into larger more resilient populations; future surveys and data from private lands would help elucidate this uncertainty), with only 10 percent of the populations having at least moderate resiliency (calculated as 100% x (moderate + high)/(total - unknown)), and only 2 populations with high resiliency, leaving portions of this unit potentially vulnerable to catastrophic events. These results are confounded by the fact that Unit 1 is the western extent of the species range, and spatial gradients in environmental factors often produce predictable patterns in which habitat quality is highest in the centers of species' ranges and becomes more unsuitable as the range edge is approached; thus, apparent lower levels of abundance seen in the western portion of the range might be driven by natural variation in climate and soils found at the edge of the species' range. Also, there are likely many populations that are unaccounted for with the limited data we had available, which if accounted for, would infer a higher degree of redundancy (i.e., more populations and greater spatial distribution).

Similarly, for Unit 2, in the western-central portion of the range, only 32 percent of the populations are of moderate or greater resiliency, but 8 populations are classified as highly resilient, potentially buffering against the potential of catastrophic events. The central (Unit 3) and eastern (Units 4 and 5) have many populations (67 percent of the total number of populations assessed), and the resiliency of many of the populations is of moderate or high condition (Unit 3 = 57 percent; Unit 4 = 68 percent; Unit 5 = 50 percent). In addition to a relatively high number of highly resilient populations within the 3 eastern analysis units, the populations are well distributed across each unit, potentially buffering against the impacts of potentially catastrophic events. The fact that there are more resilient populations in the eastern portion of the range compared to the western portion is not surprising, as the soils are not as suitable in the western portion, an important component of habitat driving habitat quality, and ultimately abundance and density.

From a rangewide perspective, although representation and redundancy have likely decreased significantly relative to the historical distribution of the species, there are still many resilient populations distributed across the range of the species, contributing to future adaptive capacity (representation), and buffering against the potential of future catastrophic events. Because the species is widely distributed across its range, it is highly unlikely any single event would put the species as a whole at risk. However, portions of analysis unit 1 are likely more vulnerable to such catastrophes given that most of the populations present in this unit are of low resiliency.

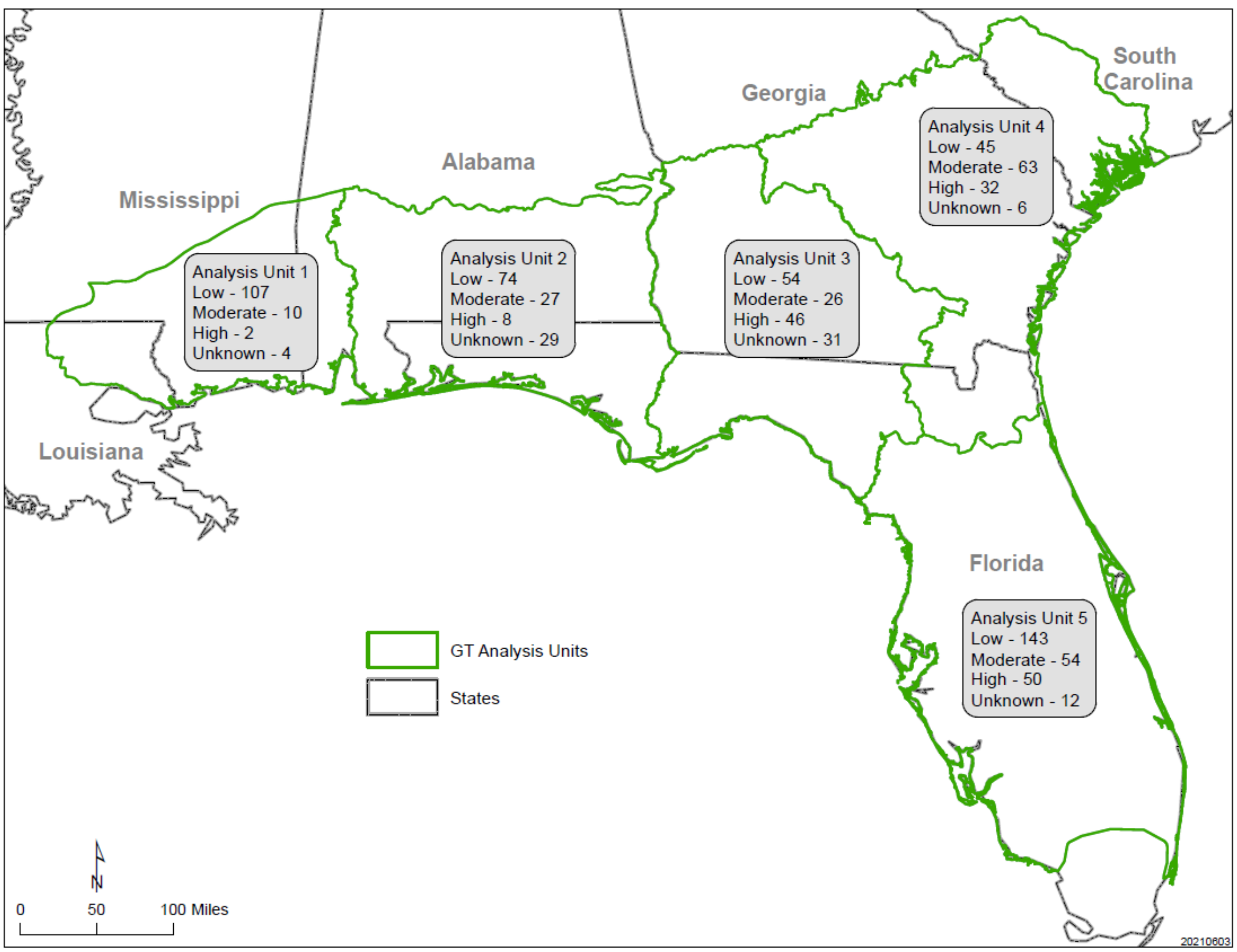


Figure 4. 17-Resiliency of gopher tortoise local populations summarized by analysis unit.

CHAPTER 5 – FUTURE CONDITIONS AND VIABILITY

We have considered what the gopher tortoise needs for viability and the current condition of those needs (Chapters 2 and 4), and we reviewed the influencing factors that are driving the current, and future conditions of the species (Chapter 3). We now consider what the species' future condition might be by projecting populations that occur on protected conservation lands. We apply our future forecasts to the concepts of resiliency, representation, and redundancy to describe the future viability of the gopher tortoise.

To assess viability for the gopher tortoise, we developed an analytical framework that integrates projections from multiple models of future anthropogenic and climatic change to project future trajectories/trends of gopher tortoise populations and identify stressors with the greatest influence on future population persistence. The modeling framework was built to support the future conditions analysis by estimating the change in population growth and persistence probability of populations while accounting for geographic variation in life history. The model links intrinsic factors (demographic vital rates) to four extrinsic anthropogenic factors that are hypothesized to threaten gopher tortoise population persistence (climate warming, sea-level rise, urbanization, and shifts in habitat management). We used published models describing extrinsic factors in the future to project gopher tortoise demographics under six future scenarios varying in threat magnitude and presence. A regression analysis of model outputs was used to identify threats that are predicted to have the greatest impact on population persistence. A detailed model description is included in Appendix B.

5.1 Models and scenarios

5.1.1. Model Structure

A population viability analysis (PVA) framework was used to predict population growth and extinction risk for the gopher tortoise. The PVA is a stage-based population model (i.e., Lefkovitch model) used to project population size and structure forward in time with simulations. For the PVA, local population demography of gopher tortoises was conceptualized in a multi-stage, female-only model, with two discrete life stages: juveniles and adults. During a given time-step, both stages had a probability of individuals surviving and staying within the stage, juveniles had a probability of maturing to become adults, and adults had a probability of reproducing and potentially recruiting individuals into the juvenile stage. Individuals that did not survive during a time-step were assumed to have either died or permanently emigrated from the population. Recruitment into the adult stage by immigration was also modeled. In the following sections of Chapter 5, we describe the methods and results of the future conditions analysis; we note that a detailed description of the model structure can be found in Appendix B.

5.1.2. Demographic parameters

We constructed a baseline population model that approximated demographic conditions experienced by gopher tortoise populations in recent decades across the species' range. However, populations of gopher tortoises experience great variation in abiotic characteristics across the species' range, and variation in abiotic characteristics influences demographic rates among populations. At more southern latitudes, populations experience significantly warmer mean annual temperature, which may afford greater overall opportunity for thermoregulation, energy acquisition, and metabolism when compared to northern populations. As a result, southern populations of gopher tortoises experience faster growth rates, younger ages of sexual maturity (hereafter, maturity age), and increased clutch size (Mushinsky et al. 1994, p. 123; Ashton et al. 2007, entire; Meshaka Jr. et al. 2019, p. 105-106). Because the goal was to predict population growth and extinction risk of populations across the species' range and predictive population models are most useful when demographic parameters are modeled specific to populations of interest (Ralls et al. 2002, entire), we extended the model to accommodate for geographic variation in demographic rates by estimating parameters specific to the geographic location of populations.

Demographic parameters used to model and project baseline population demographics of gopher tortoises are shown in Table 5.1. For parameters thought to vary substantially by abiotic features among sites, linear regression models were fit to estimate relationships between demographic rates and mean annual temperature (hereafter, MAT; degrees C) sourced from the 'WorldClim' database (Hijmans 2020, entire). If parameters were not known to vary geographically, mean values were modeled as invariant among populations. In the following subsections, we describe how parameters describing recruitment, maturity age, survival, immigration, and initial population size, were modeled.

Table 5. 1-Demographic parameters, mean estimates, and distribution shapes used to model and project baseline population demographics of gopher tortoises in conservation lands across the species' range.

Parameter	Distribution shape	Mean (SE)
Probability of breeding	Beta	0.97 (0.01)
Fecundity	Log normal	-3.54 (2.42) + 0.48 (0.12) * MAT
Nest survival	Beta	0.35 (0.10)
Probability of viable eggs	Beta	0.85 (0.05)
Probability of female	Beta	0.50 (0.04)
Hatchling survival	Beta	0.13 (0.03)
Juvenile survival	Beta	0.75 (0.06)
Adult survival	Beta	0.96 (0.03)
Maturity age	Log normal	43.52 (11.31) – 1.41 (0.53) * MAT
Juvenile abundance	Log normal	Varying by population
Adult abundance	Log normal	Varying by population
Immigration rate	Beta	0.01 (0.001)
Percent of winter days for burning	Beta	0.77 (0.05)
Percent of spring days for burning	Beta	0.80 (0.05)
Percent of summer days for burning	Beta	0.65 (0.05)
Change in winter days for burning	Beta	Varying by projection scenario
Change in spring days for burning	Beta	Varying by projection scenario
Change in summer days for burning	Beta	Varying by projection scenario
Burn probability	Beta	0.4 (0.015)
Fire effect on survival	Beta	0.96 – 0.027 (0.003) * YSB

Recruitment

We modeled the proportion of breeding females in a given year as 0.97; this estimate has recently been validated by two independent field studies (J. Goessling unpubl. data, 2021; E. Hunter unpubl. data, 2021). Because fecundity varies widely among populations and is likely driven by a north-to-south latitudinal gradient in temperature (Ashton et al. 2007, p. 360), we used linear regression to estimate the relationship between MAT and estimates of mean clutch size from the literature and then used regression coefficients to simulate mean values for populations, given the geographic location and MAT of a population. We modeled the proportion of nests that survive predation as 0.35 using an estimate from unmanipulated nests (Smith et al. 2013, p. 355). We modeled the probability of eggs being viable and hatching as 0.85, an average from reviews of field hatching rates (Landers et al. 1980, p. 359; Rostal and Jones 2002, p. 7). To account for males (and remove them) during projections, we assumed that sex ratios of eggs were even within populations and modeled the probability of eggs being female as 0.5. We modeled hatchling survival from nest emergence until the following survey period as 0.13 (0.04–0.34, 95 percent confidence interval [CI]), given results from a meta-analysis of hatchling survival of gopher tortoises (Perez-Heydrich et al. 2012, p. 342).

Maturity age

Age at maturity varies along a latitudinal gradient across gopher tortoise populations (Mushinsky et al. 1994, p. 123; Meshaka Jr. et al. 2019, p. 105-106). We used linear regression to estimate the relationship between MAT and maturity age estimates of females from the literature, then used regression coefficients to simulate mean maturity ages for populations, given the population's geographic location and MAT. Given a predicted maturity age for a population, we then calculated the probability that a juvenile will transition to adulthood during a given year.

Survival Rates

Survival rates are difficult to measure for gopher tortoises because individuals are long-lived, challenging to recapture, may become unavailable for resurvey by emigrating away from study populations, or may die. When individuals disappear from a study population, mark-recapture analyses are often unable to estimate whether individuals died or emigrated away. To this end, most mark-recapture studies of gopher tortoise seeking to understand survival have estimated apparent annual survival, which is the probability that individuals survived and stayed within a study area. Studies have found apparent annual survival to vary between adults and juveniles, with adults having higher survival than juveniles (Tuberville et al. 2014, p. 1155; Howell et al. 2020, p. 60; Folt et al. 2021, p. 624-625). We reviewed the literature for apparent annual survival estimates for gopher tortoises and performed a linear regression analysis testing for effects of age and MAT on survival, which confirmed that adults have greater survival than juveniles but failed to recover an effect of MAT on survival; rather, survival is likely most strongly influenced by habitat quality and management at sites (Howell et al. 2020, entire; Folt et al. 2021, p. 627;

Hunter and Rostal 2021, p. 661). We modeled adult survival as 0.96 and juvenile survival as 0.75 (Folt et al. 2021, p. 624-625), with a density-dependent limit on population growth where for each time-step when density increased above 2 females/ha, we prevented recruitment into the adult age class. Field studies have estimated tortoise density to range from 0.02–1.50 individuals/ha among northern populations (Guyer et al. 2012) and from 4.2–24.9 individuals/ha in southern Florida. We selected a threshold of 2 females/ha (i.e., 4 tortoises/ha, assuming even sex ratios) as a limit for density dependence because there is a considerable uncertainty when estimating tortoise density and 2 females/ha was a conservative intermediate estimate of maximum density among populations across the species' range.

Immigration

Gopher tortoises infrequently move long distances from established core home range areas; such movements can result in permanent emigration and immigration into other populations. We implicitly modeled losses to local populations due to emigration because the estimates of apparent annual survival accounts for individuals that emigrate from local populations. Given ongoing emigration, local populations within the same landscape population might receive immigrants that bolster population size. While little quantitative information is available describing the frequency or success of immigration, one study found that 2 percent of adults emigrated from local populations each year (Ott-Eubanks et al. 2003, p. 319). Given it is unlikely that all emigrants successfully immigrate into another population, the number of immigrants into local populations was modeled as a product of a randomly-drawn immigration rate (mean = 1 percent) multiplied by the total number of adult tortoises in adjacent populations (i.e., landscape population size) divided by the number of nearby local populations. Immigration rate was constrained during each time step so that the sum of immigration rate and survival rate could not exceed 1.

Initial population size

To estimate population growth and extinction risk of gopher tortoise populations across the species' range, we initialized the model with estimates of population size from spatially delineated populations. Population estimates were collected by a diverse partnership of cooperating State and Federal agencies, private organizations, and academic institutions. As discussed previously, only spatially explicit data were used in the future projection modelling. Because initial population sizes used in this analysis are the same dataset that were included in Chapter 4, the same assumptions and data limitations apply, including factors that may result in underrepresentation of initial population sizes and thus, future projections. It is important to note, data included in future condition modelling represents a subset of gopher tortoises likely to occur on the landscape, as data from private lands were lacking due to the absence of spatial information. Population estimates do not represent an assessment of all local populations of tortoises that exist in southeastern North America, but rather represent information that was provided by partners through much of the species' range. Most population estimates came from assessments of local populations on lands managed for the conservation of biodiversity or natural resources. Future inclusion of additional spatially explicit populations, particularly from private lands, would provide projections that better describe the species as a whole; our current model only makes projections about a subset of the species' populations.

We initialized starting population size using population estimates derived from data collected using burrow surveys and LTDS. Using spatial survey data associated with population estimates, we identified populations at two spatial scales as described in Chapter 4: local populations and landscape populations. We received some population estimates in aggregate from properties that were delineated to have two or more local populations of gopher tortoises; in these instances, we multiplied the population estimate (and confidence limits) by the area of each delineated local population and divided by the total survey area of the original survey. We assumed that population estimates being delineated into two or more local populations through this process would have even population densities and this process spread the population assessment evenly among local populations delineated by in the dataset. Some delineated local populations assessed in current conditions have less than 2 individuals; we removed these local populations from the future condition analysis.

The process of delineating local populations and landscape populations resulted in a dataset of 626 local populations that formed 244 landscape populations. We used population estimates from local populations to parameterize initial population size of adults and juveniles during simulated population projections. We assumed a 1:1 sex ratio and a 3:1 adult:juvenile ratio in populations (Folt et al. 2021, p. 626) and used the ratios to isolate and separate the female population into juvenile and adult components.

5.1.3. Modeling threats

We sought to model how predicted future changes to abiotic and biotic features may threaten future population growth and viability of gopher tortoises. We engaged scientists with expert knowledge in both gopher tortoise population biology and habitat management and identified a series of factors that experts considered to have high likelihood of influencing gopher tortoise demographics in the future (hereafter, threats). Using the list of threats, we reviewed the literature to identify research describing quantitative effects of how threats (or similar mechanisms) influence specific demographic parameters in the conceptual model for gopher tortoises. Below, we describe hypotheses for how four threats (climate warming, sea-level rise, urbanization, and climate-change effects on habitat management) may influence gopher tortoise demographics, and how we used quantitative estimates of the threats from the literature to parameterize and simulate how threats may influence future population growth and viability of gopher tortoises.

Climate warming

Climate change is predicted to drive warming temperatures and seasonal shifts in precipitation across Southeastern North America (Carter et al. 2018, entire). Of these two effects, warming temperatures may have the greater impact on gopher tortoises, because gopher tortoise demography is known to be sensitive to temperature gradients across the species' range. Specifically, maturity age and fecundity vary along a north-south latitudinal gradient, where warmer, southern populations have faster growth rates, younger maturity ages, and increased fecundity relative to cooler, northern populations (Ashton et al. 2007, p. 123; Meshaka Jr. et al. 2019, p. 105-106). As climate warming increases temperatures in the region, individuals in populations may experience more favorable conditions for growth and reproduction across the species' range. Because no studies have linked gopher tortoise growth or fecundity to interannual or interpopulation variation in precipitation, it seems less likely that climate-driven shifts in precipitation will influence gopher tortoise demography. Although the gopher tortoise exhibits temperature-dependent sex determination, we did not include this effect in the model as gopher tortoises can modify nest site selection and timing of nesting, as discussed in Chapter 3. We also did not model any potential range expansion or contraction that could occur due to long term climate change because there is no consensus or projection framework that we are aware of related to vegetative community changes and climate change projections; also, any significant expansion or contraction of the gopher tortoise range is likely to occur beyond our projection timeframe of 80 years.

We modeled how climate warming may influence gopher tortoise demography by using the estimated linear relationships of MAT with maturity age and fecundity to predict how warming temperatures experienced by populations in the future will drive concurrent changes in demography. For each population, we used historical estimates of MAT using the 'WorldClim' database (Hijmans 2020, entire) and then simulated step-wise climate-warming effects on MAT each year in the future where warming rates were parameterized by three treatments of climate warming: (1) a 1.0 °C (1.8 °F) increase in MAT over the next 80 years, (2) a 1.5 °C (2.7 °F) increase in MAT over the next 80 years, and (3) a 2.0 °C (3.6 °F) increase in MAT over the next 80 years (IPCC 2013, entire). The three scenarios (1.0 °C, 1.5 °C, and 2.0 °C) related to an optimistic prediction of RCP2.6, an intermediate prediction between RCP2.6 and RCP4.5, and a prediction for RCP4.5, respectively. Each year in the future, we used simulated changes in MAT to calculate mean maturity age and fecundity at sites. This analysis assumes that: (i) all local populations will respond homogeneously to warming temperatures, and (ii) there are no potential climatic ceilings that would limit growth and reproduction.

<u>Habitat management</u>

Prescribed fire is the most common management technique to maintain high-quality, open canopy conditions for gopher tortoises (Landers and Speake 1980, entire; Diemer 1986, p. 130; Yager et al. 2007, entire; Ashton et al. 2008, entire); however, when fire is not present in sufficient intervals or intensity to maintain open canopy conditions on the landscape, apparent survival of gopher tortoises decreases (Hunter and Rostal 2021, p. 661), potentially to levels that are insufficient for maintaining population viability (Folt et al. 2021, p. 627). However, wildlife managers tasked with maintaining high-quality habitat for gopher tortoises and other fire-dependent upland plant and animal species (Guyer and Bailey 1993,entire) may be challenged because regional climate warming may make habitat management with prescribed fire more difficult to accomplish. Managers require suitable fuel and weather conditions (e.g., relative humidity, temperature, wind speed; i.e., the ‘burn window’) to facilitate manageable fire behavior that will accomplish intended goals while limiting risk toward human communities. However, climate-change models predict the availability of burn window conditions to shift over future decades, with available conditions for fire management increasing in the winter but decreasing in the spring and summer (Kupfer et al. 2020, p. 769-770); summed together, seasonal shifts in the burn window conditions will decrease overall opportunity for management with prescribed fire. If managers become limited in the use of prescribed fire, resulting decreases in habitat quality may drive decreases in gopher tortoise survival. Alternatively, managers will need to rely on alternative tools to control midstory, such as chemical and mechanical treatments, which can be economically costly. Also, it should be noted that, although the ability to implement prescribed fire will likely be greatly constrained in the future, modelling for the southeastern United States suggests increased wildfire risk and a longer fire season, with at least a 30 percent increase from 2011 in lightning-ignited wildfire by 2060 (Vose et al. 2018, p. 239). It is possible that more frequent wildfires may help to mitigate predicted decreases in suitable burn days.

We estimated how habitat management influences gopher tortoise population growth by modeling habitat management of populations and linking the frequency of management to adult survival (see Appendix B for more information). We assumed that a baseline fire-return interval of 1-4 years (mean = 2.5 years) maintains high-quality habitat for the species (Guyette et al. 2012, p. 330; Crawford et al. 2020, p. 141) and then modeled the probability that the habitat associated with a population is burned during a given year (burn probability) as the inverse of the fire-return interval. Next, using historical baseline data describing average seasonal burn opportunity across southeastern North America (Kupfer et al. 2020, p. 769-771), we modeled the number of available burn days (i.e., days within the burn window) in winter (January–February), spring (March–May), and summer (June–July) as a product of the total days per season (59, 92, and 61 days, respectively) and the percentage of days historically available for burning (0.766, 0.800, and 0.645, respectively). We modeled four treatments for how the number of days available for prescribed fire may change in the future (Kupfer et al. 2020, p. 769-771): (1) ‘decreased fire’ - prescribed fire use will decrease consistent with climate shifts projected by

RCP4.5, (2) ‘very decreased fire’ - prescribed fire use will decrease with climate projections RCP8.5, (3) ‘increased fire’ - prescribed fire use will increase opposite of the effect projected by RCP4.5, and (4) ‘status quo’ - prescribed fire use will remain at current levels.

For each treatment, we modeled effects of climate change on the percentage of available burn days over the next 80 years using average effects from across southeastern North America (Kupfer et al. 2020, p. 769-771): 0.016 increase in winter, 0.040 decrease in spring, and 0.239 decrease in summer (‘decreased fire’ treatment); 0.030 increase in winter, 0.105 decrease in spring, and 0.436 decrease in summer (‘very decreased fire’ treatment); 0.016 decrease in winter, 0.040 increase in spring, and 0.239 increase in summer (‘increased fire’ treatment), and no effects on burn days (‘status quo’ treatment). The increased fire and status quo treatments could result if habitat managers can offset effects of climate change by benefiting from methodological advances in fire management or by using alternative methods rather than prescribed fire, such as mechanical or chemical treatments, to achieve similar management goals.

Urbanization

Human development of the landscape (i.e., urbanization) threatens terrestrial wildlife communities in the southeastern United States, including gopher tortoise populations that often rely on upland habitats that are popular sites for urban development or agriculture. While the local gopher tortoise populations we modeled are largely on conservation lands intended for wildlife conservation, urbanization threatens to surround these conservation lands, disrupt habitat connectivity, and decrease metapopulation dynamics that maintain connectivity and gene flow both among local populations and within landscape populations. Additionally, urbanization can disrupt habitat management by decreasing the ability of managers to use prescribed fire, with the caveat that managers have the alternative to implement other tools, such as mechanical and chemical treatments. We sought to model effects of urbanization pressure on gopher tortoise populations by linking urbanization projections from the SLEUTH urbanization model (Terando et al. 2014, entire) to habitat management of local populations with prescribed fire and with baseline immigration rates of gopher tortoises across landscape populations.

First, we modeled an effect of urbanization on habitat management by making burn probability a function of each population's distance to the nearest urban area. Studies have found evidence of fire exclusion/suppression in habitats within 600 m to 5 km (0.4 to 3.1 miles) of urban areas (Theobald & Romme, 2007, entire; Pickens, et al., 2017, p. 105). Therefore, we chose a moderate value of 10,498 feet (3.2 km) to capture the interaction between urbanization and fire frequency. Specifically, we assumed that local populations immediately adjacent to urban areas (distance less than 328 feet [0.1 km]) are unable to manage with prescribed fire. We also assumed management is uninfluenced for populations far from urban areas (greater than 10,498 feet [3.2 km]; no effect), and management of populations between 328-10,498 feet (0.1–3.2 km) from an urban area experience a negative effect on fire management with burn probability declining as a linear function of the population's proximity to the urban area (i.e., populations closer to urban areas experience less prescribed fire).

To model effects of urbanization on migration dynamics among local populations within landscape populations, we first estimated the total area and urbanized area within landscape populations in year 2020 using the SLEUTH model. Next, we estimated future urbanization and its effect on dispersal for gopher tortoises by estimating future urbanized areas using the SLEUTH model projections for 40, 60, and 80 years in the future. We then calculated the predicted change in proportion of habitat due to future urbanization for landscape populations. For each year greater or equal to 3 during population projections, we modeled the number of adult immigrants into local populations in each year as a function of the total number of individuals in the landscape population available for immigration to the local population during the previous year divided by the total number of local populations in the landscape population; this estimated a number of migrants from the landscape population that would be available to immigrate into a local population being modeled during a given timestep. We then multiplied the number of dispersing tortoises during a timestep by the proportion of non-urbanized habitat across the landscape, assuming that urbanized habitat prevented dispersal by causing mortality of dispersing tortoises (i.e., road mortality). Next, we assumed that the likelihood of a population is managed with prescribed fire varies by its distance to the nearest urban area. We first estimated the distance of each local population to the nearest urban area in the current conditions (i.e., year 2020) and in the future using the SLEUTH model by measuring the distance to urban area from the geometric center of local populations to the edge of the nearest neighbor urban area. We assumed that local populations immediately adjacent to urban areas (distance < 0.1 km) are unable to be managed with prescribed fire and forced burn probability to 0 for those populations; that management is uninfluenced for populations far from urban areas (> 3.2 km; no effect on burn probability); and that populations between 0.1–3.2 km from an urban area experience a negative effect on fire management where burn probability declined as a linear function of the population's proximity to urban area. We explain how we modeled urbanization in greater detail in Appendix B.

We estimated predicted effects of urbanization on local and landscape populations by modeling three treatments from the SLEUTH urbanization model that corresponded to different probability thresholds of urbanization:
(1) a 'low urbanization' treatment where future urbanization was limited to cells with urbanization probability greater or equal to 0.95,
(2) a 'moderate urbanization' treatment with urbanization predicted by probability greater or equal to 0.50, and
(3) a 'high urbanization' treatment with urbanization probability greater or equal to 0.20.
We assumed that: (i) immigration was limited to adults and that no juveniles successfully migrate among populations, and (ii) immigrants cannot survive or move through urbanized areas (e.g., due to road mortality) but can survive while moving through unurbanized areas.

<u>Sea level rise</u>

Because gopher tortoises are a terrestrial species and not suited for wetlands, sea-level rise may negatively affect gopher tortoise populations in low-lying coastal areas, such as coastal sand-dune environments (Blonder et al. 2021, p. 6-8). Projected sea-level rise scenarios provide a range of coastal inundation scenarios that vary in severity. We modeled effects of sea-level rise on gopher tortoises using three scenarios of sea-level rise predicted by the U.S. National Oceanic and Atmospheric Administration (NOAA), the 'intermediate-high', 'high', and 'extreme' scenarios, which correspond to projections from two of the most likely global emission scenarios, RCP6 and RCP8.5 (IPCC 2013, entire; NOAA 2020, entire). Local projections for the two scenarios are available from U.S. Geological Survey sea-level monitoring stations across the southeastern United States, providing estimates of sea-level rise for stations at decadal time steps in the future to year 2100.

We modeled three treatments of sea-level rise using projections from NOAA:
(1) the 'intermediate-high' scenario derived from RCP6.0, which projects approximately 6.0 feet (1.83 m) of sea-level rise over the next 80 years;
(2) the 'high' scenario which projects approximately 8.37 feet (2.55 m) of sea-level rise over the next 80 years; and,
(3) the 'extreme' scenario derived from RCP8.5, which projects approximately 10.37 feet (3.16 m) of sea-level rise over the next 80 years (NOAA 2020, entire).

We modeled sea-level rise effects on populations in two ways. First, assuming that gopher tortoise populations cannot persist when oceanic levels encroach too close upon their habitat, we simulated decreasing elevation of gopher tortoise populations due to sea-level rise. We extracted historical estimates of elevation Above Sea Level (ASL; in feet/m) using the centroid geographic coordinates of each local population using the 'WorldClim' database (Hijmans 2020, entire). Given the total predicted sea-level rise of each treatment over the next 80 years, we simulated incremental sea-level rise at each population in each year in the future and subtracted this incremental oceanic rise from the site's elevation through time. When the site elevation of populations decreased to less than 5.56 feet (2 m) ASL, we considered the populations functionally extirpated. Second, we assumed that habitat inundated by sea-level rise adjacent to local populations would decrease connectivity and dispersal dynamics of individuals among populations within landscape populations. We used spatial projections from NOAA to estimate future inundation area due to sea-level rise for each landscape population, and then modeled immigration to decline as a function of decreasing habitat available for dispersal at the landscape scale. The analysis of sea-level rise effects assumes that: (i) sea-level rise throughout the Southeast will be homogeneous and characterized by NOAA projections derived from data from Ft. Myers, Florida, (ii) populations less than 5.56 feet (2 m) ASL are unable to persist, and (iii) populations are unable to migrate away from sites because coastal areas are often heavily developed and there is no guarantee that adjacent properties would be available for entire populations to migrate.

5.1.4. Scenarios and population projection structure

To understand how gopher tortoise populations will respond to scenarios with multiple concurrent factors, we created a set of six scenarios with varying levels of threat magnitude and combination (Table 5.2). Specifically, we created three scenarios with different levels of stressors (low stressors, medium stressor, and high stressors) that experienced habitat management consistent with contemporary target management goals. We then used the medium stressor values and built three additional models that varied in habitat management treatments, ranging from 'more management' conditions to worsening ('less management') and much worse ('much less management') conditions (Table 5.2). Appendix B describes how uncertainty in future states of factors and scenarios were addressed, including geographic variation among populations, parametric uncertainty, and temporal stochasticity.

Table 5. 2-Six scenarios of future climate warming, sea-level rise, urbanization, and habitat management used to simulate population growth and extinction risk for gopher tortoises for 80 years into the future. Scenarios vary in the magnitude of threat influences on gopher tortoise demography; threat levels included three levels of climate warming (1.0, 1.5, and 2.0 degrees C increase; 1.8, 2.7, 3.6 degrees F, respectively), three levels of sea-level rise (intermediate-high [6.00 feet/1.83 m], high [8.37 feet/2.55 m], and extreme [10.37 feet/3.16 m] scenarios), three levels of urbanization scenarios predicted by the SLEUTH model (Terando et al. 2014, entire) at probability thresholds of 0.9 (conservative projection), 0.5 (moderate projection), and 0.1 (aggressive projection), and four levels of changes in habitat management (no changes, less management predicted by RCP4.5 [Kupfer et al. 2020, p. 769-770], much less management predicted by RCP8.5 [Kupfer et al. 2020, p. 769-770], and improved management [the opposite of the effect predicted by RCP4.5 in Kupfer et al. 2020, p. 769-770]).

Scenarios	Climate warming (deg C)	Sea-level rise (m)	Urbanization	Management
Low stressors	1.0	0.54 m	P = 0.95	Status quo
Medium stressors	1.5	1.83 m	P = 0.50	Status quo
High stressors	2.0	3.16 m	P = 0.20	Status quo
More management	1.5	1.83 m	P = 0.50	More

Less management	1.5	1.83 m	P = 0.50	Less
Much less management	1.5	1.83 m	P = 0.50	Much less

Little to no data exist describing gopher tortoise immigration rates (γ) in wild populations. Given uncertainty associated with this parameter, we sought to include a sensitivity analysis to understand the effects of γ on our results. We crafted three additional scenarios: a 'no immigration' scenario with γ = 0, a 'high immigration' scenario with γ = 0.02, and a 'very high immigration' scenario with γ = 0.04. We simulated these scenarios with stressor and habitat management values from the 'medium stressors' scenario with a projection interval of 80 years, and we compared the resulting immigration scenarios to the 'medium stressors' scenario results that were simulated with γ = 0.01.

To assess future redundancy, resiliency, and representation of the gopher tortoise, we used population projections to estimate changes in gopher tortoise populations in the future under each of the six scenarios (Table 5.2). We assessed redundancy by measuring predicted changes in the total number of individuals, local populations, and landscape populations in the future. We summarized population trends by estimating population growth rate as increasing (greater than 1.00), stable (equals 1.00), or decreasing (less than 1.00). We measured population growth of total population size, the number of local populations, and the number of landscape populations across the species' range during the projection interval by dividing the value from year 2020 by the model-predicted value at the end of the projection interval.

We assessed the resiliency of future populations to changing environments by estimating extinction risk. We chose 3 females as a lower threshold to approximate functional extinction because populations with fewer than three females are extremely likely to be inbred and at great risk of extirpation (Chesser et al. 1980, entire; Frankham et al. 2011, p. 466). For each population, we estimated persistence probability, and then categorized populations as 'extremely likely to persist' (persistence probability greater or equal to 0.95), 'very likely to persist' (P greater than or equal to 0.80 and less than 0.95), 'more likely than not to persist' (P greater than or equal to 0.50 and less than 0.80), and 'unlikely to persist' (i.e., extirpated; persistence probability less than 0.50). We then simulated the number of populations predicted to persist at the end of the projection. For each landscape population, we estimated resiliency by selecting the constituent focal population with the greatest persistence probability and used that value to categorize landscape population persistence and simulated landscape population survival.

We evaluated how representation is predicted to change in the future by examining how population growth of total population size (number of individual females), number of populations, and number of landscape populations will vary by the five population genetic groups of tortoises across the species' range (Gaillard et al. 2017, p. 501-504). For each scenario, we summarized the results among all populations across the species' range, but also by genetic units (five units; see Gaillard et al. 2017, p.501-504). All analyses were performed in the statistical program R (R Core Team 2018, entire). A more detailed methodological summary of the future conditions analysis is included in Appendix B.

5.2 Model results

Linear regression analysis of three demographic parameters reviewed in the literature (fecundity, maturity age, and apparent annual survival probability) found that fecundity and maturity age vary significantly by MAT across the species' range (Figure 5.1). For each 1 °C (1.8 °F) increase in MAT, we found that maturity age decreased by 1.41 years (0.18–2.62, 95 percent CI), which was a statistically significant effect (P = 0.029). For each 1 °C (1.8 °F) increase in MAT, we found that fecundity increased by 0.52 eggs per clutch (0.27–0.77, 95 percent CI), which was statistically significant (P less than 0.001). Survival probability showed no significant trend with respect to MAT.

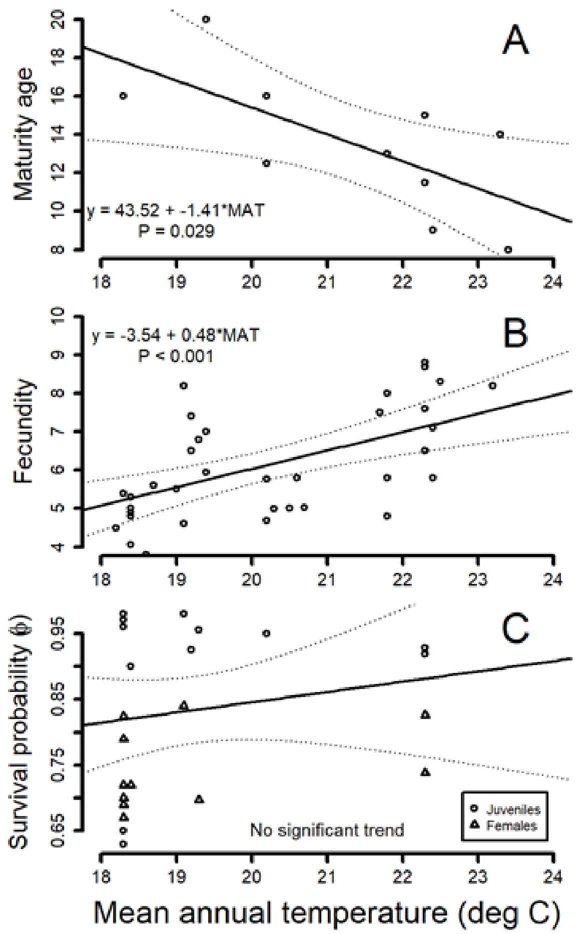


Figure 5. 1-Effect of mean annual temperature (MAT; degrees C) on (A) maturity age (MA), (B), fecundity, and (C) annual apparent survival probability of gopher tortoise (Gopherus polyphemus) populations. Geographic variation in biotic conditions (e.g., MAT) predict significant variation in maturity age and fecundity (P less than 0.05) but not in annual apparent survival probability.

We simulated population growth of 626 local populations and 244 landscape populations that were estimated to comprise approximately 70,600 individual (female) gopher tortoises. Population projections under six scenarios of future change during 40, 60, and 80-year projection intervals predicted declines in the number of gopher tortoise individuals, local populations, and landscape populations of gopher tortoises (Table 3). Relative to current levels of total population size, projections for total population size suggested declines by 2060 (λ = 0.65–0.67 among scenarios; i.e., 33–35 percent declines), 2080 (λ = 0.66–0.70 among scenarios; 30–34 percent declines), and 2100 (λ =

0.67–0.72 among scenarios; i.e., 28–33 percent declines). The six scenarios varied little in their effects on the total number of individuals, local populations, and landscape populations; but scenario effects become more magnified in each successive timestep. However, 95 percent confidence intervals for projections of future population growth overlapped with 1.00 in all scenarios and timesteps, indicating significant uncertainty in projections for each scenario at each projection interval.

Among the simulated populations, the number of local populations and landscape populations also were predicted to decline in each projection interval (Table 5.3). Declines in local populations and landscape populations were modest at the 40-year timestep (47–48 percent and 25–27 percent declines among scenarios, respectively) but were exacerbated at the 60-year (60–61 percent and 41–43 percent declines, respectively) and 80-year (68–70 percent and 53–57 percent declines, respectively) timesteps. Scenarios did not vary strongly in their effect on the predicted number of persisting local populations and landscape populations within each projection interval.

Table 5. 3-Simulated population projections for female gopher tortoises under six scenarios of future change. Columns summarize the initial number (in 2020), future predicted number, and population growth rate (λ) for the total population size, number of populations, and number of landscape populations for six scenarios projected 40, 60, and 80 years into the future. See Table 5.2 for descriptions of scenarios and parameters.

Scenarios	Total population size			Number of local populations			Number of landscape populations		
	Initial	Future	λ	Initial	Future	λ	Initial	Future	λ
Year 2060									
Low stressors	70610	47468	0.67 (0.30–1.80)	626	332	0.53 (0.51–0.55)	244	179	0.73 (0.63–0.81)
Medium stressors	70614	47630	0.67 (0.30–1.91)	626	331	0.53 (0.51–0.54)	244	183	0.75 (0.61–0.80)
High stressors	70582	45998	0.65 (0.28–1.84)	626	329	0.53 (0.51–0.55)	244	177	0.73 (0.64–0.80)
More management	70611	46646	0.66 (0.29–1.84)	626	329	0.53 (0.51–0.55)	244	178	0.73 (0.61–0.80)
Less management	70610	46826	0.66 (0.29–1.79)	626	328	0.52 (0.50–0.54)	244	180	0.74 (0.62–0.80)
Much less management	70600	46495	0.66 (0.29–1.80)	626	323	0.52 (0.50–0.54)	244	178	0.73 (0.60–0.79)
Year 2080									
Low stressors	70609	49281	0.70 (0.36–1.77)	626	249	0.40 (0.38–0.41)	244	143	0.59 (0.44–0.73)
Medium stressors	70636	48924	0.69 (0.37–1.79)	626	250	0.40 (0.38–0.41)	244	142	0.58 (0.45–0.73)
High stressors	70592	46674	0.66 (0.34–1.70)	626	246	0.39 (0.37–0.41)	244	138	0.57 (0.43–0.70)

More management	70598	49246	0.70 (0.35–1.86)	626	250	0.40 (0.38–0.42)	244	145	0.59 (0.45–0.74)
Less management	70604	48754	0.69 (0.34–1.80)	626	247	0.39 (0.38–0.41)	244	138	0.57 (0.44–0.72)
Much less management	70569	48592	0.69 (0.35–1.69)	626	243	0.39 (0.37–0.42)	244	142	0.58 (0.42–0.72)
Year 2100									
Low stressors	70614	50846	0.72 (0.37–1.77)	626	198	0.32 (0.30–0.33)	244	114	0.47 (0.36–0.62)
Medium stressors	70594	48366	0.69 (0.36–1.74)	626	196	0.31 (0.29–0.33)	244	108	0.44 (0.35–0.59)
High stressors	70578	47378	0.67 (0.35–1.70)	626	194	0.31 (0.29–0.33)	244	109	0.45 (0.33–0.60)
More management	70584	49114	0.70 (0.36–1.73)	626	196	0.31 (0.30–0.33)	244	110	0.45 (0.33–0.62)
Less management	70596	47202	0.67 (0.37–1.75)	626	193	0.31 (0.29–0.33)	244	106	0.43 (0.34–0.61)
Much less management	70608	48520	0.69 (0.37–1.67)	626	188	0.30 (0.28–0.32)	244	106	0.43 (0.34–0.59)

Categorization of populations by persistence probability revealed finer-scale variation of how scenarios varying in magnitude of stressors and management influenced persistence probability of populations (Table 5.4). Among the three projection intervals, the ‘low stressors’ scenario tended to predict higher percentages of Extremely Likely Extant populations and lower percentages of Unlikely Extant (i.e., Extirpated) populations relative to the ‘medium stressors’ and ‘high stressors’ scenarios. Similarly, the ‘more management’ scenario tended to predict higher percentages of Extremely Likely Extant populations and lower percentages of Unlikely Extant (i.e., Extirpated) populations relative to the ‘less management’ and ‘much less management’ scenarios. Figure 5.2 illustrates persistence probabilities among populations and landscape populations predicted by the ‘less management’ scenario.

Table 5. 4- Predicted population persistence probabilities categories for gopher tortoise populations in year 2100 under six future scenarios varying in the magnitude of future stressors; numbers represent number of local gopher tortoise populations, whereas numbers in parentheses represent the percentage of populations that fall into each category; persistence categories are Extremely Likely Extant (P > 95.0 percent), Very Likely Extant (P = 80.0–94.9 percent), More Likely Than Not Extant (P = 50.0–79.9 percent), and Unlikely Extant (P < 50.0 percent; i.e., extirpated). See Table 5.2 for descriptions of scenarios and their parameters.

Population persistence category	Scenario					
	Low stressors	Medium stressors	High stressors	More management	Less management	Much less management
Year 2060						
Extremely Likely Extant	104 (16.6%)	103 (16.5%)	101 (16.1%)	99 (15.8%)	102 (16.3%)	104 (16.6%)
Very Likely Extant	102 (16.3%)	97 (15.5%)	108 (17.3%)	108 (17.3%)	98 (15.7%)	91 (14.5%)
More Likely Than Not Extant	135 (21.6%)	145 (23.2%)	135 (21.6%)	134 (21.4%)	141 (22.5%)	141 (22.5%)
Unlikely Extant (i.e., Extirpated)	285 (45.5%)	281 (44.9%)	282 (45%)	285 (45.5%)	285 (45.5%)	290 (46.3%)
Year 2080						
Extremely Likely Extant	78 (12.5%)	74 (11.8%)	71 (11.3%)	79 (12.6%)	74 (11.8%)	76 (12.1%)
Very Likely Extant	35 (5.6%)	44 (7%)	41 (6.5%)	36 (5.8%)	41 (6.5%)	31 (5%)
More Likely Than Not Extant	122 (19.5%)	116 (18.5%)	117 (18.7%)	128 (20.4%)	103 (16.5%)	114 (18.2%)
Unlikely Extant (i.e., Extirpated)	391 (62.5%)	392 (62.6%)	397 (63.4%)	383 (61.2%)	408 (65.2%)	405 (64.7%)
Year 2100						
Extremely Likely Extant	76 (12.1%)	72 (11.5%)	70 (11.2%)	71 (11.3%)	70 (11.2%)	70 (11.2%)
Very Likely Extant	21 (3.4%)	20 (3.2%)	25 (4%)	24 (3.8%)	24 (3.8%)	24 (3.8%)
More Likely Than Not Extant	65 (10.4%)	62 (9.9%)	55 (8.8%)	58 (9.3%)	57 (9.1%)	54 (8.6%)
Unlikely Extant (i.e., Extirpated)	464 (74.1%)	472 (75.4%)	476 (76%)	473 (75.6%)	475 (75.9%)	478 (76.4%)

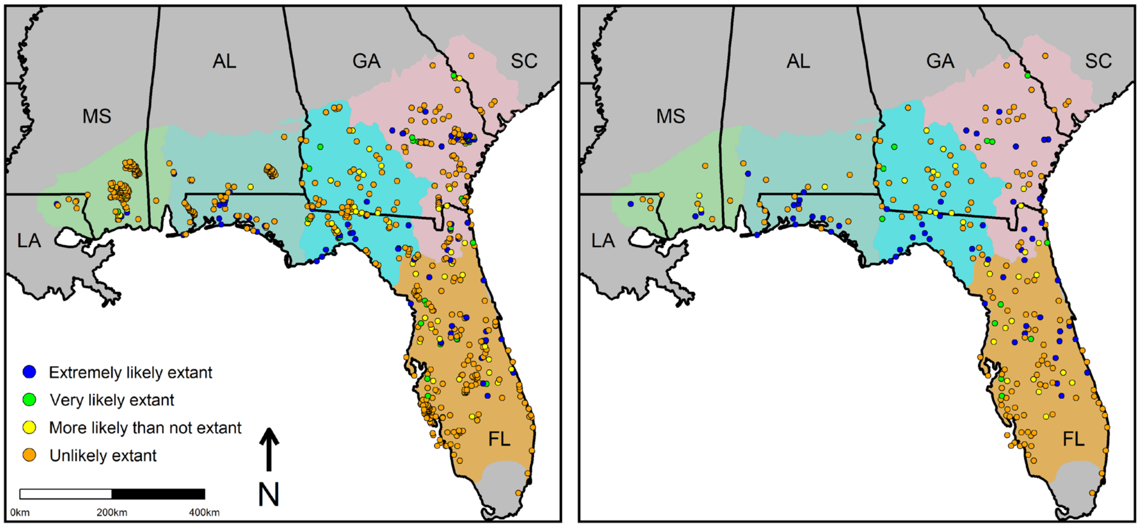


Figure 5. 2- Persistence probabilities of gopher tortoise (*Gopherus polyphemus*) local populations (left) and landscape populations (right) predicted by a future scenario of less habitat management with medium stressor (Table 2) projected 80 years into the future. Symbols are colored by persistence probability categories: Extremely Likely Extant (≥ 95.0 percent), Very Likely Extant (= 80.0–94.9 percent), More Likely Than Not Extant (= 50.0–79.9 percent), and Unlikely Extant (< 50.0 percent; i.e., extirpated). See Table 5.2 for descriptions of scenarios and their parameters.

Our analysis of representation revealed that changes in the number of individuals, local populations, and landscape populations varied by analysis unit (Figure 5.3); we provide the projections for the 80-year projection interval in Table 5.5. Among the five analysis units projected 80 years into the future, units 1, 3, and 5 were predicted to decline overall, with mean λ values ranging between 0.60–0.73, 0.47–0.49, and 0.52–0.58 among scenarios for each unit, respectively (i.e., 27–40 percent, 51–53 percent, and 42–48 percent declines, respectively); however, 95 percent CI of λ values overlapped with 1.00 in all scenarios for each of the three units, indicating uncertainty in future abundance. Unit 4 was predicted to experience more modest declines in total abundance (λ = 0.86–0.98; i.e., 2–14 percent decrease), but 95 percent CI of λ also overlapped 1.00, indicating uncertainty in predicted future abundance. Alternatively, total abundance in Unit 2 was predicted to increase substantially (λ = 2.37–2.53; i.e., 137–153 percent increase); 95 percent CI of λ exceeded 1.00, indicating a significant predicted increase.

Scenarios predicted substantial declines in the number of local populations among all units. Predicted reductions in populations were greatest in Unit 1 (λ = 0.22–0.23), Unit 2 (λ = 0.23–0.26), and Unit 5 (λ = 0.28–0.30), and slightly weaker (but still strong) in Unit 3 (λ = 0.37–0.39) and Unit 4 (λ = 0.39–0.41). The number of landscape populations was predicted to decline among all scenarios in each analysis unit, with the strongest loss of landscape populations in Unit 5 (λ = 0.36–0.41 among scenarios) and the weakest loss of landscape populations in Unit 3 (λ = 0.48–0.53 among scenarios).

Table 5. 5- Simulated population projections for gopher tortoises populations in each of the five analysis units. Six scenarios of predicted future change were projected 80 years into the future; results are summarized by the initial number, future predicted number, and population growth rate (λ) for the total population size, number of local populations, and number of landscape populations in each genetic unit. See Table 2 for descriptions of scenarios and parameters.

Scenarios	Total population size			Number of local populations			Number of landscape populations		
	Initial	Future	λ	Current	Future	λ	Initial	Future	λ
Unit 1									
Low stressors	1571	1151	0.73 (0.22–3.55)	102	23	0.23 (0.18–0.27)	13	6	0.46 (0.46–0.46)
Medium stressors	1573	1066	0.68 (0.22–3.50)	102	23	0.23 (0.18–0.27)	13	6	0.46 (0.46–0.54)
High stressors	1572	990	0.63 (0.22–3.86)	102	23	0.23 (0.18–0.26)	13	6	0.46 (0.46–0.54)
More management	1572	1066	0.68 (0.21–4.01)	102	23	0.23 (0.19–0.27)	13	6	0.46 (0.44–0.54)
Less management	1573	1026	0.65 (0.22–3.79)	102	22	0.22 (0.18–0.26)	13	6	0.46 (0.46–0.54)
Much less management	1572	947	0.60 (0.22–3.42)	102	22	0.22 (0.18–0.26)	13	6	0.46 (0.46–0.54)
Unit 2									
Low stressors	2896	7316	2.53 (1.49–4.08)	81	21	0.26 (0.21–0.30)	29	16	0.55 (0.48–0.66)
Medium stressors	2896	7022	2.42 (1.24–3.94)	81	19	0.23 (0.20–0.27)	29	15	0.52 (0.45–0.59)
High stressors	2894	6868	2.37 (1.50–4.04)	81	19	0.23 (0.20–0.28)	29	14	0.48 (0.45–0.59)
More management	2896	7086	2.45 (1.39–3.95)	81	20	0.25 (0.21–0.28)	29	15	0.52 (0.45–0.59)
Less management	2898	7007	2.42 (1.58–4.10)	81	20	0.25 (0.20–0.28)	29	15	0.52 (0.45–0.59)
Much less management	2898	7084	2.44 (1.44–3.92)	81	19	0.23 (0.20–0.27)	29	14	0.48 (0.45–0.52)
Unit 3									
Low stressors	19432	9468	0.49 (0.31–1.08)	110	42	0.38 (0.34–0.44)	55	29	0.52 (0.36–0.73)
Medium stressors	19428	9125	0.47 (0.31–1.04)	110	42	0.38 (0.34–0.44)	55	27	0.49 (0.32–0.68)
High stressors	19419	9406	0.48 (0.30–1.02)	110	42	0.38 (0.34–0.44)	55	28	0.50 (0.35–0.72)
More management	19426	9338	0.48 (0.30–1.11)	110	43	0.39 (0.35–0.45)	55	29	0.53 (0.38–0.76)
Less management	19430	9224	0.47 (0.31–1.06)	110	42	0.38 (0.33–0.43)	55	28	0.51 (0.35–0.75)

Much less management	19432	9332	0.48 (0.31–1.03)	110	41	0.37 (0.33–0.43)	55	27	0.48 (0.35–0.70)
Unit 4									
Low stressors	14032	13793	0.98 (0.55–2.20)	123	50	0.37 (0.33–0.43)	46	21	0.46 (0.35–0.65)
Medium stressors	14030	13368	0.95 (0.55–2.28)	123	50	0.39 (0.35–0.45)	46	22	0.48 (0.37–0.64)
High stressors	14040	12013	0.86 (0.42–1.98)	123	48	0.41 (0.37–0.46)	46	20	0.43 (0.35–0.62)
More management	14036	13325	0.95 (0.54–2.11)	123	51	0.40 (0.36–0.44)	46	22	0.48 (0.35–0.66)
Less management	14034	13109	0.93 (0.54–2.09)	123	49	0.41 (0.37–0.46)	46	22	0.48 (0.35–0.67)
Much less management	14039	13118	0.93 (0.56–2.11)	123	49	0.39 (0.35–0.43)	46	20	0.43 (0.36–0.63)
Unit 5									
Low stressors	32684	19120	0.58 (0.25–1.70)	210	62	0.30 (0.27–0.32)	103	41	0.40 (0.30–0.52)
Medium stressors	32666	17786	0.54 (0.24–1.65)	210	60	0.29 (0.26–0.31)	103	43	0.41 (0.27–0.53)
High stressors	32653	18102	0.55 (0.25–1.66)	210	60	0.29 (0.26–0.32)	103	39	0.38 (0.25–0.58)
More management	32655	18300	0.56 (0.24–1.64)	210	60	0.29 (0.26–0.31)	103	41	0.40 (0.26–0.57)
Less management	32662	16836	0.52 (0.23–1.71)	210	60	0.29 (0.25–0.32)	103	37	0.36 (0.27–0.54)
Much less management	32666	18038	0.55 (0.24–1.59)	210	58	0.28 (0.25–0.30)	103	40	0.38 (0.27–0.51)

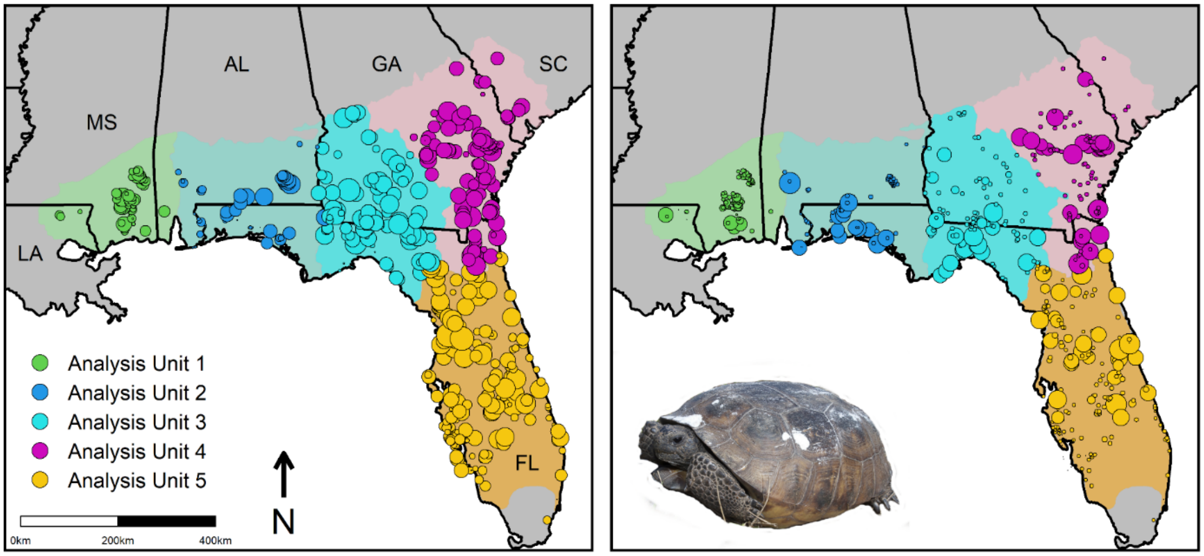


Figure 5. 3-Current (left) and future predicted abundance (right) of gopher tortoise (*Gopherus polyphemus*; right inset) populations in the southeastern United States that were modeled to predict future population growth and extinction risk for the species under scenarios of global change. Each circle represents a local population and circles are colored by analysis units. Symbol size reflects a log-transformed scale of population size; the left panel shows population size estimated during a survey during 2010–2020; the right panel shows predicted population size under a future scenario of 'medium stressors with less management' (Table 5.2). Abundance of populations during 2010–2020 was estimated from analysis of data from burrow surveys or Line Transect Distance Sampling (LTDS) at each the site within the last ten years.

We found that model projections were sensitive to input values for immigration rate (Table 5.6). The population declines predicted by the 'medium stressors' scenario were exacerbated substantially when simulated with an immigration rate of 0; conversely, elevated values for immigration produced population projections that substantially increased the total population size above initial starting population size and decreased declines in local populations and landscape populations.

Table 5. 6- Simulated population projections for gopher tortoises under scenarios varying in immigration rate (γ): no immigration (γ = 0), intermediate immigration (γ = 0.01), high immigration (γ = 0.02), and very high immigration (γ = 0.04). Columns summarize the initial number (in 2020), future predicted number, and population growth rate (λ) for the total population size, number of populations, and number of landscape populations for four scenarios projected 80 years into the future. Each scenario models stressors and management actions using input values from the 'medium stressors' scenario from Table 2, and the 'intermediate immigration' scenario has the same input values the 'medium stressors' scenario from Table 2; see Table 2 for more information about input parameters.

Scenarios	Total population size			Number of local populations			Number of landscape populations		
	Initial	Future	□	Initial	Future	□	Initial	Future	□
No immigration	70602	1566	0.02 (0.01–0.18)	626	81	0.13 (0.11–0.15)	244	46	0.19 (0.09–0.36)
Intermediate immigration	70594	48366	0.69 (0.36–1.74)	626	196	0.31 (0.29–0.33)	244	108	0.44 (0.35–0.59)
High immigration	70600	91805	1.30 (0.71–2.76)	626	247	0.39 (0.38–0.41)	244	124	0.51 (0.39–0.66)
Very high immigration	70600	151320	2.14 (1.18–4.44)	626	312	0.50 (0.48–0.52)	244	144	0.59 (0.48–0.68)

With each 50-female increase in starting population size, populations were 1.029 (1.027–1.03; 95 percent CI) times as likely to persist, which was statistically significant ($P < 0.0001$). With each 1 local population increase in landscape populations, local populations were 0.987 (0.986–0.987; 95 percent CI) times as likely to persist (i.e., 1.013 times less likely), which was statistically significant ($P < 0.0001$). For each 500-ha increase in area, populations were 1.002 (1.001–1.003; 95 percent CI) times as likely to persist, which was statistically significant ($P = 0.044$). With each 10 m increase in elevation, populations were 0.901 (0.899–0.904; 95 percent CI) times as likely to persist (i.e., 1.109 times less likely), which was statistically significant ($P < 0.0001$). For each 0.5 degree increase in latitude, populations were 1.122 (1.119–1.125; 95 percent CI) times as likely to persist, which was statistically significant ($P < 0.0001$). With each 0.01 proportional loss in landscape area due to sea-level rise, local populations were 0.57 (1.67–1.82; 95 percent CI) times as likely to persist (i.e., 1.747 times less likely), which was statistically significant ($P < 0.0001$). With each 0.1 proportional loss in landscape area due to urbanization, local populations were 0.96 (0.955–0.965; 95 percent CI) times as likely to persist (i.e., 1.042 times less likely), which was statistically significant ($P < 0.0001$). With each categorical increase in fire management (from 'very less' to 'less' to 'status quo' to 'increased'), local populations were 1.021 (1.014–1.029; 95 percent CI) times as likely to persist, which was statistically significant ($P < 0.0001$).

5.3. Summary of future conditions and viability

We synthesized literature describing gopher tortoise life history and built a predictive population model that accounted for geographic variation in demography to estimate growth of gopher tortoise populations across the species range on conservation lands. We then identified a series of influences (climate warming, sea-level rise, urbanization, and habitat management) that have been hypothesized to have significant current and future effects on gopher tortoise populations. Then, using estimates of these effects on gopher tortoise demography and/or reasonable assumptions, we linked influences to specific demographic rates and used published model projections of their prevalence in the future (Terando et al. 2014, entire; IPCC 2013, entire; Kupfer et al. 2020, entire; NOAA 2020, entire) to simulate how gopher tortoise populations will respond to future conditions across the species' range.

Using this integrative modeling framework, we simulated future resiliency, representation, and redundancy of gopher tortoise populations under six scenarios varying in the magnitude of influences at 40, 60, and 80 years in the future. Simulated growth of approximately 70,600 individuals (females) from 626 local populations and 244 landscape populations predicted future declines in the number of individuals, local populations, and landscape populations among all scenarios and projection intervals. Scenarios did not vary strongly in their effect on λ of individuals, populations, and landscape populations; no single stressor scenario or management scenario was sufficient to prevent population declines, and 95 percent confidence intervals of projections overlapped significantly among all scenarios, indicating statistical insignificance of scenario effects.

While scenarios did not have strong effects on overall trends in abundance and population redundancy, categorization of populations by persistence probabilities suggested that the ‘increased management’ and ‘low stressors’ scenarios performed better at increasing population persistence and reducing extirpation than other management and stressor scenarios. Increased habitat management promoted greater population persistence relative to decreased management scenarios because of positive effects of management on survival in local populations, which increases population growth and persistence probability of populations. While populations may experience reproductive benefits from warming temperatures in the future (i.e., positive effects with increased stressors), the ‘low stressors’ scenarios outperformed the elevated stressor scenarios because the negative effects of urbanization and sea-level rise on survival and immigration were stronger than the positive effects of warming on reproduction.

The regression analysis identified significant effects of initial abundance, number of populations per landscape population, area, elevation, urbanization, sea-level rise, and habitat management to influence persistence probabilities of local populations. For groups and agencies seeking alternatives to buffer tortoise populations from anthropogenic effects, these factors represent opportunities for management and/or conservation. We observed positive effects of initial population size, area, and fire management on population persistence. Because large areas of land support larger local populations of tortoises experience increased persistence probabilities (Fahrig and Merriam 1985, entire), management actions to conserve large tracts of land with abundant and well-connected populations on high-quality habitat might be prioritized, as well as actions to increase population size of local populations or increase the number of local populations within landscape populations (i.e., translocation and repatriation, respectively; e.g., Tuberville et al. 2008, entire; McKee et al. 2021, entire). Similarly, increased urbanization will decrease immigration and habitat management among populations, and conservation planning strategies could emphasize securing connectivity of existing local populations through strategic land acquisitions or partnerships (Ashrafzadeh et al. 2020, entire). We observed particularly strong negative effects of both sea-level rise and elevation on persistence probability. The sea-level rise effect was due in large part because we set an extinction threshold where local populations that fell to less than 2 m asl due to sea-level rise were forced to extinction. Gopher tortoise populations in low-elevation, coastal areas at risk of sea-level rise might be doomed, and future conservation actions might include assisted migration (Vitt et al. 2010, entire) to suitable areas less at risk to sea-level rise and coastal inundation (Blonder et al. 2020, entire). The effect of decreased persistence at higher elevations was likely due to increased urbanization pressure in high-elevation areas; urbanization was also predicted to have a significant negative effect on persistence of local populations, and urbanization tends to focus on upland, high-elevation habitats that are occupied by tortoise populations (Diemer 1986, entire).

The large declines in number of local populations occurred, in part, because many local populations (N = 174; 27.8%) delimited in our surveys had very few individuals to start with in the current conditions. Assuming a 3:1 adult to juvenile ratio and an even sex ratio, local populations with less than 8 individuals were functionally extirpated at the start of projections, given our quasi-extinction probability (< 3 adult females). This also likely explains the negative effect of landscape population size on population persistence we observed in our regression analysis; for example, a few extremely large landscape populations (e.g., six landscape populations contained 13–50 local populations) were dominated by local populations with <8 individuals, thus driving down mean persistence probability in the large landscape populations. This also likely explains the negative effect of landscape population size on population persistence we observed in our regression analysis; a few extremely large landscape populations (e.g., six landscape populations had 13–50 local populations) were dominated by local populations with <8 individuals, thus driving down mean persistence probability in large landscape populations.

Our analysis simulated the fate of known populations largely on protected, conservation lands that should be managed for natural resource conservation in the future. We expect populations on managed, conservation lands to be characterized by greater demographic rates and persistence probabilities relative to populations not existing on conservation lands (i.e., populations that we were unable to model in our framework). To this end, we did not project the abundance of existing populations not included in our dataset or estimate the formation of new populations outside of conservation lands. While other tortoise populations exist outside of the ones we simulated with our projection model and new tortoise populations may form due to natural dispersal and colonization dynamics, they may occur on lands lacking long-term protection from development, their demographic rates are likely reduced relative to populations on conservation lands, and we did not feel comfortable projecting those populations into the future under assumptions of land management and protection for wildlife conservation. Similarly, we could not estimate the formation of new populations outside of the sites we projected, or the migration of entire populations to new areas, because there is no guarantee that land would be available for populations to form on or migrate to.

Previous demographic models for gopher tortoises have not used immigration parameters (e.g., Tuberville et al. 2009, entire; Folt et al. 2021, entire) and modeled gopher tortoise demography as closed to immigration, perhaps due to the paucity of field estimates of immigration in wild populations. Previous models found no scenarios where populations were stable or increasing, although recent studies have documented situations where stability and population growth are achieved in the field (Folt et al. 2021, p. 624-626; Goessling et al. 2021, p. 141). This discrepancy suggests a disconnect between demographic projections that are largely influenced by apparent survival projections and actual trends occurring in populations, a discrepancy that may be resolved by incorporating immigration during projection analyses. To this end, we incorporated an immigration parameter for local populations and found projections were sensitive to inputs for this parameter. This was supported by the fact that persistence probabilities were sensitive to threats that influenced immigration rates and two scenarios of ‘no immigration’ and ‘high immigration’ produced results that strongly deviated from results of the stressor and management scenarios. Together, these lines of evidence suggest that immigration is an important parameter in gopher tortoise demography that may deserve future attention when studying gopher tortoises in the field and building models of gopher tortoise demography in the laboratory. Due to the uncertainty of true immigration rates, and the use of a small sub-set of populations used in this model relative to the true number of tortoises on the landscape, it is likely that immigration is underrepresented in this model, resulting in uncertainty in future projections.

It is important to note that we included long-term recipient sites in our population projections, although there are several assumptions that we made when including these data. While translocation is successful at removing gopher tortoises from immediate danger due to development, there are still uncertainties about its efficacy, and additional research is needed to inform improvements to translocation methodology. Gopher tortoises are long-lived, slow-growing, and are slow to reach maturity, making it difficult to determine if translocations result in viable gopher tortoise populations without long-term monitoring. Additionally, many of the recipient sites included in this analysis have not reached their permitted capacity, potentially resulting in greater uncertainty in the future condition estimates for these populations.

We modeled some parameters in our simulation exercise as invariant among populations across the species' range, largely for variables which we found lacked substantial data describing geographic variation. For example, we modeled a density-dependent limit on recruitment to the adult age class of 2.0 females/hectare and a fire-return interval of 1–4 years as necessary to create high-quality habitat for tortoises in all populations. However, tortoise populations may have different mechanisms across the species range; in Florida, populations may reach greater densities before density-dependent effects influence life history, and fire may be less important in regulating quality habitat in some areas with deep sandy soils (Hunter and Rostal 2021). More research describing geographic variation in life history, particularly how Florida populations differ from northern populations, would be useful to update and improve the utility of the model framework we used.

Literature Cited

10th Annual Gopher Tortoise Candidate Conservation Agreement Report. Submitted to U.S. Fish and Wildlife Service April 2019.

American Forest Foundation. 2021. Partnership Helps Private Landowners Manage Thriving Habitats for At-Risk Species, https://www.forestfoundation.org/aff-usfws-partnership. Accessed May 19, 2021.

America's Longleaf Restoration Initiative (ALRI). 2019. 2019 Range-Wide Accomplishment Report. 2019 ALRI Accomplishment Report (americaslongleaf.org).

America's Longleaf Restoration Initiative (ALRI). 2021. Available online (http://www.americaslongleaf.org/the-initiative/). Last accessed April 18, 2021.

Andrews, K. M. & Gibbons, J. W., 2005. How do highways influence snake movement? Behavioral responses to roads and vehicles. Copeia, pp. 772–782.

Arata, A.A. 1958. Notes on the eggs and young of *Gopherus polyphemus* (Daudin). Quart. J. Florida Academy of Sciences 21:274–280.

Aresco, M. J., and C. Guyer. 1999a. Growth of the tortoise *Gopherus polyphemus* in slash pine plantations of Southcentral Alabama. Herpetologica 55:499–506.

Aresco, M.J., and C. Guyer. 1999b. Burrow abandonment by gopher tortoises in slash pine plantations of the Conecuh National Forest. Journal of Wildlife Management. 63(1)26–35 .

Ashton, R. E., Jr., and P. S. Ashton. 2004. The gopher tortoise: a life history. Pineapple Press, Sarasota, Florida, USA. 72pp.

Ashton, K.G., R.L. Burke, and J.N. Layne. 2007. Geographic Variation in Body and Clutch Size of Gopher Tortoises. Copeia 2007:355–363.

Ashton, R. E., and P.S. Ashton. 2008. The natural history and management of the gopher tortoise *Gopherus polyphemus* (Daudin): The natural history and management of the gopher tortoise *Gopherus polyphemus*, i-xii, 1-275 p.

Ashton, K. G. and R. L. Burke. 2007. Long-term retention of a relocated population of gopher tortoises. Journal of Wildlife Management 71:783–787.

Auffenberg, W. 1969. Tortoise behavior and survival. The Biological Sciences Curriculum Study Patterns of Life Series, Rand McNally, Chicago Illinois, USA. 38pp.

Auffenberg, W. and W.G. Weaver, 1969. *Gopherus berlandieri* in southeast Texas. Bulletin of the Florida State Museum 13(3);141–203.

Auffenberg, W. and J.B. Iverson. 1979. Demography of terrestrial turtles. Pages 541-569 in M. Harless and H. Morlock (eds.). Turtles: Perspectives and Research. Wiley, New York, New York.

Auffenberg, w. and R. Franz. 1982. The status and distribution of the gopher tortoise (*Gopherus polyphemus)*. Pages 95-126 in R.B. Bury, editor. North American Tortoises: Conservation and Ecology. U.S. Fish and Wildlife Service, Wildlife Research Report 12.

Avery, M. L., E.A. Tillman, K.L. Krysko, 2009. *Gopherus polyphemus (*Gopher Tortoise). Habitat Use, Breeding Aggregation, and Interspecific Interaction. Herpetological Review 49:353–354.

Bartoszek, I.A., Andreadis, P.T., Prokop-Ervin, C., Curry, G., & Reed, R.N. 2018. *Python bivittatus* (Burmese Python) and *Gopherus polyphemus* (Gopher Tortoise). Habitat Use, Breeding Aggregation, and Interspecific Interaction. Herpetological Review 49:353−354.

Basiotis, K. 2007. The effects of invasive cogongrass (*Imperata cylindrica*) on the threatened gopher tortoise (*Gopherus polyphemus*). MS Thesis, University of South Florida.

Baskaran, L.M., V.H. Dale, R.A. Efroymson, and W. Birkhead. 2006. Habitat modeling within a regional context: an example using gopher tortoise. American Midland Naturalist 155:335–351.

Bauder, J. M., C. Castellano, J. B. Jensen, D. J. Stevenson, and C. L. Jenkins. 2014. Comparison of movements, body weight, and habitat selection between translocated and resident gopher tortoises. Journal of Wildlife Management 78:1444–1455.

Berish J. E. D., L. D. Wendland, and C. A. Gates. 2000. Distribution and prevalence of upper respiratory tract disease in gopher tortoises in Florida. Journal of Herpetology 34:5–12.

Berish J. E. D., Wendland, L.D., Keltie, R.A., Garrison, E.P., Gates, C.A. 2010. Effects of Mycoplasmal Upper Respiratory Tract Disease on Morbidity and Mortality of Gopher Tortoises in Northern and Central Florida. Journal of Wildlife Diseases 46(3):6955–705.

Birkhead R.D., C. Guyer, S.M. Hermann, and W.K. Michener. 2005. Patterns of folivory and seed ingestion by gopher tortoises (*Gopherus polyphemus*) in a southeastern pine savanna. American Midland Naturalist 154(1):143–151.

Blanchard, T.C. 2007. Population Projections of Louisiana Parishes through 2030. Report submitted to Office of Electronic Services, Division of Administration, State of Louisiana. 23pp.

Blonder, B.I., K.J. Liedtke, and S.E. Stephens. 2021. Changes in coastal gopher tortoise (*Gopherus polyphemus*) burrow characteristics and density following hurricane evens in Northeast Florida, USA: Implications for conservation planning. Global Ecology and Conservation, 25:1–12.

Boglioli, M.D., C. Guyer, and W.K. Michener. 2003. Mating Opportunities of Female Gopher Tortoises, *Gopherus polyphemus*, in Relation to Spatial Isolation of Females and Their Burrows. Copeia 2003:846–850.

Boglioli, M.D., W.K. Michener, and C. Guyer. 2000. Habitat selection and modification of the gopher tortoise (*Gopher polyphemus*) in Georgia longleaf pine forest. Chelonian Conservation and Biology 3(4):699–703.

Boyer, W.D. 1990. Longleaf pine. http://www.na.fs.fed.us/pubs/silvics_manual/Volume_1/pinus/palustris.htm. Accessed January 26, 2011.

Bramble D.M, and J.H. Hutchison. 2014. Morphology, taxonomy, and distribution of North American tortoises an evolutionary perspective. Biology and Conservation of North American Tortoises. 1–12.

Breininger, D.R., P. Schmalzer, and C. Hinkle. 1994. Gopher tortoise (*Gopherus polyphemus*) Densities in coastal scrub and slash pine flatwoods in Florida. Journal of Herpetology 28:60–65.

Buckland, S.T., D.R. Anderson, K.P. Burnham, and J.L. Laake 1993. Distance sampling: estimating abundance of Biological Populations. Chapman and Hall, London.

Burke, R. L. 1989. Florida gopher tortoise relocation: overview and case study. Biological Conservation 48:295.

Burke, Russell L. "Head-starting turtles: learning from experience." *Herpetological Conservation and Biology* 10.1 (2015): 299-308.

Butler, B.J., Hwews, J.H., Dickinson, B.J., Adrejczyk, A., Butler, S.M., Markowski_Lindsay, M. 2016. USDA Forest Service National Woodland Owner Survey: A Technical Document Supporting the Forest Service Update of the 2010 RPA Assessment. United States Department of Agriculture, Resource Bulletin NRS-99. Pp. 48.

Butler, J.A., R.D. Bowman, T.W. Hull, and S. Sowell. 1995. Movements and Home Range of Hatchling and Yearling Gopher Tortoises, *Gopherus polyphemus*. Chelonian Conservation and Biology 1:173–180.

Butler, J. A. and T. W. Hull. 1996. Reproduction of the tortoise, *Gopherus polyphemus*, in northeastern Florida. Journal of Herpetology 30:14–18.

Butler, J. A., and S. Sowell. 1996. Survivorship and predation of hatchling and yearling gopher tortoises, Gopherus polyphemus. Journal of Herpetology 30:455–458.

Burke, R., Ewert, M.A., McLemore, J.B., Jackson, D.R. 1996. Temperature-Dependent Sex Determination and Hatching Success in the Gopher Tortoise (*Gopherus polyphemus*). Chelonian Conservation and Biology 2(1);86–88.

Candidate Conservation Agreement for the Gopher Tortoise (CCA). 2019. 11th Annual Gopher Tortoise CCA Report.

Carter, L., A. Terando, K. Dow, K. Hiers, K.E. Kunkel, A. Lascurain, D. Marcy, M. Osland, and P. Schramm, 2018: Southeast. In Impacts, Risks, and Adaptation in the United States: Fourth National Climate Assessment, Volume II [Reidmiller, D.R., C.W. Avery, D.R. Easterling, K.E. Kunkel, K.L.M. Lewis, T.K. Maycock, and B.C. Stewart (eds.)]. U.S. Global Change Research Program, Washington, DC, USA, pp. 743–808.

Castellon, T.D., Rothermal, B.B., and Nomani, S.Z. 2012. Gopher Tortoise (*Gopherus polyphemus)* Burrow Densities in Scrub and Flatwoods Habitats of Peninsular Florida. Chelonian Conservation and Biology 11(2): 153-161.

Castellón, T.D., B.B. Rothermel, and J.M. Bauder. 2018. Gopher Tortoise Burrow Use, Home Range, Seasonality, and Habitat Fidelity in Scrub and Mesic Flatwoods of Southern Florida. Herpetologica 74:8–21.

Causey, M.K. and C.A. Cude. 1978. Feral dog predation of the gopher tortoise, *Gopherus polyphemus*, in southeast Alabama. Herpetological Review 9:94–95.

Chesser, R. K., M. H. Smith, and I. L. Brisbin. 1980. Management and maintenance of genetic variability in endangered species. International Zoo Yearbook 20:146–154.

Clostio, R.W., A.M. Martinez, K.E. LeBlanc, and N.M. Anthony. 2012. Population genetic structure of a threatened tortoise across the south-eastern United States: implications for conservation management. Animal Conservation 15:613–625.

Colson-Moon, J. C. 2003a. Reproductive characteristics, multiple paternity, and mating system in a central Florida population of the gopher tortoise, *Gopherus polyphemus*. M.S. Thesis. University of South Florida.

Congdon, J.D., Dunham, A.R., Van Loben Sels, R.C. 1993. Delayed Sexual Maturity and Demographics of Blanding's Turtles (E*mydoidea blandingii*): Implications for Conservation and Management of Long-Lived Organisms. Conservation Biology Vol 7(4): 826833.

Cox, Anne, C., Gordan, Doria, R., Slapcinsky, Jodi, L., and Seamon, Greg, S. 2004. Understory Restoration in Longleaf Pine Sandhills. Natural Areas Journal. Volume 24(1): 4-14.

Cox, J., D. Inkley, and R. Kautz. 1987. Ecology and habitat protection needs of gopher tortoise (*Gopherus polyphemus*) populations found on lands slated for large-scale development in Florida. Florida Game and Fresh Water Fish Commission. Nongame Wildlife Program Technical Report. No. 4.

Cox, J., R. Kautz, M. MacLaughlin, and T. Gilbert. 1994. Closing the gaps in Florida's wildlife habitat conservation system. Florida Game and Freshwater Fish Commission, Tallahassee, FL.

Cozard, R.A., S.M. Hernandex, T.M. Norton, T.D. Tuberville, N.I. Stacy, N.L. Stdman, and M.J. Aresco. 2020. Epidemiological investigation of a mortality event in a translocated gopher torotise (*Gopherus polyphemus*) population in northwest Florida. Frontiers in Veterinary Science 7:120.

Crandall, Keith, Bininda-Emonds, Olaf, Mace, Georgina, and Wayne, Robert. 2000. Considering evolutionary process in conservation biology. Trends in Ecology and Evolution. 15. 290-295.

Craft, M. 2021. Nest site choice as a potential climate response in the gopher tortoise (*Gopherus polyphemus*), a Threatened species. Masters thesis. University of South Florida, Tampa, Florida.

Craul, P.J., J.S. Kush, and W.D. Boyer. 2005. Longleaf pine site zones. General Technical Report, SRS–89, U.S. Department of Agriculture, Forest Service, Southern Research Station.

Crawford, B. A., J. C. Maerz, and C. T. Moore. 2020. Expert-informed habitat suitability analysis of at-risk species assessment and conservation planning. Journal of Fish and Wildlife Management 11:130–150.

Crooks, K.R., M.E. Soule. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563 –566.

Crumly, C.R. 1994. Phylogenetic systematics of North American tortoises (Genus *Gopherus*): evidence for their classification. In: Bury, R.B. and Germano, D.J. (Eds.). Biology of North American Tortoises. Washington, DC: U.S.D.I. National Biological Survey, pp. 7–32.

Culverhouse College of Business. 2021. Population Estimates. Retrieved from https://cber.culverhouse.ua.edu/resources/alabama-indicators. March 26, 2021.

Czaja, R.A., A.L. Scholz, M. P. Figueras, and R.L. Burke. 2020. The role of nest depth and site choice in mitigating the effects of climate change on an oviparous reptile. Diversity. 12,151. 12pp.

Dalton, M., and S. Jones. 2010. Southeast Regional Assessment Project for the National Climate Change and Wildlife Science Center. U.S. Geological Survey: U.S. Geological Survey Open-File Report.

Daudin, F.M. Dean, S., E.C. Farrer, and E.S. Menges. Fire effects on soil biogeochemistry in Florida scrubby flatwoods. Am. Mid. Nat. 174: 49–64.

Dean, Sarah, Farrer, Emily C., and Menges, Eric S. 2015. Fire Effects on Soil Biogeochemistry in Florida Scrubby Flatwoods. American Midland Naturalist. 174:49-64.

Degregorio, B.A., K.A. Buhlmann, and T.D. Tuberville. 2012. Overwintering of Gopher Tortoises (*Gopherus polyphemus*) Translocated to the Northern Limit of Their Geographic Range: Temperatures, Timing, and Survival. Chelonian Conservation and Biology 11:84–90.

Degroote, L. W., H. K. Ober, C. M. McDonough, and F. Russell. 2013. An evaluation of the nine-banded armadillo as predators of gopher tortoise and Northern bobwhite quail nests in Florida. American Midland Naturalist 169:74–85.

Demuth, J. P. 2001. The effects of constant and fluctuating incubation temperatures on sex determination, growth, and performance in the tortoise *Gopherus polyphemus*. Canadian Journal of Zoology 79:1609–1620.

Desiderio, T. M., N. I. Stacy, R. J. Ossiboff, M. Iredale, L. L. Archer, A. B. Alexander, D. J. Heard, S. E. Crevasse, W. F. Craft, D. V. E. Fredholm, K. A. Donnelly, J. F. Rosenberg, A. L. Childress, K. Russell, and J. F. X. Wellehan, Jr. 2021 Identification of a novel mortality-associated *Helicobacter* species in gopher tortoises (*Gopherus polyphemus*), qPCR test development and validation, and correlation with mortality in a wildlife rehabilitation population. Veterinary Microbiology 259. https://doi.org/10.1016/j.vetmic.2021.109136.

DeWan, A., Dubois, N., Theoharides, K., and Boshoven, J. 2010. Understanding the impacts of climate change on fish and wildlife in North Carolina. Defenders of Wildlife, Washington D.C.

Diemer, J.E., and P. E. Moler. 1982. Gopher tortoise response to site preparation in northern Florida. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 36:634–637.

Diemer, J.E. 1986. The ecology and management of the gopher tortoise in the southeastern United States. Herpetologia 42(1):125–133.

Diemer, J.E. 1989. An overview of gopher tortoise relocation. Proceedings of the gopher tortoise relocation symposium, Nongame Wildlife Program technical report number 5, Florida Game and Fresh Water Fish Commission. Tallahassee, Florida.

Diemer, J. E. 1987. The status of the gopher tortoise in Florida. Proceedings of the Southeastern Nongame and Endangered Wildlife Symposium 3:72-83, Athens, Georgia, USA.

Diemer, J. E. 1992a. Demography of the tortoise, *Gopherus polyphemus*, in northern Florida. Journal of Herpetology 26:281–289.

Diemer, J. E. 1992b. Home range and movements of the tortoise *Gopherus polyphemus* in northern Florida. Journal of Herpetology 26:158–165.

Diemer Berish, J.E., R.A. Kiltie, and T.M. Thomas. 2012. Long-Term Population Dynamics of Gopher Tortoises (*Gopherus polyphemus*) in a Pine Plantation in Northern Florida. Chelonian Conservation and Biology 11:50–58.

Diemer, J.E. and Moore, C.T. 1993. Gopher tortoise response to large-scale clearcutting in northern Florida. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 47:419–427.

Diemer, J.E. and Moore, C.T. 1994. Reproduction of Gopher Tortoises in North Central Florida. Pages 129-137 in R.B. Bury and D.J. Germano, eds. Biology of North American Tortoises. National Biological Survey fish and Wildlife Research 13.

Diffie, S., Miller, J. and Murray, K., 2010. Laboratory observations of red imported fire ant (Hymenoptera: Formicidae) predation on reptilian and avian eggs. Journal of Herpetology, 44(2), pp. 294–296.

Dodd, C. K. Jr., and R. A. Seigel. 1991. Relocation, repatriation, and translocation of amphibians and reptiles: are they conservation strategies that work? Herpetologica 47:336–350.

Douglass, J. A. 1986. Patterns of mate-seeking and aggression in a southern Florida population of the gopher tortoise, *Gopherus polyphemus*. Pp 155-199 in Daniels D., editor. Conference Proceedings. Desert Tortoise Council, Inc. Palmdale, CA.

Douglass, J. F., and C. E. Winegarner. 1977. Predators of eggs and young of the gopher tortoise, *Gopherus polyphemus* (Reptilia, Testudines, Testudinidae) in southern Florida. Journal of Herpetology 11:236–238.

Douglass, J.F., and IN. Layne. 1978. Activity and thermoregulation of the gopher tortoise (*Gopherus polyphemus*) in southern Florida. Herpetologica 34:359–374.

Dozier, H., J.F. Gaffney, S.K. McDonald, E.R.R.L. Johnson, and D.G. Shilling. 1998. Cogongrass in the United States: history, ecology, impacts, and management. Weed Technol. 12:737–743.

Dziadzio, M. C., E. R. Sievers, and D. Burr. 2018. Investigation of a large-scale gopher tortoise (*Gopherus polyphemus*) mortality event on a public conservation land in Florida. Journal of Wildlife Diseases 54(4):809-813.

Dziadzio, M.C., L.L. Smith, R.B. Chandler, and S.B. Castleberry. 2016a. Effect of nest location on gopher tortoise nest survival. Journal of Wildlife Management 80:1314–1322.

Dziadzio, M.C., R.B. Chandler, L.L. Smith, and S.B. Castleberry. 2016b. Impacts of red imported fire ants (*Solenopsis invicta*) on nestling and hatchling gopher tortoises (*Gopherus polyphemus*) in Southwest Georgia. Herpetological Conservation and Biology 11:527-538.

Edwards T, Karl AE, Vaughn M, Rosen PC, Torres CM, Murphy RW (2016) The desert tortoise trichotomy: Mexico hosts a third, new sister-species of tortoise in the *Gopherus morafkai–G. agassizii* group. ZooKeys 562: 131–158. doi: 10.3897/zookeys.562.6124

EIA 2021. US Energy Information Administration. Georgia Profile Analysis. https://www.eia.gov.state/analysis.php?sid=GA. Accessed April 19, 2021.

Enge, K. M., J. E. Berish, R. Bolt, A. Dziergowski, and H. R. Mushinsky. 2006. Biological status report - gopher tortoise. Florida Fish and Wildlife Conservation Commission, Tallahassee, USA. 60 pp.

Engeman, R. E., B. U. Constantin, M. L. Christie, and P. T. Hall. 2009. *Ctenosaura similis* (Black Spiny-Tailed Iguana), *Gopherus polyphemus* (Gopher Tortoise). Concurrent burrow use. Herpetological Review 40:84.

Engeman, R., E. Jacobson, M. L. Avery, and W. E. Meshaka, Jr. 2011. The aggressive invasion of exotic reptiles in Florida with a focus on prominent species: A review. Current Zoology 57:599-612.

Ennen, J.R. and C.P. Qualls. 2011. Distribution and habitat utilization of the gopher tortoise tick (*Amblyomma tuberculatum*) in Southern Mississippi. Journal of Parasitology 97:202-206.

Ennen, J.R., B.R. Kreiser, and C.P. Qualls. 2010. Low genetic diversity in several gopher tortoise (*Gopherus polyphemus*) populations in the Desoto National Forest, Mississippi. Herpetologica 66:31-38.

Ennen, J.R., B.R. Kreiser, C.P. Qualls, D. Gaillard, M. Aresco, R. Birkhead, T.D. Tuberville, E.D. McCoy, H. Mushinsky, T.W. Hentges, and A. Schrey. 2012. Mitochondrial DNA assessment of the phylogeography of the gopher tortoise. Journal of Fish and Wildlife Management 3:110-122.

Epperson, D. M. and C. D. Heise. 2001. Population dynamics of the gopher tortoise (*Gopherus polyphemus*) at Camp Shelby training site. The Nature Conservancy, Mississippi Chapter, Camp Shelby Field Office, Hattiesburg, MS. Department of Defense Legacy Program Project 950410 and MIPR 9855 Report.

Epperson, D.M. and C.D. Heise. 2003. Nesting and hatchling ecology of gopher tortoises (*Gopherus polyphemus*) in Southern Mississippi. Journal of Herpetology 37:315-324.

Ernst, C.H., J.E. Lovich, and R.W. Barbour. 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington, DC. 1st Ed. 578 p.

Ernst, C.H. and J.E. Lovich. 2009. Turtles of the United States and Canada. The John Hopkins University Press, Baltimore, Maryland. 2nd Ed. 827 p.

Estes, T. and T. Mann. 1996. State land 16th Section Gopher Tortoise survey. Museum Technical Report No. 43. Mississippi Museum of Natural Science, Jackson, MS. 121 p.

Falk, Bryan. 2018. Report for FWC Scientific Collecting Permit: LSSC-16-0008. Report on file U.S. Fish and Wildlife Service, Jacksonville, FL.

Federal Highway Administration. 2010. Gopher tortoise conservation area. http://www.fhwa.dot.gov/aldiv/tortoise.htm. .

Fill, J.M., J.S. Glitzenstein, D.R. Streng, J. Stowe, and T.A. Mousseau. 2017. Wiregrass (*Aristida beyrichiana*) may limit woody plant encroachment in longleaf pine (*Pinus palustris*) ecosystems. American Midland Naturalist 177:153-161.

Fitzpatrick, J. W., and G. E. Woolfenden. 1978. Red-tailed hawk preys on juvenile gopher tortoises. Florida Field Naturalist 6:49.

Florida Department of Agriculture and Consumer Services (FDACS). 2015. Agriculture Wildlife Best Management Practices for State Imperiled Species. 32 pp.

Florida Department of Agriculture and Consumer Services (FDACS). 2021. Florida Wildlife Best Management Practices. Tallahassee, Florida. 31pp.

Florida Fish and Wildlife Conservation Commission (FWC). 2007. Gopher Tortoise Management Plan. Florida Fish and Wildlife Conservation Commission, Tallahassee, Florida.

Florida Fish and Wildlife Conservation Commission (FWC). 2008. Wildlife 2060: what's at stake for Florida? Tallahassee, Florida.

Florida Fish and Wildlife Conservation Commission (FWC). 2013. A landowner's guide Managing habitat for gopher tortoises. Tallahassee, Florida. 6 pp.

Florida Fish and Wildlife Conservation Commission (FWC). 2020. Wildlife Best Management Practices Enrollment Status Report. Email Communication to Service May 27, 2021.

Florida Fish and Wildlife Conservation Commission (FWC). 2020a. State Activities Summary Document for Florida. Unpublished report on file with USFWS, Jacksonville, Florida.

Florida Fish and Wildlife Conservation Commission (FWC). 2021. Wildlife BMP Metrics. Email Communication to Service June 10, 2021.

Florida Natural Areas Inventory (FNAI). 2010. Guide to the Natural Communities of Florida: 2010 edition. Florida Natural Areas Inventory, Tallahassee, FL.

Florida Office of Economic and Demographic Research (FEDR). 2021. Population and Demographic Data – Florida Products: Population 1970-2045 by County. http://edr.state.fl.us/content/population-demographics/data/index-floridaproducts.cfm. Accessed March 26, 2021.

Folt, B., J.R. Goessling, A. Tucker, C. Guyer, S.M. Hermann, E. Shelton-Nix, and C. McGowan. 2021. Contrasting patterns of demography and population viability among gopher tortoise populations in Alabama. Journal of Wildlife Management 85(4):617–630. DOI: 10.1002/jwmg.21996.

Fowler, Cynthia and Konopi, Evelyn. 2007. The History of Fire in the Southern United States. Human Ecology Review 14(2):165-176.

Frankham, R., J. D. Ballou, M. D. B. Eldridge, R. C. Lacy, K. Ralls, M. R. Dudash, and C. B. Fenster. 2011. Predicting the Probability of Outbreeding Depression. Conservation Biology 25:465–475.

Frazer, Nat B. "Sea turtle conservation and halfway technology." *Conservation biology* 6.2 (1992): 179-184.

Frost, C.C. 1993. Four Centuries of Changing Landscape Patterns in the Longleaf Pine Ecosystem. in Hermann, S.M., Proceedings of the 18th Tall Timbers Fire Ecology Conference, The Longleaf Pine Ecosystem: ecology, restoration, and management, edited by Sharon M. Herman, Tall Timbers Research Station, Tallahassee, FL. P. 17-43

Gaillard, D., J.R. Ennen, B.R. Kreiser, C.P. Qualls, S.C. Sweat, R. Birkhead, T.D. Tuberville, M. Aresco, E.D. McCoy, H.R. Mushinsky, and T.W. Hentges. 2017. Range-Wide and regional patterns of population structure and genetic diversity in the gopher tortoise. Journal of Fish and Wildlife Management 8:497-512.

Garner, J.A. and J.L. Landers. 1981. Foods and habitat of the gopher tortoise in southwestern Georgia. Proceedings of the annual conference of the southeast association of fish and wildlife agencies. 35:120–134.

Gates C. A., M. J. Allen, J. E. D. Berish, D. M. Stillwaugh, and S. R. Shattler. 2002. Characterization of a gopher tortoise mortality event in West-Central Florida. Florida Scientist 65:185–197.

Gaya, H.E. 2019. Enhancing line-transect distance sampling to increase detectability of gopher tortoises (*Gopherus polyphemus*) in population surveys. Masters Thesis. The University of Georgia, Athens, Georgia.

Georgia Census 2020. 2021. Population Projections. Retrieved from https://census.georgia.gov/census-data/population-projections. March 26, 2021.

Georgia Department of Natural Resources (GDNR). 2014. Forest management practices to enhance habitat for the gopher tortoise [Fact Sheet]. Forsyth, Georgia. 4pp.

Georgia Department of Natural Resources, U.S. Fish and Wildlife Service, National Council for Air and Stream Improvement, Inc., Resource Management Services, LLC, Rayonier, Inc., The Westervelt Company, and Weyerhaeuser Company. 2018. Nest Conservation Practices for Gopher Torotise Habitat on Working Forest Landscapes. 5 Pages.

Gibbons, J. W. 1987. Why do turtles live so long? BioScience 37(262-269).

Ginger, S. 2010. U.S. Fish and Wildlife Service, personal communication. Discussion of threats in listed range of gopher tortoise. August 9, 2010.

Goessling, J. M., C. Guyer, J. C. Godwin, S. M. Hermann, F. C. Sandmeier, L. L. Smith, and M. T. Mendonça. 2019. Upper respiratory tract disease and associated diagnostic tests of mycoplasmosis in Alabama populations of Gopher tortoises, *Gopherus polyphemus*. PLos One, 14: 1-12.

Goessling, J.M, S.A. Koler, B.D. Overman, E.M. Hiltbold, C. Guyer, and M.T. Mendonca. 2017. Lag of immunity across seasonal acclimation states in gopher tortoises (*Gopherus polyphemus*). Journal of Experimental Zoology Part a: Ecological and Integrative Physiology 327(5):235-242.

Goessling, J.M., J.M. Stober, S.G. Gyengo, S.M. Hermann, T.D. Tuberville, and C. Guyer. 2021. Implications from monitoring tortoises at two spatial scales. Journal of Wildlife Management, 85:1:135–144.

Goetz S. M., D. A. Steen, M.A. Miller, C. Guyer, J. Kottwitz, J. F. Roberts, E. Blankenship, P. R. Pearson, D. A. Warner, and R. N. Reed. 2021. Argentine Black and White Tegu (*Salvator merianae*) can survive the winter under semi-natural conditions well beyond their current invasive range. PLoS ONE 16(3): e0245877.

Gonynor, J.L. and M.J. Yabsley. 2009. Mycoplasma related upper respiratory tract disease in gopher and desert tortoises. Southeastern Partners in Amphibian and Reptile Conservation, information sheet number 8.

Gopher Tortoise Council (GTC). 2013. Gopher tortoise minimum viable population and minimum reserve size working group report. Unpublished Report. 7 pp.

Gopher Tortoise Council (GTC). 2014. Gopher tortoise minimum viable population and minimum reserve size working group report II. Unpublished Report. 7 pp.

Greene, R.E., R.B. Iglay, K.O. Evans, T.B. Wigley, and D.A. Miller. 2019. Estimating capacity of managed pine forests in the southeastern U.S. to provide open pine woodland condition and gopher tortoise habitat. Forest Ecology and Management 432:200-208.

Greene, R. E., T. D. Tuberville, M. J. Chamberlain, D. A. Miller, T. B. Wigley, and J. A. Martin. 2020. A review of gopher tortoise demography and movements in production pine forest landscapes. Wildlife Society Bulletin 44(1):49–56.

Griffith, B. J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. Science 245:477–480.

Guyer, C., and M. A. Bailey. 1993. Amphibians and reptiles of longleaf pine communities. Proceedings of the Tall Timbers Fire Ecology Conference 18.

Guyer, C. and Valerie Johnson. 2002. Patterns of burrow use and socialization of gopher tortoises at Camp Shelby, Mississippi. Final Report for Federal Permit Number TE 036331-0. Submitted November 22, 2002; 17 pp.

Guyer, C., V.M. Johnson, and S.M. Hermann. 2012. Effects of population density on patterns of movement and behavior of gopher tortoises (*Gopherus polyphemus*). Herpetological Monographs 26:122-134.

Guyette, R. P., M. C. Stambaugh, D. C. Dey, and R. M. Muzika. 2012. Predicting Fire Frequency with Chemistry and Climate. Ecosystems 15:322–335.

Hansen, K. L. 1963. The burrow of the gopher tortoise. Q. J. Florida Acad. Sci. 26:353–360.

Haro, D., L. D. McBrayer, J. B. Jensen, J. M. Gillis, and L. Bonewell. 2020. Evidence for an established population of tegu lizards (*Salvator merianae*) in Southeastern Georgia, USA. Southeastern Naturalist 19(4):649-662.

Hawbaker, T.J., Vanderhoof, M.L., Schmidt, G.L., Beal, Y., Picotte, J.J., Takas, J.D., Falgout, J.T., Dwyer, J.L. 2020. The Landsat Burned Area algorithm and products for the conterminous United States. Remote Sensing of Environment. Pp. 21.

Hawkins, R. Z., and R. L. Burke. 1989. Of pens, pullers and pets: problems of gopher tortoise relocation. Page 99 in J. E. Diemer, D. R. Jackson, J. L. Landers, J. N. Layne, and D. A. Wood, editors. Proceedings of the gopher tortoise relocation symposium. Florida Game and Fresh Water Fish Commission, Nongame Wildlife Program Technical Report No. 5, Tallahassee, Florida, USA.

Hayhoe, K., D.J. Wuebbles, D.R. Easterling, D.W. Fahey, S. Doherty, J. Kossin, W. Sweet, R. Vose, and M. Wehner, 2018: Our Changing Climate. In Impacts, Risks, and Adaptation in the United States: Fourth National Climate Assessment, Volume II [Reidmiller, D.R., C.W. Avery, D.R. Easterling, K.E. Kunkel, K.L.M. Lewis, T.K. Maycock, and B.C. Stewart (eds.)]. U.S. Global Change Research Program, Washington, DC, USA, pp. 72–144.

Heppell, S. S., Crowder, L.B., and Crouse, D.T. 1996. Models to Evaluate Headstarting as a Management Tool for Long-Lived Turtles. Ecological Society of America 6(2):556-565. 1998:367–375.

Heppell, S. S. 1998. Application of life-history theory and population model analysis to turtle conservation. Copeia 1998:367–375.

Hermann, S.M., C. Guyer, J.H. Waddle, and M.G. Nelms. 2002. Sampling on private property to evaluate population status and effects of land use practices on the gopher tortoise, *Gopherus polyphemus*. Biological Conservation 108:289-298.

Hernandez, S. M., T. D. Tuberville, P. Frank, S. J. Stahl, M. M. McBride, K. A. Buhlmann, and S.J. Divers. 2010. Health and reproductive assessment of a free-ranging gopher tortoise (*Gopherus polyphemus*) population following translocation: Journal of Herpetological Medicine and Surgery, v. 20, p. 84-93.

Hijmans, R. J. 2020. raster: Geographic Data Analysis and Modeling. R package version 3.3-13. <https://cran.r-project.org/package=raster>.

Hinderliter, M. 2021. U.S. Fish and Wildlife Service, personal communication. Discussion of headstarting program in listed range of gopher tortoise. June 9, 2021.

Hobbs, R.J. and Huenneke, L.F. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology 6:324-337.

Hoffman, C.O. and Gottschang, J.L. 1977. Numbers, distribution, and movements of a raccoon population in a suburban residential community, Journal of Mammalogy 58:623-636.

Holbrook, A.L., Jawor, J.M., Hinderliter, M., and Lee, J.R. 2015. A Hatchling Gopher Tortoise (Gopherus polyphemus) Care Protocol for Experimental Research and Head-Starting Programs. Herpetological Review 46(4):538-543.

Holzmueller, E. J. and S. Jose. 2011. Invasion success of cogongrass, an alien C4 perennial grass, in the southern United States: exploration of the ecological basis. Biological Invasions 13:435-442.

Howarter, S. 2021. Comments submitted: gopher tortoise (*Gopherus polyphemus*) species status assessment; management and expert draft review. Email to the Service at gophertortoise@fws.gov from Stanley Howarter, Wildlife Biologist, U.S. Fish and Wildlife Service. May 28, 2021.

Howell, H. J., B. B. Rothermel, K. N. White, and C. A. Searcy. 2020. Gopher tortoise demographic responses to a novel disturbance regime. Journal of Wildlife Management 84:56–65.

Hughson, D.L., and N. Darby. 2013. Desert tortoise road mortality in Mojave National Preserve, California. California Fish and Game 99:222-232.

Hunter KW, DuPré SA, Sharp T, Sandmeier FC, Tracy CR (2008) Western blot can distinguish natural and acquired antibodies to *Mycoplasma agassizii* in the desert tortoise (*Gopherus agassizii*). Journal of Microbiological Methods 75:464-471.

Hunter, E. A., and D. C. Rostal. 2021. Fire Management Effects on Long-Term Gopher Tortoise Population Dynamics. Journal of Wildlife Management.

Iglay, R.B., B.D. Leopold, and D.A. Miller. 2014. Summer herpetofaunal response to prescribed fire and herbicide in intensively managed, mid-rotation pine stands in Mississippi. Wildlife Society Bulletin 38(1): 33–42.

Interagency Taxonomic Information System. 2019. Retrieved [November 19, 2019January 13, 2021] from the Integrated Taxonomic Information System on-line database. http://www.itis.gov.

IPCC. 2013. Summary for Policymakers. T. Stocker, D. Qin, G. K. Pattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, editors. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pages.

Iverson, J. B. 1980. The reproductive biology of *Gopherus polyphemus* (Chelonia: Testudinidae). American Midland Naturalist 103:353-359.

Jack, S.B. and K.M. McIntyre. 2017. Restoring and managing the overstory: an ecological forestry approach. Pp. 175-204. *In*: Titus, Valorie. 2017. Ecological Restoration and Management of Longleaf Pine Forests. L.K. Kirkman and S.B. Jack, Eds. CRC Press, Boca Raton, Fl, USA. 427 pp.

Jackson, D.R., and E.G. Milstrey. 1989. The fauna of gopher tortoise burrows. Technical Report Number 5, Florida Nongame Wildlife Program, Tallahassee, Florida.

Jacobson, E. R., M. B. Brown, L. D. Wendland, D. R. Brown, P. A. Klein, M. M. Christopher, and K. H. Berry. 2014. Mycoplasmosis and upper respiratory tract disease of tortoises: a review and update. The Veterinary Journal 201:257-264.

Jensen, J. B., Camp, C. D., Gibbons, J. W. & Elliot, M. J., 2008. Amphibians and Reptiles of Georgia. Athens: University of Georgia Press.

Johnson, A., A. Pessier, J. Wellehan, A. Childress, T. Norton, N. Stedman, D. C. Bloom, W. Belzer, V. Titus, R. Wagner, J. Brooks, J. Spratt, and E. Jacobson. 2008. Ranavirus infection of free-ranging and captive box turtles and tortoises in the United States. Journal of Wildlife Diseases 44:851–863.

Johnson, S.A., McGarrity M. 2017. Florida invader: tegu lizard. University of Florida/IFAS Extension, Gainesville.

Johnson, V.M., C. Guyer, S.M. Hermann, J. Eubanks, and W.K. Michener. 2009. Patterns of dispersion and burrow use support scramble competition polygyny in *Gopherus polyphemus*. Herpetologica 65:214-218.

Jones, J.C. and B. Dorr. 2004. Habitat associations of gopher tortoise burrows on industrial timberlands. Wildlife Society Bulletin 32:456-464.

Jones, P.D., S.L. Edwards, S. Demarais, and A.W. Ezell. 2009. Vegetation community responses to different establishment regimes in loblolly pine (*Pinus taeda*) plantations in southern MS, USA. Forest Ecology and Management 257: 553–560.

Kaczor, S.A. and D.C. Hartnett. 1990. Gopher tortoise (*Gopherus polyphemus*) effects on soils and vegetation in a Florida sandhill community. American Midland Naturalist 123:100-111.

Karlin, M. L. 2008. Distribution of Mycoplasma agassizii in a gopher tortoise population in south Florida. Southeastern Naturalist 7(1):145-158.

Knapp, E.E., B.L. Estes, and C.N. Skinner. 2009. Ecological effects of prescribed fire season: a literature review and synthesis for managers. Gen. Tech. Rep. PSW-GTR-224. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 80 p.

Kupfer, J.A., A.J. Terando, P. Gao, C. Teske, J.K. Hiers J. 2020. Climate change projected to reduce prescribed burning opportunities in the south-eastern United States. International Journal of Wildland Fire 29:764-778.

Kushlan, J.A. and F.J. Mazzotti. 1984. Environmental effects on a coastal population of gopher tortoises. Journal of Herpetology 18:231-239.

Lacy, R.C. and Pollak, J.P. 2014. Vortex: A Stochastic Simulation of the Extinction Process. Version 10.0, Chicago Zoological Society, Brookfield.

Landers J.L. 1980. Recent research on the gopher tortoise and its implications. Pages 8–14 in R. Franz and R.J. Bryant (Eds). The dilemma of the gopher tortoise – is there a solution? Proceedings of the first annual meeting, Gopher Tortoise Council, Florida State Museum.

Landers J.L. and J.L Buckner. 1981. The gopher tortoise, effects of forest management and critical aspects of its ecology. Technical Note number 56, Forest Productivity and Research, International Paper Company.

Landers, J. L., J. A. Garner, and W. A. McRae. 1982. Growth and maturity of the gopher tortoise in southwestern Georgia. Bulletin of the Florida State Museum, Biological Sciences 27:81-110.

Landers, J. L., Van Lear, D. H. & Boyer, W. D., 1995. The longleaf pine forests of the Southeast: requiem or renaissance? Journal of Forestry, 93(11), pp. 39-44.

Landers, J.L. and D.W. Speake. 1980. Management needs of sandhill reptiles in southern Georgia. Unpublished report on file U.S. Fish and Wildlife Service, Jacksonville Ecological Services Office, Jacksonville, Florida.

Landers, J.L., J.A. Garner, and W.A. McRae. 1980. Reproduction of the gopher tortoise (*Gopherus polyphemus*) in southwestern Georgia. Herpetologica. 36:353–361.

Lang, A., S. Baker, and B. Mendell. 2016. Forest management practices of private timberland owners and managers in the U.S. South (2016 update). Technical Release 16-R-17. Forest Resources Association, Washington, D.C., USA.

Linley, T. R. 1986. Tortoise density, age/size class distribution and reproductive parameters of a central Florida population of *Gopherus polyphemus*. Pp 21-32 in Jackson D.R. and R.J. Bryant, editors. The Gopher Tortoise and its Community. Conference Proceedings.

Lippincott, C.L. 1997. Ecological consequences of *Imperata cylindrica* (cogongrass) invasion in Florida sandhill. Ph.D. diss., Department of Botany, University of Florida, Gainesville.

Lohoefener, R. and L. Lohmeier. 1981. Comparison of gopher tortoise (Gopherus polyphemus) habitats in young slash pine and old longleaf pine areas of southern Mississippi. Journal of Herpetology; 15.2:239-242.

Lohoefener, R. and L. Lohmeier. 1984. The Status of Gopherus polyphemus (Testudines, Testudinidae) west of the Tombigbee and Mobile rivers. A report on research presented in conjunction with a petition to list the gopher tortoise west of the Tombigbee and Mobile rivers as an endangered species without critical habitat. 141 p.

Lohoefener, R. and , L. Lohmeier. 1986. Experiments with gopher tortoise (*Gopherus polyphemus*) relocation in southern Mississippi. Herpetological Review 17: 37-40.

Macdonald, L.A. and H.R. Mushinsky. 1988. Foraging ecology of the gopher tortoise, *Gopherus polyphemus*, in a sandhill habitat. Herpetologica 44:345-353.

Mangel, Marc and Charles Tier. 1993. Dynamics of Metapopulations with Demographic Stochasticity and Environmental Catastrophes. Theoretical Population Biology 44.1:1-31.

Mann, T.M. 1995. Tortoise densities and burrow occupancy rate for Gopher Tortoises on selected sites in Mississippi. Museum Technical Report No. 24. Corrected Edition Dec. 1995. Mississippi Museum of Natural Science, Jackson, MS. 54 p.

Marshall, J.E. 1987. The effects of nest predation on hatchling gopher tortoises (*Gopherus polyphemus*). Unpubl. master's thesis, Univ. of South Alabama, Mobile.

McCoy, E. D., and H. R. Mushinsky. 1988. The demography of *Gopherus polyphemus* (Daudin) in relation to size of available habitat. Unpublished report to Florida Game and Fresh Water Fish Commission, Nongame Wildlife Program, Tallahassee. 71 pp.

McCoy, E. D., H. R. Mushinsky, and J. Lindzey. 2007. Conservation strategies and emergent diseases: the case of upper respiratory tract disease in the gopher tortoise. Chelonian Conservation and Biology 6(2):170–176.

McCoy, E.D., H.R. Mushinsky, and D.S. Wilson. 1993. Pattern in the compass orientation of gopher tortoise burrows at different spatial scales. Global Ecology and Biogeography Letters 3:33-40.

McCoy, E.D., and H.R. Mushinsky. 2007. Estimates of Minimum Patch Size Depend on the Method of Estimations and the Condition of the Habitat. Ecology 88(6):1401-1407.

McDearman, W. 2006. Status of the gopher tortoise: in the federally listed range. US Fish &Wildlife Service, Jackson, MS. Unpublished Report. 34 pp.

McGuire, J. L., L. L. Smith, C. Guyer, J. M. Lockhart, G. W. Lee, and M. J. Yabsley. 2014a. Surveillance for Upper Respiratory Tract Disease and Mycoplasma in free-ranging gopher tortoises in Georgia, USA. Journal of Wildlife Diseases 50:733-744.

McGuire, J. L., L. L. Smith, C. Guyer, M. J. Yabsley. 2014b. Effects of mycoplasmal upper-respiratory-tract disease on movement and thermoregulatory behavior of gopher tortoises (*Gopherus polyphemus*) in Georgia, USA. Journal of Wildlife Diseases 50:745-756.

McIntyre, R.K., L.M. Conner, S.B. Jack, E.M. Schlimm, L.L. Smith. 2019. Wildlife habitat condition in open pine woodlands: field data to refine management targets. Forest Ecology Management 437:282-294.

McKee, R. K., K. A. Buhlmann, C. T. Moore, J. Hepinstall-Cymerman, and T. D. Tuberville. 2021. Waif gopher tortoise survival and site fidelity following translocation. Journal of Wildlife Management. DOI 10.1002/jwmg.21998.

McLaughlin, G. S. 1997. Upper respiratory tract disease in gopher tortoises, *Gopherus polyphemus*: pathology, immune responses, transmission, and implications for conservation and management. PhD Dissertation, University of Florida, Gainesville, Florida, 110 pp.

McRae, W.A., J.L. Landers, and G.D. Cleveland. 1981. Sexual dimorphism in the gopher tortoise (*Gopherus polyphemus*). Herpetologica 37:46-52.

Means, D.B. 1982. Responses to Winter Burrow Flooding of the Gopher Tortoise (*Gopherus polyphemus* Daudin). Herpetologica. 38(4): 521-525.

Means, D.B. 2009. Effects of rattlesnake roundups on the eastern diamondback rattlesnake (*Crotalus adamanteus*). Herpetological Conservation and Biology 4(2):132–141.

Mendonca, M., R. Beauman, H.E. Balbach, United States. Army. Corps of Engineers., Engineer Research and Development Center, (U. S.), and Construction Engineering Research Laboratory, (U. S.). 2007. Burrow collapse as a potential stressor on the gopher tortoise (*Gopherus polyphemus*). ERDC/CERL; TR-07-33. [US Army Corps of Engineers, Engineer Research and Development Center], Construction Engineering Research Laboratory. Champaign, Ill. vii, 55 pages: illustrations ; 28 cm. Pp.

Mengak, Michael T., "Nine-banded Armadillo (*Dasypus novemcinctus*)" (2004). USDA National Wildlife Research Center - Staff Publications. 959. https://digitalcommons.unl.edu/icwdm_usdanwrc/959

Meshaka Jr., W. E., J. N. Layne, and K. G. Rice. 2019. The effects of geography, habitat, and humans on the ecology and demography of the gopher tortoise in the southern Lake Wales Ridge region of Florida. Herpetological Journal 29:95–114.

Miller, P. S. 2001. Preliminary population viability assessment for the gopher tortoise (*Gopherus polyphemus*) in Florida. Conference Proceedings: September 11-12, 2001. Conservation Breeding Specialist Group, Species Survival Commission, IUCN-World Conservation Union. Tallahassee, FL.

Miller, J.H., S.T. Manning, and S.F. Enole. 2010. A management guide for invasive plants in southern forests. Gen. Tech. Rep. SRS-131. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 120 p.

Miller, D.A., and M.J. Chamberlain. 2008. Plant community response to burning and herbicide preparation in eastern Louisiana, USA. Forest Ecology 255: 774–780.

Minogue, P. B. Brodbeck, and J. Miller. 2018. Biology and control of Cogongrass (*Imperata cylindrica*) in Southern forests. EDIS. 2018. 10.32473/edis-fr411-2018.

Moore, J.A., A. Dornburg. 2014. Ingestion of fossil seashells, stones and small mammal bones by gravid gopher tortoises (*Gopherus polyphemus*) in South Florida. Bulletin of the Peabody Museum of Natural History 55(1):55-63.

Moore, J.A., M. Strattan, and V. Szabo. 2009. Evidence for year-round reproduction in the Gopher tortoise (*Gopherus polyphemus*) in Southeastern Florida. Bulletin of the Peabody Museum of Natural History 50:387-392.

Morafka, D.J., L.G. Aguirre, and R.W. Murphy. 1994. Allozyme differentiation among gopher tortoises (Gopherus): Conservation genetics and phylogenetic and taxonomic implications. Canadian Journal of Zoology/Revue Canadienne De Zoologie 72:1665-1671.

Murphy, R.W., K.H. Berry, T. Edwards, A.E. Leviton, A. Lathrop, and J.D. Riedle. 2011. The dazed and confused identity of Agassiz's land tortoise, *Gopherus agassizii* (Testudines, Testudinidae) with the description of a new species, and its consequences for conservation. ZooKeys 113: 39-71.

Mushinsky, H. R. and E. D. McCoy. 1994. Comparison of gopher tortoise populations on islands and on the mainland in Florida. Pp. 39-47 in Bury R.B. and D.J. Germano, eds. Biology of North American Tortoises. Volume 13. Fish and Wildlife Research.

Mushinsky, H. R., D. S. Wilson, and E. D. McCoy. 1994. Growth and sexual dimorphism of *Gopherus polyphemus* in central Florida. Herpetologica 50:119-128.

Mushinsky, H. R., E. D. McCoy, J. E. Berish, R. E. Ashton, Jr., and D. S. Wilson. 2006. *Gopherus polyphemus*, Gopher Tortoise. In P. A. Meylan, (ed). Biology and conservation of Florida's turtles. Chelonian Research Monographs, Lunenburg, Massachusetts.

Mushinsky, H.R., T.A. Stilson, and E.D. McCoy. 2003. Diet and dietary preference of the juvenile gopher tortoise (*Gopherus polyphemus*). Herpetologica 59:475-483.

Myers, D.A., R. Isaza, G. Ben–Shlomo, J. Abbott, and C.E. Plummer. 2009. Fungal keratitis in a gopher tortoise (*Gopherus polyphemus*). Journal of Zoo and Wildlife Medicine 40(3):579–582.

National Aeronautics and Space Administration DEVELOP National Program (NASA DEVELOP). 2018. Solar Energy Development in Georgia. Retrieved April 19, 2021 from website: https://usg.maps.arcgis.com/apps/MapJournal/index.html?appid=9d50b5415d1542d59c222751e45610c9

National Council for Air and Stream Improvement, Inc. (NCASI). 2020. Response to information request: gopher tortoise (Gopherus polyphemus) species status assessment and the need for species information throughout its range. Letter on file with USFWS, Jacksonville, Florida.

Natural Resources Conservation Service (NRCS). 2018. Working Lands for Wildlife Gopher tortoise status: At Risk 2018 Progress Report. 2 pp. https://www.nrcs.usda.gov/wps/PA_NRCSConsumption/download?cid=nrcseprd1452021&ext=pdf

Natural Resources Conservation Service (NRCS). 2020. Working Lands for Wildlife gopher tortoise: FY 2020-2024 Implementation Strategy. 24 pp. https://www.nrcs.usda.gov/wps/PA_NRCSConsumption/download?cid=nrcseprd1643225&ext=pdf

Nicotra A.B., Beever, E.A., Robertson, A.L., Hofmann, G.E., O'Leary, J. 2015. Assessing the components of adaptive capacity to improve conservation and management efforts under global change. Conservation Biology Vol. 29,5:1268-78.

NOAA. 2020. Sea Level Rise Viewer. <https://coast.noaa.gov/slr/#>. Accessed 5 Jan 2021.

Noel, K.M., Qualls, C.P., and J.R. Ennen, 2012. A comparison of artificial incubation and natural incubation hatching success of gopher tortoise (*Gopherus polyphemus*) eggs in south Mississippi. Herpetologica 68:324–333.

Nomani, S.Z., Carthy, R.R., and Oli, M.K. 2008. Comparison of methods for estimating abundance of gopher tortoises. Applied Herpetology5:13-31.

Nordman, C., R. White, R. Wilson, C. Ware, C. Rideout, M. Pyne, and C. Hunter. 2016. Rapid assessment metrics to enhance wildlife habitat and biodiversity within southern open pine ecosystems, version 1.0. U.S. Fish and Wildlife Service and NatureServe, for the Gulf Coastal Plains and Ozarks Landscape Conservation Cooperative. 115 p.

O'Brien, S., R. Bourou, and T. Hafany. 2005. Hatch size, somatic growth rate and size-dependent survival in the endangered ploughshare tortoise. Biological Conservation 126.2: 141-145.

Offner, M.T. 2017. Spatial ecology and diet of the Argentine black and white tegu (*Salvator merianae*) in Central-Florida. Masters thesis. University of Florida, Gainesville, Florida.

Osentoski, M.F. and T. Lamb. 1995. Intraspecific phylogeography of the gopher tortoise, *Gopherus polyphemus*: RFLP analysis of amplified mtDNA segments. Molecular Ecology 4:709-718.

Oswalt, S.N.; Smith, W. B.; Miles, P.D.; Pugh, S.A. 2014. Forest resources of the United States, 2012: a technical document supporting the Forest Service update of the 2010 RPA assessment. Gen. Tech. Rep. WO-91. Washington, DC: U.S. Department of Agriculture, Forest Service. 218 p

Ott, J.A., M.T. Mendonça, C. Guyer, and W.K. Michener. 2000. Seasonal changes in sex and adrenal steroid hormones of gopher tortoises (*Gopherus polyphemus*). General and Comparative Endocrinology 117:299-312.

Ott-Eubanks, J., W. K. Michener, and C. Guyer. 2003. Patterns of movement and burrow use in a population of gopher tortoises (*Gopherus polyphemus*). Herpetologica. 59:311-321.

Ong, S., Campbell, C., Denholm, P., Margolis, R., and Heath, G. 2013. Land-use requirements for solar power plants in the United States. Technical report 6A20-56290. National Renewable Energy Laboratory. Golden, Colorado. 47pp.

Ozgul, A., M. K. Oli, B. M. Bolker and C. Perez-Heydrich. 2009. Upper respiratory tract disease, force of infection, and effects on survival of gopher tortoises. Ecological Applications 19:786-798.

Perez-Heydrich, C., K. Jackson, L. D. Wendland, and M. B. Brown. 2012. Gopher tortoise hatchling survival: field study and meta-analysis. Herpetologica 68:334–344.

Pickens, B. A. et al., 2017. The effect of urban growth on landscape-scale restoration for a fire dependent songbird. Journal of Environmental Management, Volume 191, pp. 105-115.

Pike, David, A. 2006. Movement Patterns, Habitat Use, and Growth of Hatchling Tortoises, *Gopherus polyphemus*. Copeia. 1:68-76.

Pike, D. A., and R. A. Seigel. 2006. Variation in hatchling tortoise survivorship at three geographic localities. Herpetologica 62:125-131.

Platt, W.J., Entrup, A.K., Babl, E.K., Coryell-Turpin, C., Dao, V., Herbert, J.A., LaBarbara, Noto, J.F.L., Ogundare, S.O., Stamper, L.K., and Timilsina, N. Short-term effects of herbicides and a prescribed fire on restoration of a shrub-encroached pine savanna. Restoration Ecology 23:909–917.

Population Projections, United States, 2004-2030, by state, age, and sex, on CDC WONDE Online Database. September 2005. Retrieved from http://wonder.cdc.gov/population-projections.html. Mar 26, 2021.

Prieto-Ramirez, A.M, Röhler, L., Cord, A.F., Pe'er, G., Rödder, D., Henle, K. 2020. Differential effects of habitat loss on occupancy patterns of the eastern green lizard *Lacerta viridis* at the core and periphery of its distribution range. PLoSONE 15(3):e0229600.https://doi.org/10.1371/journal.pone.0229600

Quinn, D.P., Tuberbille, T.D., and Buhlmann, K.A. 2016. Post-release movement and survivorship of head-started gopher tortoises. Journal of Wildlife Management 82:1545-1554.

Rabatsky, A., and B. Blihovde. 2002. Gopher tortoise die-off at Rock Springs Run State Reserve, Lake County, Florida. Turtle and Tortoise Newsletter 6:27–28.

Rautsaw, R.M., Martin, S.A., Lanctot, K., Vincent, B.A., Bolt, M. R., Seigel, R.A., Parkinson, C.L. 2018. On the road again: assessing the use of roadsides as wildlife corridors for gopher tortoises (*Gopherus polyphemus*). Journal of Herpetology 52(2);136-144.

Redford, K.H., G. Amoto, J. Baillie, P. Beldomenico, E.L. Bennett, N. Clum, R. Cook, G. Fonseca, S. Hedges, F. Launay, S. Lieberman, G. M. Mace, A. Murayama, A. Putnam, J.G. Robinson, H. Rosenbaum, E.W. Sanderson, S.N. Stuart, P. Thomas, and J. Thorbjarnarson. 2011. What does it mean to successfully conserve a (vertebrate) species? Bioscience 61:39– 48.

Richardson, J.C., and P. Stiling. 2019. Gopher tortoise herbivory increases plant species richness and diversity. Plant Ecology, 220:383–391.

Richter, S.C., J.A. Jackson, M. Hinderliter, D. Epperson, C.W. Theodorakis, and S.M. Adams. 2011. Conservation genetics of the largest cluster of federally threatened gopher tortoise (*Gopherus polyphemus*) colonies with implications for species management. Herpetologica 67:406-419.

Riedl, S. C., H. R. Mushinsky, and E. D. McCoy. 2008. Translocation of the gopher tortoise: difficulties associated with assessing success. Applied Herpetology 5:145-160.

Rostal, D. C. and D. N. J. Jones. 2002. Population biology of the gopher tortoise (*Gopherus polyphemus*) in southeast Georgia. Chelonian Conservation and Biology 4(2):479-487.

Rostal, D. C., E. D. McCoy, and H. R. Mushinsky. 2014. Biology & conservation of North American tortoises. Johns Hopkins University Press, Baltimore, MD, USA.

Ruppert, T.K., T. Ankerson, C. Coverington, R. Feinberg, Y. Huang, M. McDonnell, and A. Miller. 2008. Eroding long-term prospects for Florida's beaches: Florida's coastal management policy. Final report for Sea turtle grant program, contract number 07-019E. Sea Turtle Conservancy, Gainesville, Florida.

Sandmeier, F. C., C. R. Tracey, S. duPre, and K. Hunter. 2009. Upper respiratory tract disease (URTD) as a threat to desert tortoise populations: a reevaluation. Biological Conservation 142:1255–1268.

Schwartz, T.S. and S.A. Karl. 2005. Population and conservation genetics of the gopher tortoise (*Gopherus polyphemus*). Conservation Genetics 6:917-928.

Seigel, R. A. and J. Hurley. 1993. Ecology and management of the gopher tortoise (*Gopherus polyphemus*) at Bens Creek Wildlife Management Area. U.S. Fish and Wildlife Service, Division of Federal Aid, Atlanta, GA. Report to U.S. Fish and Wildlife Service and Louisiana Department of Wildlife and Fisheries.

Seigel, R. A. and C. K. Dodd Jr. 2000. Manipulation of turtle populations for conservation: halfway technologies or viable populations? *In* Turtle conservation: 218–238. Klemens, M. W. (Ed). Washington, DC: Smithsonian Institute Press.

Seigel, R.A., and K.R. Smith. 1995. Demography and reproduction of gopher tortoises in Mississippi. Museum Technical Report No. 32. Submitted to: Mississippi Museum of Natural Science, Jackson, MS. 15 p.

Seigel, R.A. and K.R. Smith. 1996. Demography and reproduction of gopher tortoises in Mississippi. Museum Final Report March 1996. Submitted to Mississippi Museum of Natural Science, Jackson, MS. 29 p.

Seigel, Richard A., and C. Kenneth Dodd Jr. 2000. Manipulation of turtle populations for conservation: Half-way technologies or viable options?: Chapter 9218-238.

Sellers, B.A., Ferrell, J.A., MacDonald, G.E., Enloe, S.F., and Flory, S.L. 2018. Cogongrass (Imperata cylindrica) Biology, Ecology, and Management in Florida Grazing Lands. EDIS:8.

Sgro, Carla M., Lowe, Andrew, J., Hoffmann, Ary, A. 2011. Building evolutionary resilience for conserving biodiversity under climate change. Evolutionary Applications. 326-327.

Shaffer, M. L. 1981. Minimum population sizes for species conservation. BioScience 1:131-134.

Shearin, M. E. 2011. The direct and indirect effects of the red imported fire ant (*Solenopsis invicta*) on seed fate in the longleaf pine ecosystem. M.S. thesis, University of Georgia, Athens, GA. 84 pp.

Schulte, P. 2020. Social Network Formation in Translocated Gopher Tortoises (*Gopherus polyphemus*). Auburn University. Master's Thesis.

Simberloff, D., 1993. Species-area and fragmentation effects on old growth forests: prospects for longleaf pine communities. *In*: S. M. Hermann, ed. The longleaf pine ecosystem: ecology, restoration, and management. Tall Timber Fire Ecology Conference Proceedings, No. 18. Tallahassee: Tall Timber Research Station, pp. 1-14.

Sinclair-Winters, C., Moler, P.E., and Berish, J.D. 2011. Microsatellite assessment of *Gopherus polyphemus* populations in the Florida panhandle. Florida Scientist 80:151–158.

Smallwood, K.S. 2001.Linking Habitat Restoration to Meaningful Unitos of Animal Demography. Restoration Ecology 9(2):253-261.

Smith, K. R., J. A. Hurley, and R. A. Seigel. 1997a. Reproductive biology and demography of gopher tortoises (*Gopherus polyphemus*) from the western portion of their range. Chelonian Conservation and Biology 2:596-600.

Smith, L. L. 1995. Nesting ecology, female home range and activity, and populations size-class structure of the gopher tortoise, *Gopherus polyphemus*, on the Katherine Ordway Preserve, Putnam County, Florida. Bulletin of the Florida Museum of Natural History 37:97-126.

Smith, L. L., D. A. Steen, L. M. Conner, and J. L. Rutledge. 2013. Effects of predator exclusion on nest and hatchling survival in the gopher tortoise. Journal of Wildlife Management 77:352-358.

Smith, L. L., J. M. Linehan, J. M. Stober, M. J. Elliott, and J. B. Jensen. 2009a. An evaluation of distance sampling for large-scale gopher tortoise surveys in Georgia, U.S.A. Applied Herpetology 6:355–368.

Smith, L.L., Hinderliter, M., Taylor, R.S., and Howze, J.M. 2015. Recommendation for Gopher tortoise Burrow Buffer to Avoid Collapse from Heavy Equipment. Journal of Fish and Wildlife Management 6(2):456-463.

Smith, L.L., J. Stober, H.E. Balbach, and W.D. Meyer. 2009b. Gopher tortoise survey handbook. Final Report prepared for U.S. Army Corps of Engineers, Washington, D.C. 59 pp.

Smith, L.L., T. D. Tuberville, and R.A. Seigel. 2006. Workshop on the ecology, status, and management of the gopher tortoise (*Gopherus polyphemus*), Joseph W. Jones Ecological Research Center, 16–17 January 2003: Final Results and Recommendations. Chelonian Conservation and Biology, 5(2): 326–330.

South Carolina Budget and Control Board. 2009. South Carolina Statistical Abstract. Office of Research and Statistics. Columbia, South Carolina. 2pp.

Southeast Regional Partnership for Planning and Sustainability (SERPPAS). 2020, 12th Annual Report – Candidate Conservation Agreement for the Gopher Tortoise. 171 pp.

Southern Environmental Law Center (SELC). 2017. The environmental review of solar farms in the Southeast U.S. Maximizing benefits & minimizing impacts to Drive Smart, Sustainable Development of Solar Power. Chapel Hill, North Carolina. 22pp.

Speake, D. W., and R. H. Mount. 1973. Some possible ecological effects of "Rattlesnake Roundups" in the southeastern coastal plain. Proceedings of the Annual Conference of Association of Game and Fish Commissioners 27:267-277.

Spencer, R.J., Van Dyke, J.U., and Thompson M.B. 2017. Critically evaluating best management practices for preventing freshwater turtle extinctions. Conservation Biology 31(6):1340-1349.

Steen, D. A., and J. P. Gibbs. 2004. Effects of roads on the structure of freshwater turtle populations. Conservation Biology 18:1143-1148.

Steen, D. A., M. J. Aresco, S. G. Beilke, B. W. Compton, E. P. Condon, C. K. Dodd, Jr., H. Forrester, J. W. Gibbons, J. L. Greene, G. Johnson, T. A. Langen, M. J. Oldham, D. N. Oxier, R. A. Saumure, F. W. Schueler, J. M. Sleeman, L. L. Smith, J. K. Tucker, and J. P. Gibbs. 2006. Relative vulnerability of female turtles to road mortality. Animal Conservation 9:269-273.

Stewart, M.C., D.F. Austin, and G.R. Bourne. 1993. Habitat structure and the dispersion of gopher tortoise on a nature preserve. Florida Scientist 56(2):70–81.

Stiles, J.H., R.H. Jones. 1998. Distribution of the red imported fire ant, *Solenopsis invita*, in road and powerline habitats. Landscape Ecology 13:335–346 https://doi.org/10.1023/A:1008073813734

Sustainable Forestry Initiative (SFI). 2021. SFI Database. https://www.sfidatabase.org/ Accessed June 7, 2021.

Sutherland, R. W., 2009. The effects of urbanization on reptiles and amphibians in the Sandhills region of North Carolina. Dissertation. Durham: Duke University.

Taulman, J. F. and L. W. Robbins. 1996. Recent range expansion and distributional limits of the nine-banded armadillo (*Dasypus novemcinctus*) in the United States. Journal of Biogeography 23:635-648.

Taylor, Robert W., JR. 1982. Human Predation on the Gopher Tortoise (*Gopherus polyphemus*) in North-Central Florida. Bul. Florida State Museum. Biol. Sci. 26(4):79-102.

Terando A.J., Costanza J., Belyea C., Dunn R.R., McKerrow A., and Collazo J.A. 2014. The Southern Megalopolis: Using the Past to Predict the Future of Urban Sprawl in the Southeast U.S. PLoS ONE 9(7): e102261. https://doi.org/10.1371/journal.pone.0102261

Thaxton, J.M. and W.J. Platt. 2006. Small-scale fuel variation alters fire intensity and shrub abundance in pine savanna. Ecology 87:1331-1337.

Theobald, D. M. & Romme, W. H., 2007. Expansion of the US wildland–urban interface. Landscape and Urban Planning, Volume 83, pp. 340-354.

Thomas, L., S.T. Buckland , E.A. Rexstad, J.L. Laake, S. Strindberg, S.L. Hedley, J.R.B. Bishop, T.A. Marques, and K.P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5-14.

Tuberville, T. D., E. E. Clark, K. A. Buhlmann, and J. W. Gibbons. 2005. Translocation as a conservation tool: site fidelity and movement of repatriated gopher tortoises (*Gopherus polyphemus*). Animal Conservation 8:349-358.

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

Tuberville, T. D., T. M. Norton, B. J. Waffa, C. Hagen, and T. C. Glenn. 2011. Mating system in a gopher tortoise population established through multiple translocations: apparent advantage of prior residence. Biological Conservation 144:175–183.

Tuberville, T. D., B. D. Todd, S. M. Hermann, W. K. Michener, and C. Guyer. 2014. Survival, demography, and growth of gopher tortoises (*Gopherus polyphemus*) from three study sites with different management histories. Journal of Wildlife Management 78:1151–1160.

Tuberville, T.D., T.M. Norton, K.A. Buhlman and V. Greco. 2015. Head-starting as a management component for gopher tortoises (*Gopherus polyphemus*). Herpetological Conservation and Biology 10:455-471.

Tuberville, T.D., J.W. Gibbons, and H.E. Balbach. 2009. Estimating viability of gopher tortoise populations. Final report ERDC/CERL TR-09-2 U.S. Army Corps of Engineers, Washington, D.C.

Tubberville, T.D., Quinn, D.P., and Buhlmann, K.A. 2021. Movement and Survival to Winter Dormancy of Fall-Released Hatchling and Heastarted Yearling Gopher Tortoises. Journal of Herpetology. 55(1):89-94.

Tuma, M.W. 1996. Life history and population structure of the gopher tortoise (*Gopherus polyphemus*) on Camp Shelby, Mississippi. Annual report for Gopher Tortoise Legacy Research.

Tuma M, Stanford CB. 2014. History of human interaction with North American tortoises. In: Rostal DC, McCoy ED, Mushinsky HR (eds) Biology & conservation of North American tortoises. John Hopkins University Press, Baltimore, pp 143–148.

Turtle Conservation Fund. 2002. A global action plan for conservation of tortoises and freshwater turtles, Strategy and funding prospectus 2002-2007. Conservation International and Chelonian Research Foundation, Washington, DC.

U.S. Census Bureau. 2021. Quick Facts. Retrieved from https://www.census.gov/quickfacts/fact/table/SC,MS,LA,AL,GA,FL/PST120219. March 26, 2021

U.S. Department of Agriculture (USDA). 2017. Imported Fire Ant and Household Insects Research. Retrieved from https://www.ars.usda.gov/southeast-area/gainesville-fl/center-for-medical-agricultural-and-veterinary-entomology/imported-fire-ant-and-household-insects-research/docs/potential-united-states-range-expansion-of-the-invasive-fire-ant/. April 20, 2021.

U.S. Environmental Protection Agency (EPA), 2013, Level III ecoregions of the continental United States: Corvallis, Oregon, U.S. EPA – National Health and Environmental Effects Research Laboratory, map scale 1:7,500,000, https://www.epa.gov/eco-research/level-iii-and-iv-ecoregions-continental-united-states.

U.S. Forest Service (USFS). 2020. Mission, vision, and operational strategy; De Soto Ranger District; De Soto National Forest; National Forests in Mississippi. July 8, 2020. De Soto Ranger District, Wiggins, MS. 36 pp.

U.S. Fish and Wildlife Service [Service]. 1990. Gopher Tortoise Recovery Plan. U.S. Fish and Wildlife Service, Jackson, Mississippi. 28 pp.

U.S. Fish and Wildlife Service. 2008. Guidelines for activities occurring within occupied gopher tortoise habitat. Jackson, Mississippi. 4pp.

U.S. Fish and Wildlife Service[Service]. 2008a. Candidate Conservation Agreement for the Gopher Tortoise (*Gopherus polyphemus*) Eastern Population November 2008 (Revised October 2018). Atlanta, Georgia, 87pp.

U.S. Fish and Wildlife Service [Service]. 2013. Range-wide conservation strategy for the gopher tortoise. May 2013. 22 pages.

U.S. Fish and Wildlife Service [Service]. 2016. Service Species Status Assessment Framework: an integrated analytical framework for conservation. Version 3.4 dated August 2016., Washington D.C.: U.S. Fish and Wildlife Service.

U.S. Fish and Wildlife Service [Service]. 2017. Department of Defense Gopher Tortoise (Gopherus polyphemus) Conservation and Crediting Strategy. Atlanta, Georgia. 62pp.

U.S. Fish and Wildlife Service [Service]. 2019. Gopher Tortoise Candidate Notice of Review: 84 FR 54732 54757.

U.S. Fish and Wildlife Service [Service]. 2020. Partners for Fish and Wildlife 2010 to 2019 Project information. Unpublished data on file with USFWS, Jacksonville, FL.

Ultsch, G. R. and J. F. Anderson. 1986. The respiratory microenvironment within the burrows of gopher tortoises (*Gopherus polyphemus*). Copeia 1986:787-795.

Waddle, J.H., F.J. Mazzotti, K.G. Rice. 2006. Changes in abundance of gopher tortoise burrows at Cape Sable, Florida. Southeastern Naturalist, 5:2:277–284.

Ware, S.C., Frost, C., and Doer, P.D. 1993. Southern mixed hardwoods; the former longleaf pine forest, in WH Martin ed., Biodiversity of the southeastern United States: lowland terrestrial communities. New York, J. Wiley p. 447-493.

Wear, D.N. and J.G. Greis, editors. 2002. The southern forest resource assessment. USDA, Forest Service, Southern Research Station. Asheville, North Carolina. 628 pp.

Wear, D.N. and J.G. Greis, editors. 2013. The southern forest futures project: technical report 178, USDA, Forest Service, Southern Research Station, Asheville, North Carolina. 542 pp.

Weatherford, P., S.P. Prisley, A.L. Larsen-Gray, E.B. Schilling, and D.A. Miller. 2020. Report submitted as comments: gopher tortoise (*Gopherus polyphemus*) species status assessment and the need for species information throughout its range. Email to the Service at gophertortoise@fws.gov from representatives of the National Council for Air and Stream Improvement (NCASI). April 30, 2020.

Wendland, L.D. Epidemiology of mycoplasmal upper respiratory tract disease in tortoises. Dissertation. University of Florida, Gainesville, Florida.

Wendland, L. D., Wooding, J., White, C. L., Demcovitz, D., Littell, R., Berish, J. D., Ozgul, A., Oli, M. K., Klein, P. A., Christman, M. C., and Brown, M. B. 2010. Social behavior drives the dynamics of respiratory disease in threatened tortoises. Ecology (Washington D C), v. 91, p. 1257-1262.

Wester, Edward, E. 2005. Distribution and Status of the Threatened Gopher Tortoise on Camp Shelby, Mississippi 1995-2004. Mississippi Army National Guard, State of Mississippi Contract number 03-A&E-10-F.

Wester, E.E., and J.W. Kolb. 2008. Impact of natural gas pipeline operation and maintenance on long-term population viability of the threatened gopher tortoise. Environment Concerns in

Rights-of-Way Management : 8th International Symposium 12-16 September 2004 Saratoga Springs, New York, USA.

Wetterer, J. K. and J. A. Moore. 2005. Red imported fire ants (Hymenoptera: Formicidae) at gopher tortoise (Testundines:Testunididae) burrows. Florida Entomologist 88(4):349-354.

White, C.L. 2009. Gopher tortoise (*Gopherus polyphemus*) habitat selection, health, and fecundity. Dissertation. University of Florida, Gainesville, Florida.

Wigley, T.B., Hedman, C.W., Loehle, C., Register, M., Poirier, J.R., and P.E. Durfield. 2012. Density of gopher tortoise burrows on commercial forestland in Alabama and Mississippi. South. J. Appl. For. 36:38–43.

Wilcove, D.S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:121-1214.

Wilcox, E. & Giuliano, W. M., 2014. Red imported fire ants and their impacts on wildlife. Gainesville: Florida Cooperative Extension Service, Institute of Food and Agricultural Science, University of Florida. WEC 207.

Wilson, D. S. 1991. Estimates of survival for juvenile gopher tortoises, *Gopherus polyphemus*. Journal of Herpetology 25:376-379.

Wilson, D. S., H. R. Mushinsky, and E. D. McCoy. 1994. Home range, activity, and use of burrows of juvenile gopher tortoises in central Florida. Pages 147-160 *In* R. B. Bury and D. J. Germano (eds.). Biology of North American tortoises. National Biological Survey, Fish and Wildlife Research 13.

Wolf. S., B. Hartl, C. Carroll, M.C. Neel, and D.N. Greenwald. 2015. Beyond PVA: why recovery under the Endangered Species Act is more than population viability. BioScience 65:200-207.

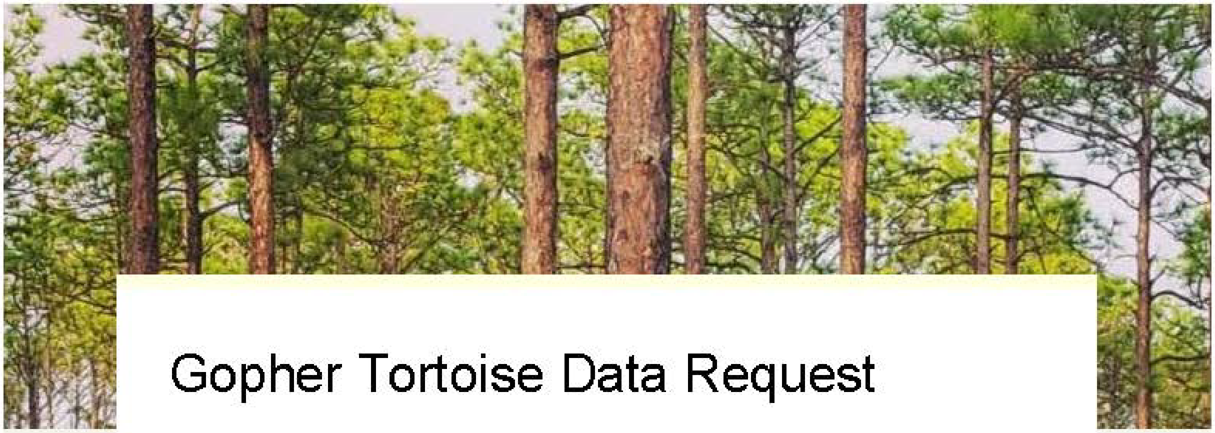
Wright, J.S. 1982. Distribution and population biology of the gopher tortoise, *Gopherus polyphemus*, in South Carolina. Clemson University. Master Thesis. 74 pp.

Yager, L.Y., M.G. Hinderliter, C.D. Heise, and D.M. Epperson. 2007. Gopher tortoise response to habitat management by prescribed burning. Journal of Wildlife Management 71:428–434.

Yager, L.Y., Miller, D.L., Jones, J. 2010. Susceptibility of longleaf pine forest associations in south Mississippi to invasion by Cogongrass [*Imperata cylindrica* (L.) Beauv.]. Natural Areas Journal 30:226–232.

APPENDIX A

GOPHER TORTOISE PRIVATE LANDOWNER QUESTIONNAIRE



Gopher Tortoise Data Request

To support the development of a Species Status Assessment (SSA) for the gopher tortoise, the U.S. Fish and Wildlife Service (Service) is collecting, compiling, synthesizing, and analyzing the best available science on habitat and management of the species. This form is being used to gather data and information for the gopher tortoise SSA, which will be used to inform the classification decision for the gopher tortoise. Classification decisions are based only on the best available science. Multiple groups have requested additional clarification in the type of information that the Service will need to do the evaluation for this species, and therefore, we are providing this form for you to consider. However, the Service will accept information in any format that you can provide.

Please answer the below questions to the best of your ability. If there is other important information you think we should know about your property, please feel free to provide that in the last question on the form. We appreciate your time and effort! We would appreciate your response by September 15, 2019, if possible, to ensure we have adequate time to consider the information during our status review, but we will accept information throughout the entire process. All data and information submitted to us, including names and addresses, would become part of the administrative record.

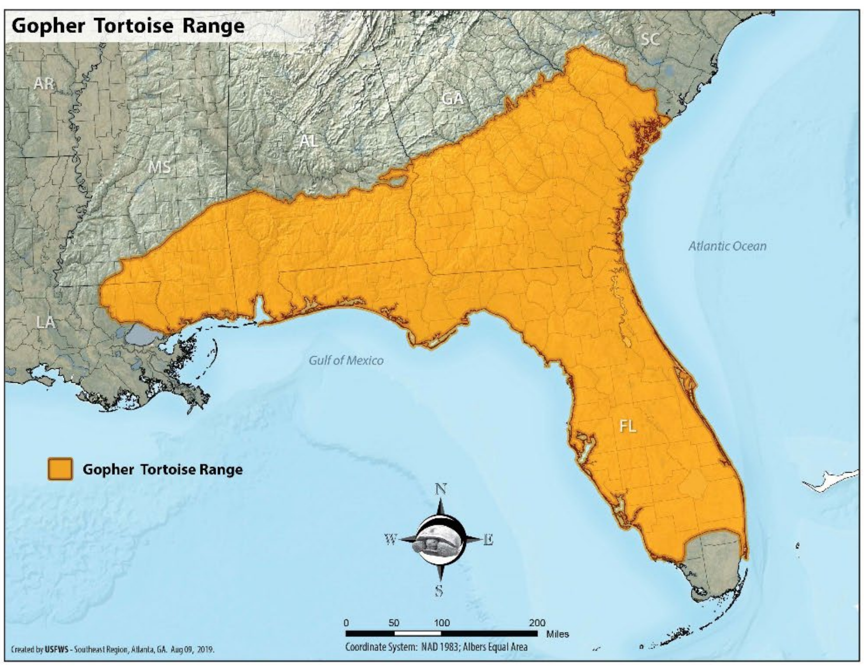
In order to avoid duplication, please submit this form only once (via internet or PDF version). If PDF version, please provide to the Service at gophertortoise@fws.gov or through your respective association to provide to the Service.

Gopher Tortoise Data Request

Basic Property Information

Please provide as much information about your property as you feel comfortable. If you would like to submit additional information or data, please do so at gophertortoise@fws.gov.

State



County (if you own property in multiple counties, please fill out separate forms for each county).

Counties with Gopher Tortoises

Alabama: *Baldwin, Choctaw, Clarke, Marengo, Mobile, Sumter, Washington, Baldwin, Barbour, Bullock, Butler, Choctaw, Clarke, Coffee, Conecuh, Covington, Crenshaw, Dale, Dallas, Escambia, Geneva, Henry, Houston, Lee, Lowndes, Macon, Marengo, Mobile, Monroe, Montgomery, Pike, Russell, Washington, Wilcox*; **Louisiana**: *Livingston, St. John the Baptist, St. Tammany, Tangipahoa, Washington*; **Mississippi**: *Clarke, Covington, Forrest, George, Greene, Hancock, Harrison, Jackson, Jasper, Jefferson Davis, Jones, Lamar, Lawrence, Marion, Pearl River, Perry, Pike, Stone, Walthall, Wayne*; **Georgia**: *Appling, Atkinson, Bacon, Baker, Ben Hill, Berrien, Bleckley, Brantley, Brooks, Bryan, Bulloch, Burke, Calhoun, Camden, Candler, Charlton, Chatham, Chattahoochee, Clay, Clinch, Coffee, Colquitt, Cook, Crawford, Crisp, Decatur, Dodge, Dooly, Dougherty, Early, Echols, Effingham, Emanuel, Evans, Glascock, Glynn, Grady, Houston, Irwin, Jeff Davis, Jefferson, Jenkins, Johnson, Lanier, Laurens, Lee, Liberty, Long, Lowndes, McDuffie, McIntosh, Macon, Marion, Miller, Mitchell, Montgomery, Muscogee, Peach, Pierce, Pulaski, Quitman, Randolph, Richmond, Schley, Screven, Seminole, Stewart, Sumter, Talbot, Tattnall, Taylor, Telfair, Terrell, Thomas, Tift, Toombs, Treutlen, Turner, Twiggs, Ware, Washington, Wayne, Webster, Wheeler, Wilcox, Wilkinson, Worth*; **Florida**: *Alachua, Baker, Bay, Bradford, Brevard, Broward, Calhoun, Charlotte, Citrus, Clay, Collier, Columbia, DeSoto, Dixie, Duval, Escambia, Flagler, Franklin, Gadsden, Gilchrist, Glades, Gulf, Hamilton, Hardee, Hendry, Hernando, Highlands, Hillsborough, Holmes, Indian River, Jackson, Jefferson, Lafayette, Lake, Lee, Leon, Levy, Liberty, Madison, Manatee, Marion, Martin, Miami-Dade, Monroe, Nassau, Okaloosa, Okeechobee, Orange, Osceola, Palm Beach, Pasco, Pinellas, Polk, Putnam, St. Johns, St. Lucie, Santa Rosa, Sarasota, Seminole, Sumter, Suwannee, Taylor, Union, Volusia, Wakulla, Walton, Washington*; **South Carolina**: *Aiken, Allendale, Barnwell, Bamberg, Colleton, Dorchester, Hampton, Jasper*

Is your property subject to a conservation easement?

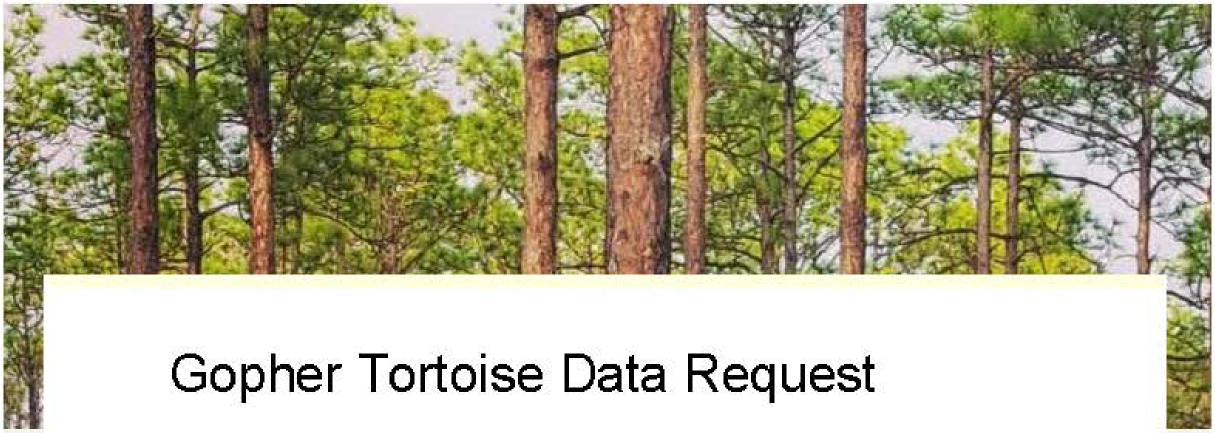
○ Yes ○ No

Is your property third party certified (e.g., SFI, FSC, ATFS)?

○ Yes ○ No

Do you implement any wildlife conservation or land best management practices?

○ Yes ○ No



Gopher Tortoise Data Request

Gopher Tortoise Habitat Type Information

How many acres of potential gopher tortoise type habitat are on your property? Potential gopher tortoise habitat includes well-drained, sandy soils, and can be found in a variety of habitats such as longleaf pine forests/ sandhills, xeric oak hammocks, scrub, pine flatwoods, dry prairies, coastal dunes, and pastures. This number will be called your "GT Acres", and can either be an exact number or a high and low estimate.

Which of the following community types best describes your GT acres? (choose all that apply)

- ☐ Pine
- ☐ Hardwood
- ☐ Mixed-pine hardwood
- ☐ Pasture/Open
- ☐ Other

We can describe gopher tortoise habitat suitability as low, moderate, or high depending on the condition of the canopy, mid-story/shrub layer, and herbaceous ground cover. Please estimate the approximate amount of your GT acres that fall in the Low suitability class as described below:

How many acres do you have that meet the Low Suitability as described below?

Description and examples of low suitability

Low	Dense canopy; uniform stand condition, characterized by minimal herbaceous groundcover	Metric	
		Pine Basal Area (ft^2/acre)	Less than 10 or greater than 105 (ft^2/acre)
		Pine Canopy Cover	Less than 10% or more than 85%
		Mid-story Cover	More than 40%
		Native Herbaceous Ground Cover	Less than 20%

Please estimate the approximate amount of your GT acres that fall in the Medium suitability class as described below:

How many acres do you have that meet the Medium Suitability as described below?

Description and examples of Medium suitability

Medium	**Fairly open canopy, with low to dense mid-story/shrub layer so only a few areas have adequate light reaching the ground to support herbaceous groundcover**	**Metric**	
		Pine Basal Area (ft^2/acre)	10 to 20 or 90 to 105
		Pine Canopy Cover	10 to 20 % or 75 to 85%
		Mid-story Cover	30 to 40%
		Native Herbaceous Ground Cover	20 to 30%

Please estimate the approximate amount of your GT acres that fall in the High suitability class as described below:

How many acres do you have that meet the High Suitability as described below?

Description and examples of high suitability

High	Open canopy; minimal shrub/mid-story layer; abundant native herbaceous groundcover	Metric	
		Pine Basal Area (ft^2/acre)	20 to 90
		Pine Canopy Cover	20 to 75%
		Mid-story Cover	Less than 30%
		Native Herbaceous Ground Cover	30 to 98%

Land Management Information

If prescribed fire is used on the GT acres, how many acres are treated with fire?

If prescribed fire is used on the GT acres, what is the prescribed burning frequency?

- ○ 1 to 3 years
- ○ 3 to 5 years
- ○ 5 to 7 years
- ○ More than 7 years
- ○ Other:

What other beneficial management practices do you use on your property? check all that apply

- ☐ Herbicide application for hardwood control
- ☐ Roller Chopping
- ☐ Mowing/Mulching
- ☐ Thinning
- ☐ Longleaf planting
- ☐ Invasive species control
- ☐ Marking/flagging burrows before thinning or disruptive practices
- ☐ Other:

On how many GT acres do you manage mid-story woody vegetation by methods other than prescribed fire (e.g. mechanical or herbicide)?

Do you anticipate the land use, management objectives, or fire regime to change in the next 20-30 years?

- ○ Yes
- ○ No

If yes, explain how.

Gopher Tortoise Information

Have there been gopher tortoises observed on your property in the last 5 years?

- ◯ Yes
- ◯ No

Has a complete survey of the property been done?

- ◯ Yes
- ◯ No

If Yes, what was the type of survey conducted?

- ☐ Line-transect distance sampling
- ☐ 100% survey method
- ☐ Opportunistic
- ☐ Other: ____________

What is the estimated number of individual tortoises on your property?

- ◯ 1 to 25
- ◯ 25 to 50
- ◯ 50 to 100
- ◯ 100 to 250
- ◯ 250 or more
- ◯ Unknown

What is the estimated number of tortoise burrows on your property?

- ◯ 1 to 25
- ◯ 25 to 50
- ◯ 50 to 100
- ◯ 100 to 250
- ◯ 250 or more
- ◯ Unknown

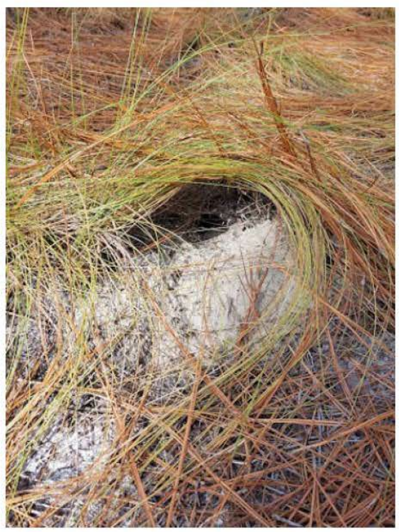
Have juvenile gopher tortoises or juvenile burrows (i.e. burrow opening <5 inches) been seen on your property?

◯ Yes

◯ No

No (image NOT of a gopher tortoise burrow)

Examples of juvenile burrows. You can go here (https://www.outdooralabama.com/sites/default/files/GT%20vs%20other%20burrows%20Identification%20Guide%20Handout.pdf) for additional examples.



Anything important you think we should know about your property and conservation practices for gopher tortoises?

APPENDIX B

Gopher Tortoise Population Modelling

Predicting Population Growth of Gopher Tortoises (*Gopherus polyphemus*) under Future Scenarios of Climate Warming, Sea-level Rise, Urbanization, and Habitat Management

Brian Folt

Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville, Florida 32611 U.S.A.

Author e-mail: brian.folt@gmail.com

Introduction

In this paper, I describe an analytical framework that integrates predictions from multiple models of future anthropogenic change to: (1) predict future population growth of an imperiled, ecologically significant species, (2) identify stressors with the greatest influence on future population persistence, and (3) support decisions about conservation and management during, for example, a Species Status Assessment for the gopher tortoise (*Gopherus polyphemus*). I reviewed the literature describing gopher tortoise life history and adapted a previously published population model for gopher tortoises (Folt et al. 2021) to estimate population growth and persistence probability of populations while accounting for geographic variation in life history. I expanded the model to link intrinsic factors (demographic vital rates) to four extrinsic anthropogenic factors that are hypothesized to threaten gopher tortoise population persistence (climate warming, sea-level rise, urbanization, and shifts in habitat management). I used published models describing predictions for extrinsic factors in the future to project gopher tortoise demographics under six future scenarios varying in threat magnitude and presence. I performed a regression analysis of model outputs to identify threats that are predicted to have the greatest impact on population persistence.

Methods

I sought to predict population growth and extinction risk for the gopher tortoise in a population viability analysis (PVA) framework. I built a stage-based population model (i.e., Lefkovitch model) (Lefkovitch 1965) and used the model to project population size and structure forward in time with simulations. For the PVA, I conceptualized local population demography of tortoises in a multi-stage, female-only model with two discrete life stages: juveniles and adults (Figure 1). During a given time-step, both stages had a probability of individuals surviving and remaining within the stage, juveniles had a probability of maturing to become adults, and adults had a probability of reproducing and potentially recruiting individuals into the juvenile stage. Individuals that did not survive during a time-step were assumed to have either died or permanently emigrated from the population. I also modeled recruitment into the adult stage by immigration (see below).

Model structure

I used the model structure to predict future abundance of populations across the range of the gopher tortoise using a first-order Markovian process in which adult abundance at time *t* was a function of adult and juvenile abundance at time *t*-1 with vital rates stochastically drawn from parameter distributions:

$$N_t^a = N_{t-1}^a \times \varphi_{t-1}^a + N_{t-1}^j \times \varphi_{t-1}^j \times \tau_{t-1} + N_{t-1}^i, \tag{1}$$

where *N* is abundance, φ is the apparent annual survival rate, and τ is an annual transition rate from juvenile to adult (i.e., maturation) during each time step *t* (year); superscripts a, j, and i denote adults, juveniles, and immigrants, respectively.

Juvenile abundance at time *t* was a function of juvenile and hatchling abundance at time *t*-1 with vital rates similarly drawn from parameter distributions:

$$N_t^j = N_{t-1}^j \times \varphi_{t-1}^j \times (1 - \tau_{t-1}) + R_{t-1}, \tag{2}$$

where *N* is abundance, φ is survival, τ is the juvenile-adult transition rate, and R is recruitment (below) during each time step t (year).

For individuals to recruit into the juvenile stage, adult females must lay eggs that hatch into offspring and survive until the next survey period (i.e., time step). Therefore, to estimate annual recruitment by reproduction, we modeled the probability of females breeding (PB), the mean number of eggs laid per individual (fecundity; F), the probability of nests surviving predation (NS), the proportion of eggs that are viable and hatch (VE), the probability of eggs being female (PF) and the survival probability of hatchlings through the first year to the next survey period (φ^h) at time *t* (Noon and Sauer 1992). I modeled probabilities (*PB, NS, VE,* PF, φ^h) as beta-distributed random variables, and I modeled fecundity as a log-normal random variable. Together, I then modeled recruitment (R) at time *t* as a product of:

$$R_t = PB_t \times F_t \times NS_t \times VE_t \times PF \times \varphi_t^h, \tag{3}$$

where the superscript *h* denotes hatchling.

Demographic parameters

I sought to construct a baseline population model that approximated demographic conditions experienced by gopher tortoise populations in recent decades across the species' range. However, populations of gopher tortoises experience variation in abiotic characteristics across the species' range, and variation in abiotic characteristics influences demographic rates among populations. At southern latitudes, populations experience significantly warmer mean annual temperature, which may afford greater overall opportunity for thermoregulation, energy acquisition, and metabolism when compared to northern populations. As a result, southern populations of tortoises experience faster growth rates, younger ages of sexual maturity (hereafter, maturity age), and increased clutch size (Mushinsky et al. 1994, Ashton et al. 2007, Meshaka Jr. et al. 2019). Because my goal was to predict population growth and extinction risk of populations across the species' range and predictive population models are most useful when demographic parameters are modeled specific to populations of interest (Ralls et al. 2002), I extended the model to accommodate for geographic variation in demographic rates by estimating parameters specific to the geographic location of populations.

I reviewed the literature for demographic estimates from gopher tortoise populations in the wild (Appendix 1). For parameters thought to vary by abiotic features among sites, I fit linear regression models to estimate relationships between demographic rates and mean annual temperature (hereafter, MAT; degrees C) sourced from the 'WorldClim' database (Hijmans 2020). After testing whether the data met assumptions of parametric statistics, I evaluated whether regression models estimated statistically significant effects of independent variables on response variables with α = 0.05. I used observed statistically significant linear relationships between MAT and demographic rates among populations as a predictive tool to generate mean parameter estimates with error for populations in our predictive modeling framework, given georeferenced data describing MAT at sites. If parameters were not known to vary geographically, I modeled mean values as invariant among populations. In the following paragraphs, I describe how I modeled parameters describing recruitment, maturity age, survival, immigration, and initial population size, respectively; however, all stochastic parameters and the distributions used to model them are summarized in Table 1.

I modeled the proportion of breeding females (oviposition; PB) in a given year as 0.97; this estimate has recently been validated by two independent field studies (Jeffrey Goessling, Eckerd

College, personal communication; Elizabeth Hunter, personal communication). Because fecundity (F) varies widely among populations and is likely driven by a north-to-south latitudinal gradient in temperature (Ashton et al. 2007), I used linear regression to estimate the relationship between MAT and estimates of mean clutch size (F) from the literature and then used regression coefficients to simulate mean values of F for populations, given the geographic location and MAT of a population. I modeled the probability of nests that survive predation (NS) as 0.35 using an estimate from unmanipulated nests (Smith et al. 2013). I modeled the probability of eggs being viable and hatching (VE) as 0.85, an average from a review of field hatching rates (Landers et al. 1980, Rostal and Jones 2002). To account for males (and remove them) during projections, I assumed that sex ratios of eggs were even within populations and modeled the probability of eggs being female (PF) as 0.5. I modeled hatchling survival (φ^h) from nest emergence until the following survey period as 0.13 (0.04–0.34, 95% CI), given results from a meta-analysis of hatchling survival of gopher tortoises (Perez-Heydrich et al. 2012). I modeled mean values of PB, NS, VE, PF, and φ^h as invariant among populations; I modeled F as a function of MAT at local populations using regression coefficients from my analysis of literature values (Table 1). For each recruitment parameter, I modeled parameters using appropriate statistical distributions (below) and randomly estimated the parameter in each year using stochastic draws using estimates of variance associated with parameter estimates (Table 1).

Maturity age also varies along a latitudinal gradient among gopher tortoise populations (Mushinsky et al. 1994, Meshaka Jr. et al. 2019). I used linear regression to estimate the relationship between MAT and maturity age estimates of females from the literature (Table 1); I then used regression coefficients to simulate mean maturity ages for populations, given the population's geographic location and MAT. Given a predicted maturity age for a population, I then calculated the probability that a juvenile will transition to adulthood, τ, during a given year with:

$$\tau = \frac{1}{Maturity\ age - 1}. \quad (4)$$

This formula assumes that all individuals in the juvenile age class at a population have an equal probability, τ, of transitioning to the adult state (i.e., maturing), and that this probability is the inverse of the age of sexual maturity minus one, to account for one year spent as a hatchling.

Survival rates are difficult to measure for gopher tortoises because individuals are long-lived, challenging to recapture, may become unavailable for resurvey by emigrating away from study populations, or may die (e.g., Folt et al. 2021). When individuals disappear from a study population, mark-recapture analyses are often unable to estimate whether individuals died or emigrated away (Williams et al. 2002). To this end, most mark-recapture studies of gopher tortoise seeking to understand survival have estimated apparent annual survival (φ), which is the probability that individuals survived and stayed within a study area. Studies have found φ to vary between adults and juveniles, with adults having higher survival than juveniles (Tuberville et al. 2014, Howell et al. 2020, Folt et al. 2021). I reviewed the literature for apparent annual survival estimates for gopher tortoises (Appendix 1) and performed a linear regression analysis testing for effects of age and MAT on survival. This heuristic analysis confirmed that adults have greater survival than juveniles but failed to recover an effect of MAT on survival; rather, survival is likely most strongly influenced by habitat quality and management at sites (Howell et al. 2020, Folt et al. 2021, Hunter and Rostal 2021). I modeled adult survival (φ^a) as 0.96 and juvenile survival (φ^j) as 0.75, given demographic rates reported from relatively stable populations in Alabama (Folt et al. 2021). I modeled a density-dependent limit on population growth where for each time-step when density increased above 2 females/ha, I prevented recruitment into the adult age class. This was meant to simulate population conditions where juveniles may elect to disperse away from high-density conditions to other populations with lower density, while also enforcing a limit on maximum population size (i.e., carrying capacity). Field studies have estimated tortoise density to range from 0.02–1.50 individuals/ha among northern populations (Guyer et al. 2012) and from 4.2–24.9 individuals/ha in southern Florida. I selected a threshold of 2 females/ha (i.e., 4 tortoises/ha, assuming even sex ratios) as a limit for density dependence because there is a considerable uncertainty when estimating tortoise density and 2 females/ha was a conservative intermediate estimate of maximum density among populations across the species' range.

Gopher tortoises infrequently move long distances from established core home range areas; such movements can result in permanent emigration and immigration into other populations. I implicitly modeled losses to local populations due to emigration because the estimates of apparent annual survival (φ) account for mortality and permanent emigration away from local populations. Given ongoing emigration, local populations that are spatially proximate to other local populations might receive immigrants that bolster population size. While little quantitative information is available describing the frequency or success of immigration, one study found that 2% of adults emigrated from local populations each year (Ott-Eubanks et al. 2003). Given it is unlikely that all emigrants successfully immigrate into another population, I modeled the number of immigrants into local populations as a product of a randomly-drawn, beta distributed, time-varying annual immigration rate (γ; mean = 0.01) multiplied by the total number of adult tortoises in adjacent populations (i.e., landscape population size, N^m; see below) divided by the number of nearby local populations. I constrained γ during each time step such that its randomly-drawn value could never exceed $1 - \varphi^a$. Demographic parameters were modeled as random variables that accounted for both parametric uncertainty and temporal variability. We provide a full description of how the model treated uncertainty below, after describing simulation scenarios and other aspects of the model.

I sought to estimate population growth and extinction risk of tortoise populations across the species' range. To do so, I initialized the model with estimates of population size from populations on protected, conservation lands (e.g., national forests, state forests, state wildlife management areas), military installations, and some private lands across the species' range during the last ten years. Population estimates were collected by a diverse partnership of cooperating state agencies, private organizations, and academic institutions (see Acknowledgments) using burrow surveys burrow scope surveys, and lLine Transect Distance Sampling (LTDS) surveys. Population estimates do not represent an assessment of all local populations of tortoises that exist in southeastern North America, but rather represent information that was provided by partners through much of the species' range. Most population estimates came from assessments of local populations on lands managed for the conservation of biodiversity or natural resources.

I initialized starting population size using population estimates derived from data collected using burrow surveys, burrow scope surveys, and LTDS surveys. Burrow surveys involved a team of researchers searching a site to count the number of gopher tortoise burrows that were present and detected at a given site. Only burrows that were clearly identifiable as being constructed by a tortoise were counted. Because gopher tortoises often construct and/or use more than one burrow per individual, I used a published estimate of the relationship between the number of tortoises and burrows among six populations (0.4 tortoises/burrow; Guyer et al. 2012) to estimate the number of tortoises at sites from burrow count data. The burrow survey method assumes the tortoise-per-burrow estimate from Guyer et al. (2012) is generalizable to tortoise populations range-wide and that no burrows are missed during surveys; this method likely underestimates total population size, because small burrows are undetected (Gaya 2019). Burrow scope surveys used the same field survey methods as burrow surveys but included an additional step of using a burrow-scope camera to verify the presence of tortoises in burrows. Burrow scope surveys attempted to directly estimate abundance of local populations by counting individuals directly; this method assumes that all tortoise burrows were detected at sites and that only a single tortoise is present in a burrow. Burrow scope surveys also likely underestimate total population size because small burrows are difficult to detect during field surveys.

LTDS surveys are a population estimation method where a research team walks transects through habitat, observes tortoise burrows, searches the burrow for a tortoise with a burrow scope, records the spatial location of occupied tortoise burrows, and measures the perpendicular distance of each occupied burrow to the transect line. Invariably, burrows and individuals are imperfectly sampled, because detection probability of burrows is less than one. However, analysis of the LTDS survey data generates functions estimating the decay of the detection rate with increasing distance from the transect line, and this detection function can then be used to account for undetected burrows and therefore estimate the total number of occupied burrows in the search area (i.e., total population size). I note that because juvenile tortoises have small burrows that are difficult to observe, detection of juveniles during LTDS is lower than adults, and LTDS surveys may underrepresent smaller size classes in the population estimates.

Population estimates from surveys allowed us to parameterize initial population size during simulated projections of populations. However, many population estimates were measured at spatial scales that may not necessarily reflect the target unit for demographic projection models, the population, but rather express the number of individuals that exist across a larger spatial scale (e.g., a property boundary) that may functionally represent more than one local populations. Using spatial survey data associated with population estimates, I sought to operationally identify populations at two spatial scales: local populations and landscape populations. I defined local populations as geographic aggregations of individuals that interact significantly with one another in social contexts that make reproduction significantly greater between individuals within the aggregation than with individuals outside of the aggregation (*sensu* Smallwood 1999). I operationally delimited local populations by identifying aggregations of individuals or burrows where individuals were clustered together within a 600 m buffer to the exclusion of other adjacent individuals or burrows. Studies of gopher tortoise populations in Alabama (Conecuh National Forest; C. Guyer, unpublished data), Georgia (Ft. Stewart

Army Reserve; E. Hunter and D. Rostal, unpublished data), and Florida (Boyd Hill Nature Preserve; J. Goessling and G. Heinrich, unpublished data) have found that >80% of gopher tortoise movements within and among years were less than 500 m. I selected a 600 m distance to buffer populations to encompass typical movement distances and adjacent habitat around surveyed populations that might include tortoises. I assumed that unsuitable habitat for tortoises (i.e., interstates, freeways, and expressways (HPMS 2019); major rivers and lakes (Sciencebase.org); wetlands, and highly urbanized areas as determined by visual inspection with ESRI imagery)e.g., major rivers and lakes, wetlands, paved roads [interstates, freeways, and expressways], urban areas) were unsuitable for tortoise movement or survival and considered those strict barriers when delimiting local populations. Adjacent local populations connected to each other by suitable habitat through which dispersal might occur formed a landscape population. I operationally delimited landscape populations by identifying local populations connected by suitable habitat within a 2.5 km buffer around each local population or any single population that was isolated from other populations by greater than 2.5 km. I received some population estimates from properties that were delimited to have two or more local populations of tortoises; in these instances, I multiplied the population estimate (and confidence limits) by the area of each delimited local population and divided by the total survey area of the original survey. I assumed that population estimates being delimited into two or more local populations through this process would have even population densities and this process spread the population assessment evenly among local populations delimited by in the dataset.

The process of delimiting local populations and landscape populations resulted in a dataset of 626 local populations that formed 244 landscape populations; Florida had the greatest number of local (314) and landscape populations (152), followed by Georgia (151, 63, respectively), Mississippi (94, 7), Alabama (54, 14), Louisiana (7, 5), and South Carolina (6, 4). I used population estimates from local populations to parameterize initial population size of adults (N^a) and juveniles (N^j) during simulated population projections. I assumed a 1:1 sex ratio and a 3:1 adult:juvenile ratio in populations, given observations from stable local populations in Alabama (Folt et al. 2021), and used the ratios to isolate and separate the female population into juvenile and adult components.

Modeling threats

Climate warming – The world is rapidly changing in the 21st century, and numerous anthropogenic factors threaten the stability and persistence of natural ecosystems worldwide. I sought to model how predicted future changes to abiotic and biotic features in southeastern North America may threaten future population growth and viability of gopher tortoises. I met with scientists with expert knowledge in both gopher tortoise population biology and habitat management and identified a series of factors that experts considered to have high likelihood of influencing tortoise demographics in the future (hereafter, threats). Using the list of threats, I reviewed the literature to identify research describing quantitative effects of how threats (or similar mechanisms) influence specific demographic parameters in the conceptual model for tortoises. Here, I describe hypotheses for how four threats (climate warming, sea-level rise, urbanization, and climate-change effects on habitat management) may influence tortoise demographics, and how I used quantitative estimates of the threats from the literature to parameterize and simulate how threats may influence future population growth and viability of gopher tortoises.

Climate change is predicted to drive warming temperatures and seasonal shifts in precipitation across southeastern North America (Dalton and Jones 2010). Of these two effects, warming temperatures may have the greater impact on gopher tortoises, because tortoise demography is known to be sensitive to temperature gradients across the species' range. Specifically, maturity age and F vary along a north-south latitudinal gradient, where warmer, southern populations have faster growth rates, younger maturity ages, and increased fecundity relative to cooler, northern populations (Ashton et al.

2007, Meshaka Jr. et al. 2019). As climate warming increases temperatures in the region, individuals in populations may experience more favorable conditions for growth and reproduction across the species' range. Because no studies have linked tortoise growth or fecundity to interannual or interpopulation variation in precipitation, it seems less likely that climate-driven shifts in precipitation will influence tortoise demography. I modeled how climate warming may influence gopher tortoise demography by using the estimated linear relationships of MAT with maturity age and F (above) to predict how warming temperatures experienced by populations in the future will drive concurrent changes in demography. For each population, I extracted historic estimates of MAT using the 'WorldClim' database (Hijmans 2020) and then simulated step-wise climate-warming effects on MAT each year in the future where warming rates were parameterized by three treatments of climate warming: (1) a 1.0 °C increase in MAT over the next 80 years, (2) a 1.5 °C increase in MAT over the next 80 years, and (3) a 2.0 °C increase in MAT over the next 80 years (IPCC 2013). Each year in the future, I used simulated changes in MAT to calculated mean maturity age and F at sites. This analysis assumes that: (i) all local populations will respond homogeneously to warming temperatures, and (ii) there are no potential climatic ceilings that would limit growth and reproduction.

Habitat management – Through much of its range, gopher tortoises prefer upland habitat with open canopy, sparse midstory, and an understory plant community that provides diverse food sources (Aresco and Guyer 1999, Birkhead et al. 2005, McCoy et al. 2013, Bauder et al. 2014, Nussear and Tuberville 2014). Prescribed fire is the most common management technique to maintain high-quality, open habitat for gopher tortoises (Landers and Speake 1980, Diemer 1986, Yager et al. 2007, Ashton et al. 2008); however, when fire is not present in sufficient intervals or intensity to maintain open habitat on the landscape, apparent survival of gopher tortoises decreases (Hunter and Rostal 2021), potentially to levels that are insufficient for maintaining population viability (Folt et al. 2021). However, wildlife managers tasked with maintaining high-quality upland habitat for gopher tortoises and other fire-dependent upland plant and animal species (Guyer and Bailey 1993) may be challenged because regional climate warming may make habitat management with prescribed fire more difficult to accomplish. Managers require suitable fuel and weather conditions (e.g., relative humidity, temperature, wind speed; i.e., the 'burn window') to facilitate manageable fire behavior that will accomplish intended goals while limiting risk toward human communities. However, climate-change models predict the availability of burn window conditions to shift over future decades, with available conditions for fire management increasing in the winter but decreasing in the spring and summer (Kupfer et al. 2020); summed together, seasonal shifts in the burn window conditions will decrease overall opportunity for management with prescribed fire. If managers become limited in the use of prescribed fire, resulting decreases in habitat quality may drive decreases in gopher tortoise survival (Hunter and Rostal 2021). I modeled how habitat management influences gopher tortoise population growth by modeling habitat management of populations and linking the frequency of management to adult survival. I assumed that a baseline fire-return interval (FRI) of 1–4 years (mean = 2.5 years) maintains high-quality habitat for gopher tortoises (Guyette et al. 2012, Crawford et al. 2020) and then modeled the probability that a population is burned during a given year (burn probability; BP) as the inverse of the fire-return interval:

$$BP_t = \frac{1}{FRI}. \tag{5}$$

For example, an intended two-year FRI for a population would yield a BP of 0.5. Next, using historic baseline data describing average seasonal burn opportunity across southeastern North America (Kupfer et al. 2020), I modeled the number of available burn days (i.e., days within the burn window) in winter (January–February; W), spring (March–May; Sp), and summer (June–July; Su) as a product of the total days per season (59, 92, and 61 days, respectively) and the stochastically-drawn percentage of days historically available for burning (0.766, 0.800, and 0.645, respectively). I modeled four treatments for how the number of days available for prescribed fire may change in the future (Kupfer et al. 2020): (1) prescribed fire use will decrease consistent with climate shifts predicted by RCP4.5 (‘decreased fire’), (2) prescribed fire use will decrease with climate predictions RCP8.5 (‘very decreased fire’), (3) prescribed fire use will increase opposite of the effect predicted by RCP4.5 (‘increased fire’), and (4) prescribed fire use will remain at current levels (‘status quo’). For each treatment, I modeled effects of climate change on the percentage of available burn days over the next 80 years using average effects from across southeastern North America (Kupfer et al. 2020): 0.016 increase in winter, 0.040 decrease in spring, and 0.239 decrease in summer (‘decreased fire’ treatment); 0.030 increase in winter, 0.105 decrease in spring, and 0.436 decrease in summer (‘very decreased fire’ treatment); 0.016 decrease in winter, 0.040 increase in spring, and 0.239 increase in summer (‘increased fire’ treatment), and no effects on burn days (‘status quo’ treatment). The third and fourth scenarios could result if habitat managers can offset effects of climate change by benefiting from methodological advances in fire management or by using alternative methods rather than prescribed fire, such as mechanical or chemical treatments, to achieve similar management goals. We extracted all mean values and predicted effects from the text in Kupfer et al. (2020).

For the first three treatments, I used the predicted effects to model stepwise changes in the percentage of available burn days per season in each year. Assuming that changes in total burn opportunity result in changes in total burn frequency, I modeled BP in each year t as a product of the function of the inverse of FRI and predicted changes in the total number of burn days available due to climate change:

$$BP_t = \frac{1}{FRI} * \frac{W_t + Sp_t + Su_t}{W_1 + Sp_1 + Su_1}. \quad (6)$$

where subscript 1 is the first year of the projection and t is each year ranging from 1 to the last year in the projection. For the fourth treatment, I modeled no effects of climate on the number of available burn days per year; burn probability did not vary by fixed effects through time in an attempt to simulate unvarying management ability in the future. I used estimates of BP to simulate whether a population was burned in each year. Apparent annual survival probability of female gopher tortoises is highest in the first year after a site is burned, but declines by 0.027 each year without fire (Hunter and Rostal 2021). During each year of projections, I simulated adult survival as a stochastic effect of the number of years since last burn (YSB):

$$\varphi_t^a = 0.96 - 0.027 \times YSB. \quad (7)$$

Because Hunter and Rostal (2021) only estimated the effect of year-since-burn on survival of adults up to three years since burn, I did not extrapolate this effect beyond 3 years or to juveniles. This formulation assumes that: (i) changes in the number of days available to burn result in changes in burn frequency (i.e., management is limited by available burn days), the season that a burn is performed does not influence habitat quality (but see: Aresco and Guyer 1999, Yager et al. 2007), and (iii) effects of YSB on survival from Georgia (Hunter and Rostal 2021) is generalizable to all populations of gopher tortoises.

Urbanization – Human development of the landscape (i.e., urbanization) threatens terrestrial wildlife communities in the southeastern United States, including gopher tortoise populations that often rely on upland habitats that are popular sites for urban development or agriculture. While the local tortoise populations I modeled are largely on conservation lands intended for wildlife conservation, urbanization threatens to surround these lands, disrupt habitat connectivity, and decrease metapopulation dynamics that maintain connectivity and gene flow both among local populations and within landscape populations. Additionally, urbanization can disrupt habitat management by decreasing the ability of managers to use prescribed fire. I sought to model effects of urbanization pressure on tortoise populations by linking urbanization predictions from the SLEUTH urbanization model (Clarke 2000) to habitat management of local populations with prescribed fire and with baseline immigration rates (γ) of tortoises across landscape populations. First, I modeled an effect of urbanization on habitat management by making BP a function of each population's distance to the nearest urban area ($dNUA$). Specifically, I assumed that local populations immediately adjacent to urban areas (distance < 0.1 km) are unable to manage with prescribed fire and forced BP to 0, management is uninfluenced for populations far from urban areas (> 3.2 km; no effect on BP), and management of populations between 0.1–3.2 km from an urban area experience a negative effect on fire management with BP declining as a linear function of the population's proximity to the urban area (i.e., populations closer to urban areas experience less prescribed fire). For populations between 0.1–3.2 km of an urbanized area, I added an additional term to Equation 6 to estimate BP as a consequence of $dNUA$ at time t:

$$BP_t = \frac{1}{FRI} * \frac{W_t + Sp_t + Su_t}{W_1 + Sp_1 + Su_1} * \frac{dNUA_t}{3.2}. \tag{8}$$

To model effects on urbanization on migration dynamics among local populations within landscape populations, I first estimated the total area (A; ha) and urbanized area (UA; ha) within landscape populations in year 2020 using the SLEUTH model. Assuming that tortoises cannot survive and/or move through urbanized areas but can survive and move in unurbanized areas, I estimated the initial proportion of suitable dispersal habitat (PDH_i) for tortoise dispersal in landscape populations at the start of population projections as:

$$PDH_i = \frac{A_i - UA_i}{A_i}. \tag{9}$$

I next estimated future urbanization and its effect on dispersal habitat for tortoises using the SLEUTH model predictions for 40, 60, and 80 years in the future. I estimated predicted urbanized area in the future (UA_f; ha). Similar to Equation 9, I estimated the future proportion of suitable dispersal habitat (PDH_f) around populations in the future:

$$PDH_f = \frac{A_i - UA_f}{A_i}. \quad (10)$$

I calculated the predicted change in proportion of dispersal habitat (ΔPDH) due to future urbanization for landscape populations by taking the difference between PDH_f and PDH_i. For each year $t \geq 3$ during population projections, I modeled the number of adult immigrants (N_t^i) into local populations in each year as a function of the number of individuals in the landscape population available for immigration to the local population during the previous year (N_{t-1}^{mp}), the total number of local populations in the landscape population (N^{lp}), γ_t, PDH_i, ΔPDH, and the time-step in the future:

$$N_t^i = \frac{N_{t-1}^{mp}}{N^{lp} - 1} * \gamma_t * \left[PDH_i + \Delta PDH * \frac{t}{total}\right], \quad (11)$$

where t is the year in the population projection, ranging from t_i = 1 to the total projection interval ($total$). I estimated N^{mp} at t = 1 by summing the starting population size of all local populations in the landscape population and subtracting the abundance of the focal population, because individuals from the focal population would be unavailable for immigration into their own population. I assumed that population growth of the landscape population term would change through time similarly to that of the local population being modeled in any instance; therefore, I modeled changes in N^{mp} through time as a function of changes in abundance of the local adult population size during the previous time step, $\frac{N_t^a}{N_{t-1}^a}$, during year 3 and beyond. I next estimated the distance of each local population to the nearest urban area currently and in the future using the SLEUTH model. I measured distance to urban area from the geometric center of local populations to the edge of the nearest neighbor urban area. I estimated predicted effects of urbanization on local and landscape populations by modeling three treatments from the SLEUTH urbanization model that corresponded to different probability thresholds of urbanization: (1) a low urbanization treatment where future urbanization was limited to cells with urbanization probability ≥0.95, (2) a moderate urbanization treatment with urbanization predicted by probability ≥0.50, and (3) a high urbanization treatment with urbanization probability ≥0.20. I assumed that: (i) immigration was limited to adults and that no juveniles successfully migrate among populations, and (ii) immigrants cannot survive or move through urbanized areas (e.g., due to road mortality) but survive perfectly while moving through unurbanized areas.

Sea-level rise – Warming temperatures across Earth are causing the polar ice caps to shrink, release freshwater into the oceans, and drive substantial increases in oceanic levels worldwide (hereafter, sea-level rise) (IPCC 2013). In southeastern North America, sea-level rise is predicted to influence low-lying coastal habitats by causing floods, inundation, and shifts in land-cover types (Marcy et al. 2011). Because gopher tortoises are a terrestrial species and not suited to wetland habitats, sea-level rise may negatively affect gopher tortoise populations in low-lying coastal areas, such as coastal sand-dune environments (Blonder et al. 2020). Projected sea-level rise scenarios provide a range of coastal inundation scenarios that vary in severity. I modeled effects of sea-level rise on tortoises using three scenarios of sea-level rise predicted by NOAA, the 'intermediate-high', 'high', and 'extreme' scenarios, which correspond to predictions from two of the most likely global emission scenarios, RCP6.0 and RCP8.5 (IPCC 2013, NOAA 2020). Local predictions for the two scenarios are available from USGS sea-level monitoring stations across the southeastern United States, providing estimates of sea-level rise for stations at decadal time steps in the future to year 2100. I modeled three treatments of sea-level rise using predictions from NOAA: (1) the 'intermediate-high' scenario derived from RCP6.0, which predicts ca. 1.83 m of sea-level rise over the next 80 years, (2) the 'high' scenario which predicts 2.55 m of sea-level rise over the next 80 years, and (3) the 'extreme' scenario derived from RCP8.5, which predicts 3.16 m of sea-level rise over the next 80 years (NOAA 2020). I modeled sea-level rise effects on populations in two ways. First, assuming that gopher tortoise populations cannot persist when oceanic levels encroach too close upon their habitat, I simulated decreasing elevation of tortoise populations due to sea-level rise. I extracted historic estimates of elevation above sea level (asl; in m) using the centroid geographic coordinates of each local population using the 'WorldClim' database (Hijmans 2020). Given the total predicted sea-level rise of each treatment over the next 80 years, I simulated incremental sea-level rise at each population in each year in the future and subtracted this incremental oceanic rise from the site's elevation through time. When the site elevation of populations decreased to less than 2 m asl, I considered the populations functionally extirpated and forced the population size vectors, N^j and N^a, to zero. Second, I assumed that habitat inundated by sea-level rise adjacent to local populations would decrease connectivity and dispersal dynamics of individuals among populations within landscape populations. I used spatial predictions from NOAA to estimate future inundation area due to sea-level rise for each landscape population, and then I modeled γ to decline as a function of decreasing habitat available for dispersal at the landscape scale. Assuming that tortoises cannot survive and/or move through inundated areas but can survive and move in inundated areas, I extended Equation (11) to subtract the proportion of area lost to sea-level rise (SLR) from the proportion of dispersal habitat (PDH_i) in each year:

$$N_t^i = \frac{N_{t-1}^{mp}}{N^{lp} - 1} * \gamma_t * \left[PDH_i + \Delta PDH * \frac{t}{total} - SLR * \frac{t}{total}\right], \qquad (12)$$

The analysis of sea-level rise effects assumes that: (i) sea-level rise throughout southeastern North America will be homogeneous and characterized by NOAA predictions derived from data from Ft. Myers, Florida, (ii) populations less than 2 m asl are unable to persist, and (iii) populations are unable to migrate away from sites because coastal areas are often heavily developed and there is no guarantee that adjacent properties would be available for entire populations to migrate.

Population projection structure

I conceptualized and mathematically articulated different scenarios for how four factors (climate warming [3 treatments]; habitat management [4 treatments]; urbanization [3 treatments]; sea-level rise [3 treatments]) might influence future population growth of gopher tortoises. However, factors of global change are not independent; rather, most factors that I considered depend on other factors (e.g., sea-level rise is a consequence of climate warming). To understand how tortoise populations will respond to scenarios with multiple concurrent factors, I created a set of six scenarios with varying levels of threat magnitude and combination (Table 2). Specifically, I created three models with different levels of stressors (low stressors, medium stressor, and high stressors) that experienced habitat management consistent with contemporary target management goals. I then used the medium stressor values and built three additional models that varied in habitat management treatments, ranging from 'more management' conditions to worsening ('less management') and much worse ('much less management') conditions (Table 2). The three stressor models were meant to estimate the effects of uncertainty in unmanageable future stressors (climate warming, sea-level rise, urbanization), while the management models were meant to estimate the effects of uncertainty in actionable management practices (e.g., habitat management).

To encompass uncertainty in future states of risk factors and scenarios, I projected population growth for each local population under each of the six model scenarios using a stochastic projection uncertainty structure that accounted for scenario uncertainty, geographic variation among populations, parametric uncertainty, and temporal stochasticity (Figure 2). For each scenario, I parameterized certain stochastic variables specific to the scenario and then projected gopher tortoise populations across the species' range into the future. For each population, I specified mean demographic rates specific to the MAT of the population's geographic location (Table 1) and then simulated future population trajectories with 100 replicates each projected 80 years into the future. During simulations, I applied an uncertainty structure that accounted for both parametric uncertainty (among replicates) and temporal stochasticity (within replicates; McGowan et al. 2011). For each replicate, I drew mean values (and an associated error term) to model parametric uncertainty; I then modeled temporal stochasticity by drawing stochastically from the mean (given its error) during each time step within the replicate. I simulated parameters by drawing replicate-level means stochastically from either beta distributions (e.g., probabilities) with shape parameters calculated from mean and standard deviation estimates (Morris and Doak 2002), log-normal distributions (e.g., counts), or binomial distributions (e.g., probabilities simulating discrete events). I projected populations 80 years into the future because this interval overlapped with the maximum duration of future predictions of the climate, urbanization, and sea-level rise models that I used and the interval also encompassed ca. two generations of gopher tortoises (B. Folt, pers. obs.). I felt uncomfortable making predictions past 80 years into the future because of uncertainty among models and parameters.

Little to no data exist describing gopher tortoise immigration rates, γ, in wild populations. Given uncertainty associated with this parameter, I sought to include a sensitivity analysis to understand the effects of γ on our results. I crafted three additional scenarios: a ‘no immigration’ scenario with $\gamma = 0$, a ‘high immigration’ scenario with $\gamma = 0.02$, and a ‘very high immigration’ scenario with $\gamma = 0.4$. I simulated these scenarios with stressor and habitat management values from the ‘medium stressors’ scenario with a projection interval of 80 years, and I compared the resulting immigration scenarios to the ‘medium stressors’ scenario results that were simulated with $\gamma = 0.01$.

To understand redundancy, resiliency, and representation of the gopher tortoise in the future, I used the population projections to estimate future changes in tortoise populations under each of the six scenarios (Table 2). I assessed resiliency by measuring the predicted population rate of change in the total number of individuals, local populations, and landscape populations in the future relative to current conditions. I summarized population trends by estimating population growth rate (λ), a metric that describes change in population size as increasing ($\lambda > 1.00$), stable ($\lambda \sim 1.00$), or decreasing ($\lambda <$

1.00) over a projection interval; I measured population growth rate of total population size (N^{total}), the number of local populations (N^{p}), and the number of landscape populations (N^{m}) across the species' range during the projection interval. I report changes in population size (total, local, or landscape populations) with λ values or by expressing λ values as percent increases or decreases from initial current population size during the projection interval (e.g., a λ = 1.25 is a 25% increase; λ = 0.66 is a 34% reduction), and I report ranges of λ values among the six scenarios. I assessed the resiliency of future populations to changing environments by estimating extinction risk. Within populations, I evaluated extinction risk with a quasi-extinction probability (P_e), where I estimated P_e by the proportion of simulations resulting in < 3 females alive at the end of the simulation period. I chose < 3 females as a threshold to approximate functional extinction because populations with fewer than three females are extremely like to be inbred (Chesser et al. 1980, Frankham et al. 2011). For each population, I estimated persistence probability (P_p) as 1–P_e, and then I used P_p to categorize populations as 'extremely likely to persist' (P_p ≥ 0.95), 'very likely to persist' (0.80 ≤ P_p < 0.95), 'more likely than not to persist' (0.50 ≤ P_p < 0.80), and 'unlikely to persist' (i.e., extirpated; P_p < 0.50). I then took a random draw from a Bernoulli distribution with *p* = P_p for each population to simulate the likely number of populations predicted to persist at the end of the projection; I summarized this simulation with the median (95% CI) of 1000 replications. For each landscape population, I estimated resiliency by selecting the constituent focal population with the greatest persistence probability and used that value to categorize landscape population persistence and simulated landscape population survival by drawing from a Bernoulli distribution in the future. I evaluated how representation is predicted to change in the future by examining how population growth of total population size (number of individuals), number of populations, and number of landscape populations will vary by the five analysis units across the species' range. For each scenario, I summarized the results among all populations across the species' range, but also by analysis units (five units) and state (six states: Alabama, Florida, Georgia, Louisiana, Mississippi, South Carolina).

My demographic model for gopher tortoises included biotic, abiotic, and anthropogenic effects on demography. To understand the relative importance of how each hypothesized factor contributed to population persistence among the 626 populations modeled, I used model outputs from each scenario projected 80 years into the future and regressed P_p of populations by hypothesized fixed effects. Specifically, I built a generalized linear model where I evaluated how biotic (initial population size, number of populations per landscape population), abiotic (population area, elevation, latitude), and anthropogenic (sea-level rise, urbanization, management level) factors influenced population persistence; I fit the model with a binomial distribution to accommodate a response variable with values ranging between 0–1. To simplify the model, I treated management as a continuous variable with four values: more management (1), status quo (0), less management (-1), and much less management (-2). I evaluated statistical significance of mixed-effects model parameters using α = 0.05 and I reported the size of statistically significant effects using odds ratios.

I performed all analyses in the statistical program R (R Core Team 2018).

Results

Linear regression analysis of three demographic parameters reviewed in the literature (fecundity, maturity age, and apparent annual survival probability) found that fecundity and maturity age vary significantly by MAT across the species' range (Figure 3). For each 1 °C increase in MAT, I found that maturity age decreased by 1.41 years (0.18–2.62, 95% CI), which was a statistically significant effect ($P = 0.029$). For each 1 °C increase in MAT, I found that fecundity increased by 0.48 eggs per clutch (0.24–0.72, 95% CI), which was statistically significant ($P < 0.001$). I used linear functions describing geographic variation in demographic rates to randomly simulated mean fecundity and age of maturity for each population during simulations, given the patterns of MAT at each population's location (Table 1).

I simulated population growth of an estimated 70,600 individual (female) gopher tortoises comprising 626 local populations and 244 landscape populations in the current conditions. Population projections under six scenarios of future change during 40, 60, and 80-year projection intervals predicted declines in the number of gopher tortoise individuals, local populations, and landscape populations of gopher tortoises (Table 3). Relative to current levels of total population size, predictions for total population size suggested declines by 2060 (λ = 0.65–0.67 among scenarios; i.e., 33–35% declines), 2080 (λ = 0.66–0.70 among scenarios; 30–34% declines), and 2100 (λ = 0.67–0.72 among scenarios; i.e., 28–33% declines). The six scenarios varied little in their effects on the total number of individuals, local populations, and landscape populations; but scenario effects become more magnified in each successive timestep. However, 95% confidence intervals (CI) for predictions of λ all overlapped with 1.00 in all scenarios and timesteps, indicating significant uncertainty in predictions for each scenario at each projection interval. Among the simulated populations, the number of local populations and landscape populations also were predicted to decline in each projection interval (Table 3). Declines in local populations and landscape populations were modest at the 40-year timestep (47–48% and 25–27% declines among scenarios, respectively) but were exacerbated at the 60-year (60–61% and 41–43% declines, respectively) and 80-year (68–70% and 53–57% declines, respectively) timesteps. Scenarios did not vary strongly in their effect on the predicted number of persisting local populations and landscape populations within each projection interval.

Categorization of populations by persistence probability revealed finer-scale variation of how scenarios varying in magnitude of stressors and management influenced persistence probability of populations (Table 4). Among the three projection intervals, the 'low stressors' scenario tended to predict higher percentages of Extremely Likely Extant populations and lower percentages of Unlikely

Extant (i.e., Extirpated) populations relative to the 'medium stressors' and 'high stressors' scenarios. Similarly, the 'more management' scenario tended to predict higher percentages of Extremely Likely Extant populations and lower percentages of Unlikely Extant (i.e., Extirpated) populations relative to the 'less management' and 'much less management' scenarios. Figure 5 illustrates persistence probabilities among populations and landscape populations predicted by the 'less management' scenario.

Changes in the number of individuals, local populations, and landscape populations varied by analysis unit and state (Appendix 2, Appendix 3). Among the five analysis units projected 80 years into the future, units 1, 3, and 5 were predicted to decline overall, with mean λ values ranging between 0.60–0.73, 0.47–0.49, and 0.52–0.58 among scenarios for each unit, respectively (i.e., 27–40%, 51–53%, and 42–48% declines, respectively); however, 95% CI of λ overlapped with 1.00 in all scenarios for each of the three units, indicating uncertainty in future abundance. Unit 4 was predicted to experience more modest declines in total abundance (λ = 0.86–0.98; i.e., 2–14% decrease), but 95% CI of λ also overlapped 1.00, indicating uncertainty in predicted future population growth. Alternatively, total abundance in Unit 2 was predicted to increase substantially (λ = 2.37–2.53; i.e., 137–153% increase); 95% CI of λ did not overlap 1.00, indicating a significant predicted increase in population size. Scenarios predicted substantial declines in the number of local populations among all units. Predicted reductions in populations were greatest in Unit 1 (λ = 0.22–0.23), Unit 2 (λ = 0.23–0.26), and Unit 5 (λ = 0.28–0.30), and slightly weaker (but still strong) in Unit 3 (λ = 0.37–0.39) and Unit 4 (λ = 0.39–0.41). The number of landscape populations was predicted to decline among all scenarios in each analysis unit, with the strongest loss of landscape populations in Unit 5 (λ = 0.36–0.41 among scenarios) and the weakest loss of landscape populations in Unit 3 (λ = 0.48–0.53 among scenarios).

Among the six states, total population size was predicted to decline in four states (Florida, Georgia, Mississippi, South Carolina) and increase in two (Alabama, Louisiana; Appendix 3; e.g., Figure 4). The number of local populations and landscape populations were predicted to decline among all scenarios for all states. In South Carolina, reductions in the number of individuals and populations were predicted to be particularly strong, where scenarios predicted substantial declines in individuals (λ = 0.03 among all scenarios; i.e., 97% declines), local populations (λ = 0.17 among all scenarios; i.e., 83% declines), and landscape populations (median λ = 0 among all scenarios; i.e., no remaining landscape populations). Similarly, Louisiana was predicted to lose all local populations and landscape populations except for one by 2100; however, growth of a single surviving population/landscape population caused the total population size to increase in the state during the projections. Similarly, Alabama was predicted to experience an 85–87% reduction in local populations (λ = 0.13–0.15 among scenarios), but predicted increases in the number of individuals in surviving populations caused predictions for the number of individuals in the state to increase substantially over the next 80 years. Mississippi was projected to lose 40–54% of total population size and 77–78% of local populations, but while maintaining 71% of its landscape populations. Predicted changes in the number of populations for Florida and Georgia were similar, with the number of local populations declining 66–68% and 61–62% among scenarios and landscape populations declining 52–55% and 52–57% among scenarios for each respective state (Appendix 3).

I found that model predictions were highly sensitive to input values for immigration rate, γ (Table 5). The population declines predicted by the 'medium stressors' scenario were exacerbated substantially when simulated with γ = 0; conversely, elevated values for γ produced population projections that substantially increased the total population size (overall λ > 1.00) and decreased declines in populations and landscape populations.

Regression analysis of how abiotic, biotic, and anthropogenic factors influenced persistence probability of local populations found support for significant effects of initial population size, number of populations per landscape population, area, elevation, latitude, sea-level rise, urbanization, and prescribed fire on persistence probability. With each 50-female increase in starting population size, populations were 1.029 (1.027–1.03; 95% CI) times as likely to persist, which was statistically significant (P < 0.0001). With each 1 local population increase in the landscape population, local populations were 0.987 (0.986–0.987; 95% CI) times as likely to persist (i.e., 1.013 times less likely), which was statistically significant (P < 0.0001). For each 500-ha increase in area, populations were 1.002 (1.001–1.003; 95% CI) times as likely to persist, which was statistically significant (P = 0.044). With each 10-m increase in elevation, populations were 0.901 (0.899–0.904; 95% CI) times as likely to persist (i.e., 1.109 times less likely), which was statistically significant (P < 0.0001). For each 0.5 degree increase in latitude, populations were 1.122 (1.119–1.125; 95% CI) times as likely to persist, which was statistically significant (P < 0.0001). With each 0.01 proportional loss in landscape area due to sea-level rise, local populations were 0.57 (1.67–1.82; 95% CI) times as likely to persist (i.e., 1.747 times less likely), which was statistically significant (P < 0.0001). With each 0.1 proportional loss in landscape area due to urbanization, local populations were 0.96 (0.955–0.965; 95% CI) times as likely to persist (i.e., 1.042 times less likely), which was statistically significant (P < 0.0001). With each categorical increase in fire management, local populations were 1.021 (1.014–1.029; 95% CI) times as likely to persist, which was statistically significant (P < 0.0001).

Discussion

I synthesized a large literature describing gopher tortoise life history and built a predictive population model that accounted for geographic variation in demography to estimate growth of populations across the species range. I then identified a series of stressors (climate warming, sea-level rise, urbanization, and habitat management) that have been hypothesized to have current and future negative effects on gopher tortoise populations; then, using estimates of stressor effects on tortoise demography and/or reasonable assumptions, I linked stressors to specific demographic rates and then used published model predictions of stressor prevalence in the future (Clarke 2000, IPCC 2013, Kupfer et al. 2020, NOAA 2020) to simulate how gopher tortoise populations will respond to plausible future conditions across the species range.

Using this integrative modeling framework, I simulated future population size, redundancy, and resiliency of gopher tortoises under six scenarios varying in the magnitude of threats at intervals of 40, 60, and 80 years in the future. Simulated growth of ca. 70,600 females from 626 local populations and 244 landscape populations predicted future declines in the number of individuals, local populations, and landscape populations among all scenarios and projection intervals. Scenarios did not vary strongly in their effect on λ of individuals, populations, and landscape populations; no single stressor scenario or management scenario was sufficient to prevent population declines, and 95% confidence intervals of predictions overlapped significantly among all scenarios, indicating statistical insignificance of scenario effects.

While scenarios did not have strong effects on overall trends in abundance and population redundancy, categorization of populations by persistence probabilities suggested that the 'increased management' and 'low stressors' scenarios performed better at increasing population persistence and reducing extirpation than other management and stressor scenarios. Increased habitat management promoted greater population persistence relative to decreased management scenarios because of positive effects of management on survival in local populations, which increases population growth and persistence probability of populations. While populations may experience reproductive benefits from warming temperatures in the future (i.e., positive effects with increased stressors), the 'low stressors' scenarios outperformed the elevated stressor scenarios because the negative effects of urbanization and sea-level rise on survival and immigration were stronger than the positive effects of warming on reproduction.

The regression analysis identified significant effects of initial abundance, number of populations per landscape population, area, elevation, urbanization, sea-level rise, and habitat management to influence persistence probabilities of local populations. For groups and agencies seeking alternatives to buffer tortoise populations from anthropogenic effects, these factors represent opportunities for management and/or conservation.

Previous demographic models for gopher tortoises have largely ignored including immigration parameters (e.g., Tuberville et al. 2009, Folt et al. 2021) and modeled tortoise demography as closed to immigration, perhaps due to the paucity of field estimates of immigration in wild populations. These models often predicted population declines, even though recent evidence was more consistent with population stability (Folt et al. 2021, Goessling et al. 2021). This discrepancy suggests a disconnect between demographic projections that are largely influenced by apparent survival projections and actual trends occurring in populations, a discrepancy that may be resolved by incorporating immigration during projection analyses. To this end, I incorporated an immigration parameter, γ, for local populations and found predictions were highly sensitive to variation in γ. This was supported by the fact that persistence probabilities were sensitive to threats that influenced immigration rates and two scenarios of 'no immigration' and 'high immigration' produced results that strongly deviated from results of the stressor and management scenarios. Together, these lines of evidence suggest that immigration is an important parameter in tortoise demography that may deserve future attention when studying tortoises in the field and building models of tortoise demography in the laboratory.

While the number of individuals, populations, and landscape populations were all expected to decline across each projection interval, overall projections suggest that extinction risk for the gopher tortoise is low in the future. Of the populations modeled here, mean predictions among scenarios for 80 years in the future suggested the presence of 47,202–50846 individuals (females) among 188–198 local populations within 106–114 landscape populations. The persistence of relatively large numbers of individuals and populations suggests resiliency of the species in the face of global change and also redundancy to buffer from future catastrophic events. The spatial distribution of populations predicted to persist in the future are distributed somewhat evenly among analysis units (e.g., Figure 5), which suggests the persistence of representation in the future as well. However, we note that the number of local populations in genetic analysis Unit 1 was the predicted decline by 27–40% among scenarios; this analysis unit includes the populations in Louisiana, Mississippi, and southwest Alabama that are currently protected federally as 'Threatened' under the ESA. The large declines in number of populations occurred, in part, because many local populations (N = 174) delimited in our surveys had very few individuals to start with in the current conditions. Assuming a 3:1 adult to juvenile ratio and an even sex ratio, local populations with less than 8 individuals were functionally extirpated at the start of projections, given our quasi-extinction probability (< 3 adult females). Thus, many local populations were doomed for extirpation from the start, because of insufficiently large population size in the current conditions. This also likely explains the negative effect of landscape population size on population persistence we observed in our regression analysis; a few extremely large landscape populations (e.g., six landscape populations had 13–50 local populations) were dominated by local populations with <8 individuals, thus driving down mean persistence probability in large landscape populations.

I sought to build a population modeling framework that accounts for important elements of population viability analyses, including clear objectives, detailed demographic data and knowledge of life history, temporal stochasticity, parametric uncertainty, density dependence, relevant extrinsic factors (i.e., threats), and sensitivity analysis, to name a few (Chaudhary and Oli 2020). However, like all models, the framework has limitations and opportunities for improvement. The model was sensitive to immigration, a parameterization that we derived largely from a single estimate of emigration (Ott-Eubanks et al. 2003). I modeled demography as an effect of predicted values of climate warming and fire management at broad spatial scales to support an impending listing decision for the species. Future models could evaluate regional variation in effects of warming and fire management for more realistic predictions of threat effects at more detailed spatial scales. The model also focused on simulating the fate of known populations and did not estimate the formation of new populations or project the abundance of existing populations not included in the dataset. Therefore, predictions for of local and landscape populations were constrained by an upper limit of 1 and therefore were unable to exceed this limit. My analysis provides an objective assessment of how stressors and management actions will influence future population growth, overall extinction risk of both populations and the species across landscape genetic group and by state, and how uncertainty in important input parameters (e.g., immigration) influences predictions.

Acknowledgments

Funding for this analysis was provided by a grant from the U.S. Fish and Wildlife Service (sub-contacted through Texas A&M University). I thank the following experts who participated in a workshop to help develop the model: J. Diemer-Berish, D. Burr, C. Guyer, S. Hermann, H. Mushinksy, B. Nuse, B. Rothermel, D. Rostal, and L.L. Smith. I thank all the wildlife researchers and agencies who provided data or information about gopher tortoise populations, particularly the following groups: J. Berish-Diemer (Florida FWC), J. Goessling (Eckerd College), T. Radzio (Georgia Sea Turtle Center), Alabama Department of Conservation and Natural Resources (E. Shelton-Nix), Alabama Forestry Commission (R. Metzler), Florida Fish and Wildlife Conservation Commission (D. Burr, M. Dziadzio), Georgia Department of Natural Resources (M. Elliott), Louisiana Department of Wildlife and Fisheries (K. Lejeune), The Jones Center at Ichauway (L. Smith), and Auburn University (S. Hermann). I thank F. Erickson, A. Goode, K. Gregory, C. McGowan, C. Guyer, B. Rothermel, and B. Nuse for comments that improved the document.

REFERENCES

Aresco, M. J., and C. Guyer. 1999. Burrow abandonment by gopher tortoises in slash pine plantations of the Conecuh National Forest. Journal of Wildlife Management 63:26–35.

Ashton, K. G., R. L. Burke, and J. N. Layne. 2007. Geographic Variation in Body and Clutch Size of Gopher Tortoises. Copeia 2007:355–363.

Ashton, K. G., B. M. Engelhardt, and B. S. Branciforte. 2008. Gopher Tortoise (*Gopherus polyphemus*) abundance and distribution after prescribed fire reintroduction to Florida scrub and sandhill at Archbold Biological Station. Journal of Herpetology 42:523–529.

Bauder, J. M., C. Castellano, J. B. Jensen, D. J. Stevenson, and C. L. Jenkins. 2014. Comparison of movements, body weight, and habitat selection between translocated and resident gopher tortoises. Journal of Wildlife Management 78:1444–1455.Birkhead, R. D., C. Guyer, S. M. Hermann, and W. K. Michener. 2005. Patterns of Folivory and Seed Ingestion by Gopher Tortoises (*Gopherus polyphemus*) in a Southeastern Pine Savanna. American Midland Naturalist 154:143–151.

Blonder, B. I., K. J. Liedtke, and S. E. Stephens. 2020. Changes in Coastal Gopher Tortoise (Gopherus polyphemus) Burrow Characteristics and Density Following Hurricane Events in Northeast Florida, USA: Implications for Conservation Planning. Global Ecology and Conservation e01437.

Chesser, R. K., M. H. Smith, and I. L. Brisbin. 1980. Management and maintenance of genetic variability in endangered species. International Zoo Yearbook 20:146–154.

Clarke, K. 2000. SLEUTH: Land Cover transition Model, version 3.0.

Crawford, B. A., J. C. Maerz, and C. T. Moore. 2020. Expert-informed habitat suitability analysis of at-riskspecies assessment and conservation planning. Journal of Fish and Wildlife Management

11:130–150.

Dalton, M., and S. Jones. 2010. Southeast Regional Assessment Project for the National Climate Change and Wildlife Science Center. U.S. Geological Survey: U.S. Geological Survey Open-File Report.

Diemer, J. E. 1986. The Ecology and Management of the Gopher Tortoise in the Southeastern United States. Herpetologica 42:125–133.

Folt, B., J. M. Goessling, A. Tucker, C. Guyer, S. Hermann, and E. Shelton-Nix. 2021. Contrasting Patterns of Demography and Population Viability among Gopher Tortoise Populations in Alabama. Journal of Wildlife Management. <https://doi.org/10.1002/jwmg.21996>.

Frankham, R., J. D. Ballou, M. D. B. Eldridge, R. C. Lacy, K. Ralls, M. R. Dudash, and C. B. Fenster. 2011. Predicting the Probability of Outbreeding Depression. Conservation Biology 25:465–475.

Gaillard, D., J. R. Ennen, B. R. Kreiser, C. P. Qualls, S. C. Sweat, R. Birkhead, T. D. Tuberville, M. Aresco, E. D. McCoy, H. R. Mushinsky, and T. W. Hentges. 2017. Range-wide and regional patterns of population structure and genetic diversity in the gopher tortoise. Journal of Fish and Wildlife Management 8:497–512.

Gaya, H. E. 2019. Enhancing line-transect distance sampling to increase detectability of gopher tortoises (Gopherus polyphemus) in population surveys. University of Georgia.

Goessling, J. M., J. Stober, S. Gyengo, S. M. Hermann, T. D. Tuberville, and C. Guyer. 2021. Implications from monitoring gopher tortoises at two spatial scales. Journal of Wildlife Management in press.

Guyer, C., and M. A. Bailey. 1993. Amphibians and reptiles of longleaf pine communities. Proceedings fo the Tall Timbers Fire Ecology Conference 18.

Guyer, C., V. M. Johnson, and S. M. Hermann. 2012. Effects of population density on patterns of movement and behavior of gopher tortoises (*Gopherus polyphemus*). Herpetological Monographs 26:122–134.

Guyette, R. P., M. C. Stambaugh, D. C. Dey, and R. M. Muzika. 2012. Predicting Fire Frequency with Chemistry and Climate. Ecosystems 15:322–335.

Hijmans, R. J. 2020. raster: Geographic Data Analysis and Modeling. R package version 3.3-13. <https://cran.r-project.org/package=raster>.

Howell, H. J., B. B. Rothermel, K. N. White, and C. A. Searcy. 2020. Gopher tortoise demographic responses to a novel disturbance regime. Journal of Wildlife Management 84:56–65.

Hunter, E. A., and D. C. Rostal. 2021. Fire Management Effects on Long-Term Gopher Tortoise Population Dynamics. Journal of Wildlife Management.

IPCC. 2013. Summary for Policymakers. T. Stocker, D. Qin, G. K. Pattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, editors. Climate Change 2013: The Physical Science Basis. Conribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Kupfer, J. A., A. J. Terando, J. K. H. D, and C. T. D. 2020. Climate change projected to reduce prescribed burning opportunities in the south-eastern United States. International Journal of Wildland Fire 29:764–778.

Landers, J. L., J. A. Garner, and W. A. McRae. 1980. Reproduction of gopher tortoises (*Gopherus polyphemus*) in southwestern Georgia. Herpetologica 36:353–361.

Landers, L. J., and D. W. Speake. 1980. Management needs of sandhill reptiles in southern Georgia. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife

Agencies 34:515–529.

Lefkovitch, L. 1965. The Study of Population Growth in Organisms Grouped by Stages. Biometrics1 21:1–18.

Lunney, D., S. Gresser, L. E. O'neill, A. Matthews, and J. Rhodes. 2007. The impact of fire and dogs on Koalas at Port Stephens, New South Wales, using population viability analysis. Pacific Conservation Biology 13:189–201.

Marcy, D., W. Brooks, K. Draganov, and B. Hadley. 2011. Flooding Impacts. Pages 474–490 *in* L. A. Wallendorf, C. Jones, L. Ewing, and B. Battalio, editors. Proceedings of the 2011 Solutions to Coastal Disasters Conference. American Society of Civil Engineers, Reston, VA.

McCoy, E. D., K. A. Basiotis, K. M. Connor, and H. R. Mushinsky. 2013. Habitat selection increases the isolating effect of habitat fragmentation on the gopher tortoise. Behavioral Ecology and Sociobiology 67:815–821.

McGowan, C. P., M. C. Runge, and M. A. Larson. 2011. Incorporating parametric uncertainty into population viability analysis models. Biological Conservation 144:1400–1408.

Meshaka Jr., W. E., J. N. Layne, and K. G. Rice. 2019. The effects of geography, habitat, and humans on the ecology and demography of the gopher tortoise in the southern Lake Wales Ridge region of Florida. Herpetological Journal 29:95–114.

Miller, P. S. 2001. Preliminary population viability assessment for the gopher tortoise (*Gopherus polyphemus*) in Florida. Apple Valley, Minnesota, USA. <https://www.cpsg.org/sites/cbsg.org/files/documents/Gopher Tortoise PVA.pdf>. Accessed 24 Jun 2020.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, Massachusetts.

Mushinsky, H. R., D. S. Wilson, and E. D. McCoy. 1994. Growth and Sexual Dimorphism of *Gopherus polyphemus* in Central Florida. Herpetologica 50:119–128.

NOAA. 2020. Sea Level Rise Viewer. <https://coast.noaa.gov/slr/#>. Accessed 5 Jan 2021.

Noon, B. R., and J. Sauer. 1992. Population models for passerine birds: structure, parameterization, and analysis. Pages 441–464 *in* D. R. McCulloug and R. H. Barrett, editors. Wildlife 2001: Populations. Elsevier Applied Science, New York, New York, USA.

Nussear, K. E., and T. D. Tuberville. 2014. Habitat characteristics of North American tortoises. Pages 77–84 *in* D. Rostal, E. McCoy, and H. Mushinsky, editors. Biology and conservation of North American tortoises. Johns Hopkins University Press, Baltimore, Maryland.

Ott-Eubanks, J., W. K. Michener, and C. Guyer. 2003. Patterns of movement and burrow use in a population of gopher tortoises (*Gopherus polyphemus*). Herpetologica 59:311–321.

Perez-Heydrich, C., K. Jackson, L. D. Wendland, and M. B. Brown. 2012. Gopher tortoise hatchling survival: field study and meta-analysis. Herpetologica 68:334–344.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org/>.

Ralls, K., S. R. Beissinger, and J. F. Cochrane. 2002. Guidelines for using population viability analysis in endangered-species management. Pages 521–550 *in* S. R. Beissinger and D. McCullough, editors. Population viability analysis. The University of Chicago Press, Chicago, IL.

Rostal, D. C., and D. N. Jones. 2002. Population biology of the gopher tortoise (*Gopherus polyphemus*) in southeast Georgia. Chelonian Conservation and Biology 4:479–487.

Smallwood, K. S. 1999. Scale domains of abundance amongst species of mammalian Carnivora. Environmental Conservation 26:102–111.

Smith, L. L., D. A. Steen, L. M. Conner, and J. C. Rutledge. 2013. Effects of predator exclusion on nest and hatchling survival in the gopher tortoise. Journal of Wildlife Management 77:352–358.

Tuberville, T. D., J. W. Gibbons, and H. E. Balbach. 2009. Estimating viability of gopher tortoise populations. Final Report, US Army Corps of Engineers, Washington, DC. <https://apps.dtic.mil/sti/pdfs/ADA520821.pdf>. Accessed 24 Jun 2020.

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

Tuberville, T. D., B. D. Todd, S. M. Hermann, W. K. Michener, and C. Guyer. 2014. Survival, demography, and growth of gopher tortoises (*Gopherus polyphemus*) from three study sites with different management histories. Journal of Wildlife Management 78:1151–1160.

Wiegand, T., J. Naves, T. Stephan, and A. Fernandez. 1998. Assessing the risk of extinction for the brown bear (*Ursus arctos*) in the Cordillera Cantabrica, Spain. Ecological Monographs 68:539–570.

Williams, B., J. Nichols, and M. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego.

Yager, L. Y., M. G. Hinderliter, C. D. Heise, and D. M. Epperson. 2007. Gopher Tortoise Response to Habitat Management by Prescribed Burning. Journal of Wildlife Management 71:428–434.

Table 1. Mean and standard error values used to estimate stochastic variables in our population projection model for gopher tortoises (*Gopherus polyphemus*) in conservation lands across the species' range. MAT = mean annual temperature (degrees C) of a population's locality; YSB = years since last burn of habitat using prescribed fire. See Appendix 1 for the full list of references used to compile parameter estimates for variables in the table.

Parameter	Distribution shape	Mean (variance)	Source
Probability of breeding	Beta	0.97 (0.01)	E. Hunter, pers. comm.
Fecundity	Log normal	-3.54 (2.42) + 0.48 (0.12) * MAT	Meshaka Jr. et al. (2019); this study
Nest survival	Beta	0.35 (0.10)	Smith et al. (2013)
Probability of viable eggs	Beta	0.85 (0.05)	Landers et al. (1980), Rostal and Jones (2002)
Probability of female	Beta	0.50 (0.04)	This study
Hatchling survival	Beta	0.13 (0.03)	Perez-Heydrich et al. (2012)
Juvenile survival	Beta	0.75 (0.06)	Appendix 1
Adult survival	Beta	0.96 (0.03)	Appendix 1
Maturity age	Log normal	43.52 (11.31) – 1.41 (0.53) * MAT	Appendix 1; this study
Juvenile abundance	Log normal	Varying by population	This study
Adult abundance	Log normal	Varying by population	This study
Immigration rate	Beta	0.01 (0.001)	Ott-Eubanks et al. (2003)
Percent of winter days for burning	Beta	0.77 (0.05)	Kupfer et al. (2020)

Percent of spring days for burning	Beta	0.80 (0.05)	
Percent of summer days for burning	Beta	0.65 (0.05)	
Change in winter days for burning	Beta	Varying by prediction scenario	
Change in spring days for burning	Beta	Varying by prediction scenario	
Change in summer days for burning	Beta	Varying by prediction scenario	
Burn probability	Beta	0.4 (0.015)	Guyette et al (2012), Crawford et al. (2020)
Fire effect on survival	Beta	0.96 – 0.027 (0.003) * YSB	Hunter and Rostal (2021)

Table 2. Six scenarios of future climate warming, sea-level rise, urbanization, and habitat management used to simulated population growth and extinction risk for gopher tortoises (*Gopherus polyphemus*) for 80 years into the future. Scenarios vary in the magnitude of threat influences on gopher tortoise demography; threat levels included three levels of climate warming (1.0, 1.5, and 2.0 degrees C increase), three levels of sea-level rise (intermediate-high [1.83 m], high [2.55 m], and extreme [3.16 m] scenarios), three levels of urbanization scenarios predicted by the SLEUTH model [Clarke 2000] at probability thresholds of 0.9 (conservative prediction), 0.5 (moderate prediction), and 0.1 (aggressive prediction), and four levels of changes in habitat management (no changes, less management predicted by RCP4.5 [Kupfer et al. 2020], much less management predicted by RCP8.5 [Kupfer et al. 2020], and improved management [the opposite of the effect predicted by RCP4.5 in Kupfer et al. 2020]).

Scenarios	Climate warming (deg C)	Sea-level rise (m)	Urbanization	Management
Low stressors	1.0	0.54 m	P = 0.95	Status quo
Medium stressors	1.5	1.83 m	P = 0.50	Status quo
High stressors	2.0	3.16 m	P = 0.20	Status quo
More management	1.5	1.83 m	P = 0.50	More
Less management	1.5	1.83 m	P = 0.50	Less
Much less management	1.5	1.83 m	P = 0.50	Much less

Table 3. Simulated population projections for female gopher tortoises under six scenarios of future change. Columns summarize the initial number (in 2020), future predicted number, and population growth rate (λ) for the total population size, number of populations, and number of landscape populations for six scenarios projected 40, 60, and 80 years into the future. See Table 2 for descriptions of scenarios and parameters.

Scenarios	Total population size			Number of local populations			Number of metapopulations		
	Initial	Future	λ	Initial	Future	λ	Initial	Future	λ
Year 2060									
Low stressors	70610	47468	0.67 (0.30–1.80)	626	332	0.53 (0.51–0.55)	244	179	0.73 (0.63–0.81)
Medium stressors	70614	47630	0.67 (0.30–1.91)	626	331	0.53 (0.51–0.54)	244	183	0.75 (0.61–0.80)
High stressors	70582	45998	0.65 (0.28–1.84)	626	329	0.53 (0.51–0.55)	244	177	0.73 (0.64–0.80)
More management	70611	46646	0.66 (0.29–1.84)	626	329	0.53 (0.51–0.55)	244	178	0.73 (0.61–0.80)
Less management	70610	46826	0.66 (0.29–1.79)	626	328	0.52 (0.50–0.54)	244	180	0.74 (0.62–0.80)
Much less management	70600	46495	0.66 (0.29–1.80)	626	323	0.52 (0.50–0.54)	244	178	0.73 (0.60–0.79)
Year 2080									
Low stressors	70609	49281	0.70 (0.36–1.77)	626	249	0.40 (0.38–0.41)	244	143	0.59 (0.44–0.73)
Medium stressors	70636	48924	0.69 (0.37–1.79)	626	250	0.40 (0.38–0.41)	244	142	0.58 (0.45–0.73)
High stressors	70592	46674	0.66 (0.34–1.70)	626	246	0.39 (0.37–0.41)	244	138	0.57 (0.43–0.70)
More management	70598	49246	0.70 (0.35–1.86)	626	250	0.40 (0.38–0.42)	244	145	0.59 (0.45–0.74)
Less management	70604	48754	0.69 (0.34–1.80)	626	247	0.39 (0.38–0.41)	244	138	0.57 (0.44–0.72)
Much less management	70569	48592	0.69 (0.35–1.69)	626	243	0.39 (0.37–0.42)	244	142	0.58 (0.42–0.72)

Year 2100									
Low stressors	70614	50846	0.72 (0.37–1.77)	626	198	0.32 (0.30–0.33)	244	114	0.47 (0.36–0.62)
Medium stressors	70594	48366	0.69 (0.36–1.74)	626	196	0.31 (0.29–0.33)	244	108	0.44 (0.35–0.59)
High stressors	70578	47378	0.67 (0.35–1.70)	626	194	0.31 (0.29–0.33)	244	109	0.45 (0.33–0.60)
More management	70584	49114	0.70 (0.36–1.73)	626	196	0.31 (0.30–0.33)	244	110	0.45 (0.33–0.62)
Less management	70596	47202	0.67 (0.37–1.75)	626	193	0.31 (0.29–0.33)	244	106	0.43 (0.34–0.61)
Much less management	70608	48520	0.69 (0.37–1.67)	626	188	0.30 (0.28–0.32)	244	106	0.43 (0.34–0.59)

Table 4. Predicted population persistence probabilities (P_p) categories for gopher tortoise populations in year 2100 under six future scenarios varying in the magnitude of future stressors. Persistence categories are Extremely Likely Extant (P_p > 95.0%), Very Likely Extant (P_p = 80.0–94.9%), More Likely Than Not Extant (P_p = 50.0–79.9%), and Unlikely Extant (P_p < 50.0%; i.e., extirpated). See Table 2 for descriptions of scenarios and their parameters.

Population persistence category	Scenario					
	Low stressors	Medium stressors	High stressors	More management	Less management	Much less management
Year 2060						
Extremely Likely Extant	104 (16.6%)	103 (16.5%)	101 (16.1%)	99 (15.8%)	102 (16.3%)	104 (16.6%)
Very Likely Extant	102 (16.3%)	97 (15.5%)	108 (17.3%)	108 (17.3%)	98 (15.7%)	91 (14.5%)
More Likely Than Not Extant	135 (21.6%)	145 (23.2%)	135 (21.6%)	134 (21.4%)	141 (22.5%)	141 (22.5%)
Unlikely Extant (i.e., Extirpated)	285 (45.5%)	281 (44.9%)	282 (45%)	285 (45.5%)	285 (45.5%)	290 (46.3%)
Year 2080						
Extremely Likely Extant	78 (12.5%)	74 (11.8%)	71 (11.3%)	79 (12.6%)	74 (11.8%)	76 (12.1%)
Very Likely Extant	35 (5.6%)	44 (7%)	41 (6.5%)	36 (5.8%)	41 (6.5%)	31 (5%)
More Likely Than Not Extant	122 (19.5%)	116 (18.5%)	117 (18.7%)	128 (20.4%)	103 (16.5%)	114 (18.2%)
Unlikely Extant (i.e., Extirpated)	391 (62.5%)	392 (62.6%)	397 (63.4%)	383 (61.2%)	408 (65.2%)	405 (64.7%)
Year 2100						
Extremely Likely Extant	76 (12.1%)	72 (11.5%)	70 (11.2%)	71 (11.3%)	70 (11.2%)	70 (11.2%)

Very Likely Extant	21 (3.4%)	20 (3.2%)	25 (4%)	24 (3.8%)	24 (3.8%)	24 (3.8%)
More Likely Than Not Extant	65 (10.4%)	62 (9.9%)	55 (8.8%)	58 (9.3%)	57 (9.1%)	54 (8.6%)
Unlikely Extant (i.e., Extirpated)	464 (74.1%)	472 (75.4%)	476 (76%)	473 (75.6%)	475 (75.9%)	478 (76.4%)

Table 5. Simulated population projections for gopher tortoises under scenarios varying in immigration rate (γ): no immigration (γ = 0), intermediate immigration (γ = 0.01), high immigration (γ = 0.02), and very high immigration (γ = 0.04). Columns summarize the initial number (in 2020), future predicted number, and population growth rate (λ) for the total population size, number of populations, and number of metapopulations for four scenarios projected 80 years into the future. Each scenario models stressors and management actions using input values from the 'medium stressors' scenario from Table 2, and the 'intermediate immigration' scenario has the same input values the 'medium stressors' scenario from Table 2; see Table 2 for more information about input parameters.

Scenarios	Total population size			Number of local populations			Number of metapopulations		
	Initial	Future	λ	Initial	Future	λ	Initial	Future	λ
No immigration	70602	1566	0.02 (0.01–0.18)	626	81	0.13 (0.11–0.15)	244	46	0.19 (0.09–0.36)
Intermediate immigration	70594	48366	0.69 (0.36–1.74)	626	196	0.31 (0.29–0.33)	244	108	0.44 (0.35–0.59)
High immigration	70600	91805	1.30 (0.71–2.76)	626	247	0.39 (0.38–0.41)	244	124	0.51 (0.39–0.66)
Very high immigration	70600	151320	2.14 (1.18–4.44)	626	312	0.50 (0.48–0.52)	244	144	0.59 (0.48–0.68)

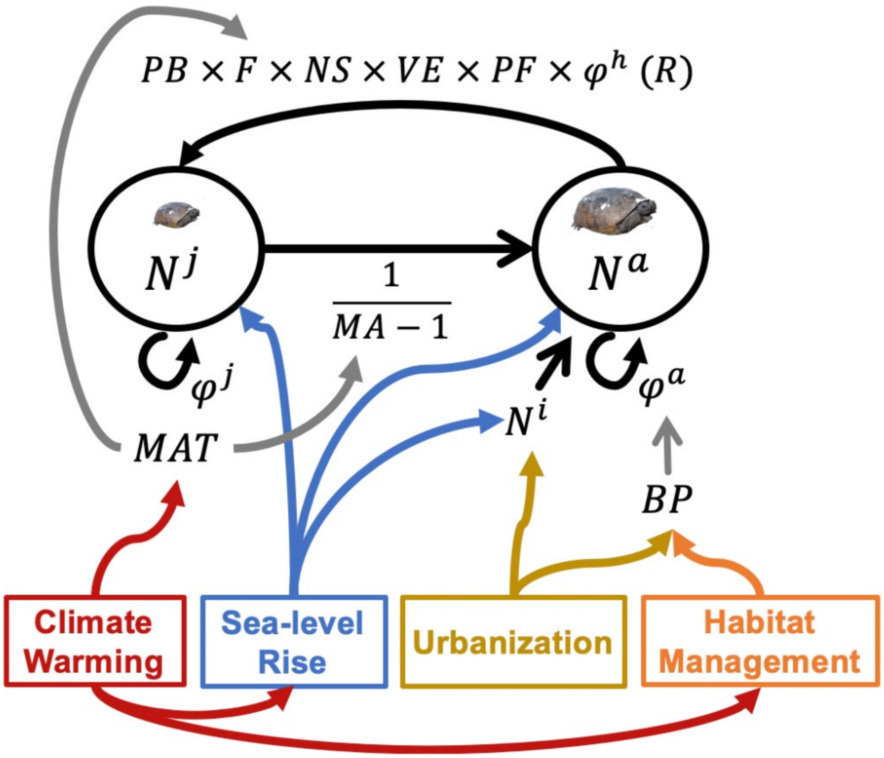


Figure 1. A conceptual model illustrating a stage-based, female-only population model (black text) used to simulate demography and project population size of the Gopher Tortoise (*Gopherus polyphemus*) into the future. Black arrows and circles indicate gopher tortoise demographic parameters (survival, growth, abundance); colored arrows and text indicate predicted threat effects on tortoise demography simulated through scenario analysis. See Table 1 for demographic variable definitions and baseline estimates; MAT = mean annual temperature (°C) and BP is burn probability with prescribed fire (see Methods). For each threat (colored box), I modeled three or four scenarios of future change in the threat magnitude (Table 2).

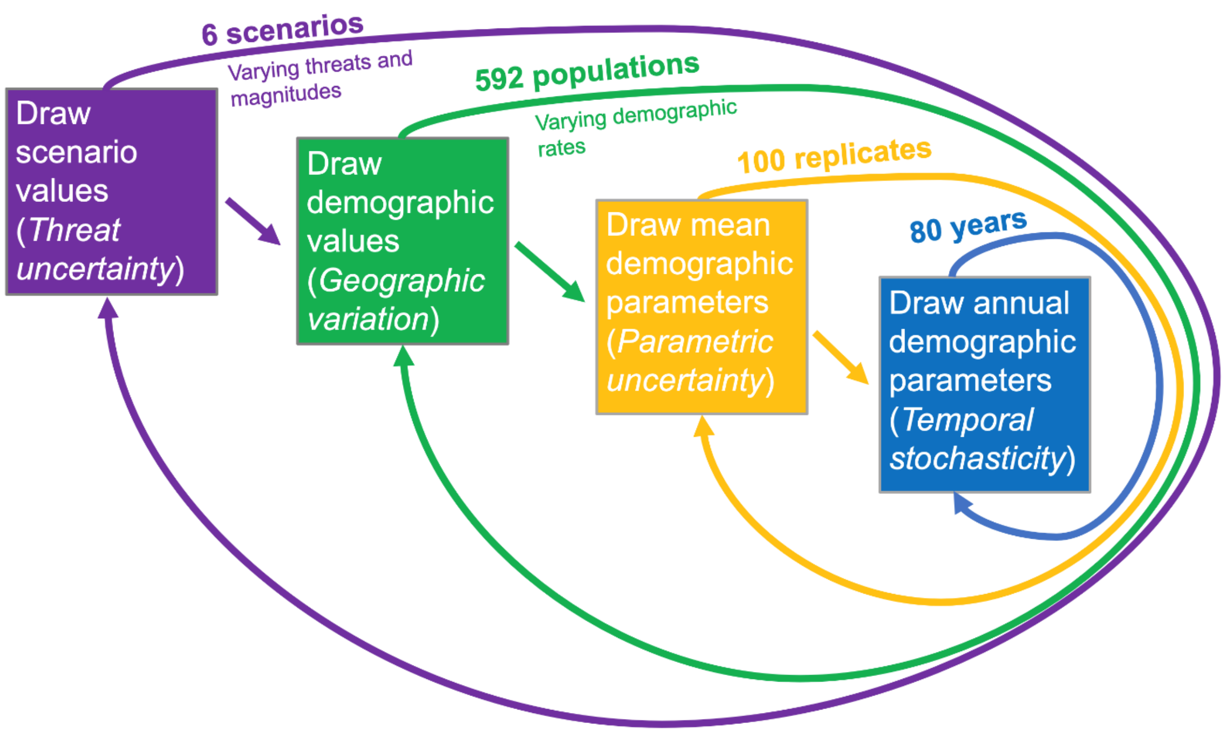


Figure 2. I used a four-loop uncertainty structure to simulate uncertainty in threats, geographic variation, parameter estimates, and temporal stochasticity of stochastic variables during population projections for gopher tortoises. For each scenario, I simulated each population using 100 replicates and projected each replicate into the future for 80 years.

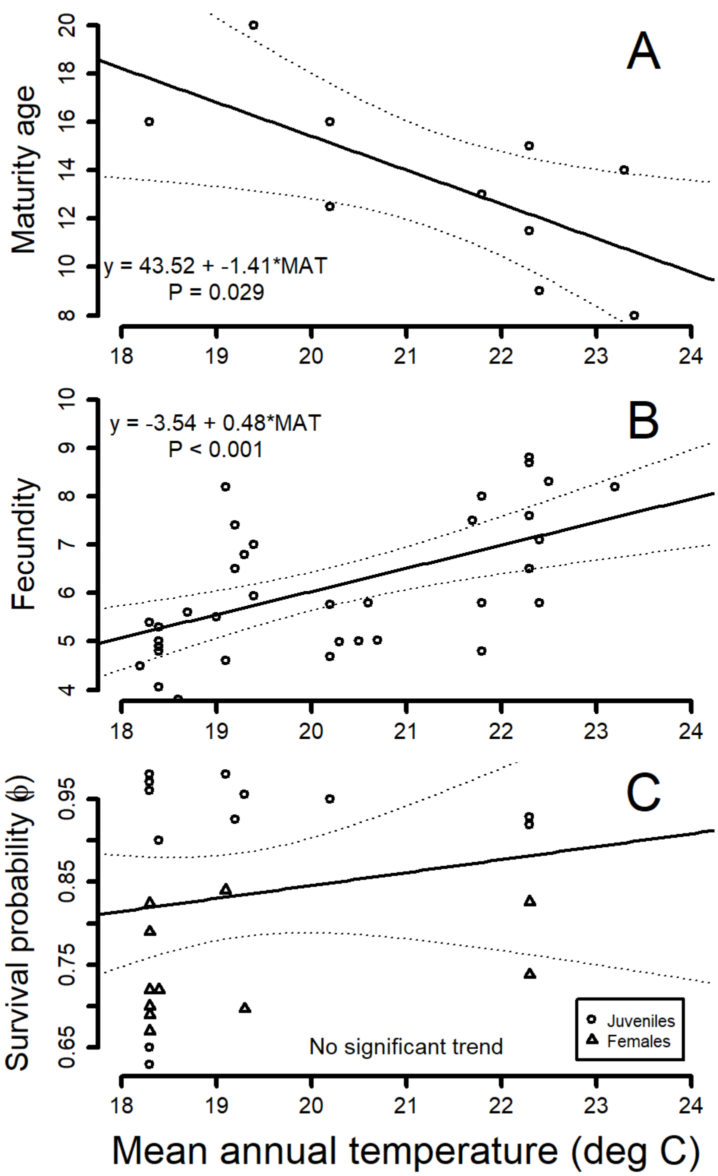


Figure 3. Effect of mean annual temperature (MAT; degrees C) on (A) maturity age (MA), (B), fecundity, and (C) annual apparent survival probability (φ) of gopher tortoise (*Gopherus polyphemus*) populations. Geographic variation in biotic conditions (e.g., MAT) predict significant variation in maturity age and fecundity ($P < 0.05$) but not in annual apparent survival probability (see inset text).

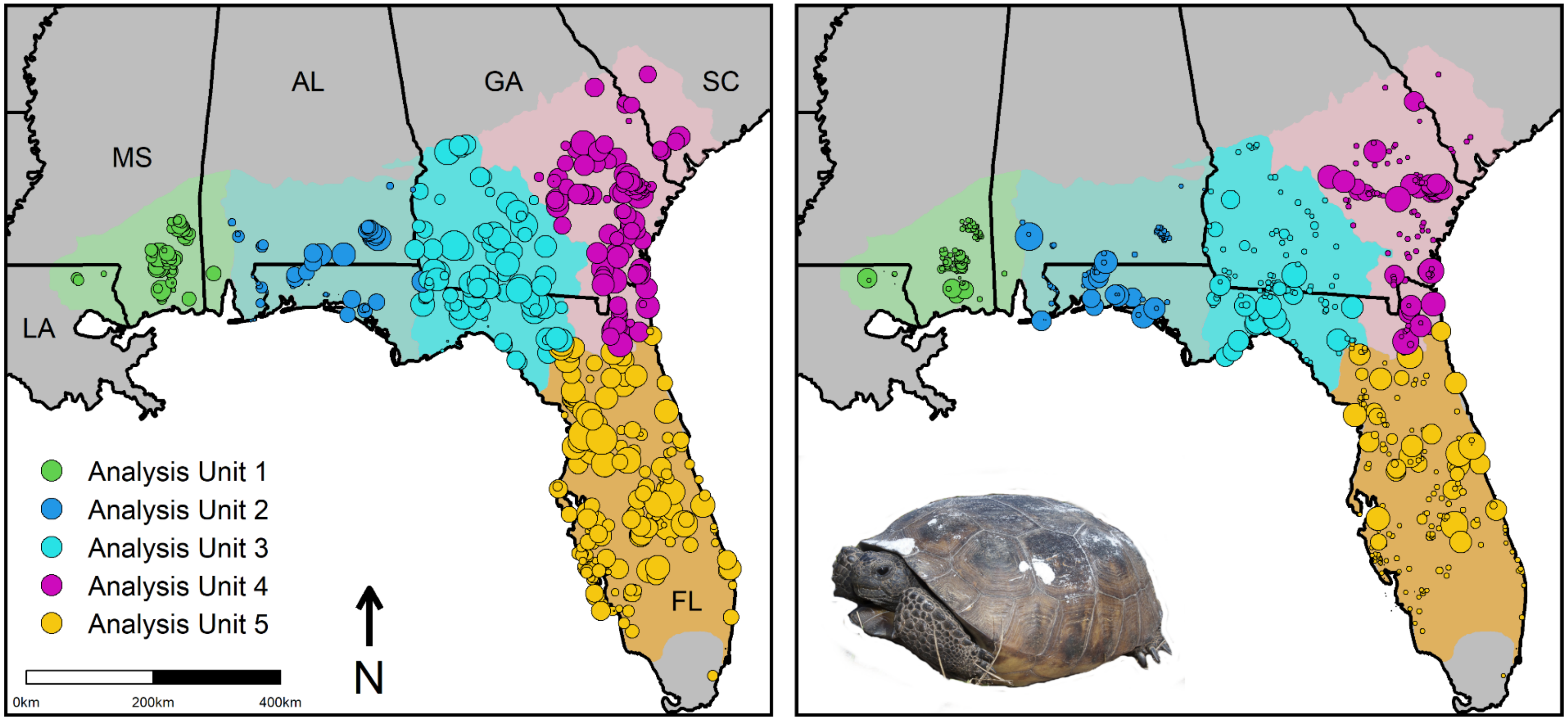


Figure 4. Current abundance (left) and predicted abundance 80 years in the future (right) of gopher tortoise (*Gopherus polyphemus*; right inset) populations in the southeastern United States that were modeled to predict future population growth and extinction risk for the species under scenarios of global change. Each circle represents a local population and circles are colored by analysis unit. Symbol size reflects a log-transformed scale of population size; the left panel shows population size estimated during a survey during 2010–2020; the right panel shows predicted population size under a future scenario of 'medium stressors with less management' (Table 2). Abundance of populations during

2010–2020 was estimated from analysis of data from burrow surveys or Line Transect Distance Sampling (LTDS) surveys at each the site within the last ten years.

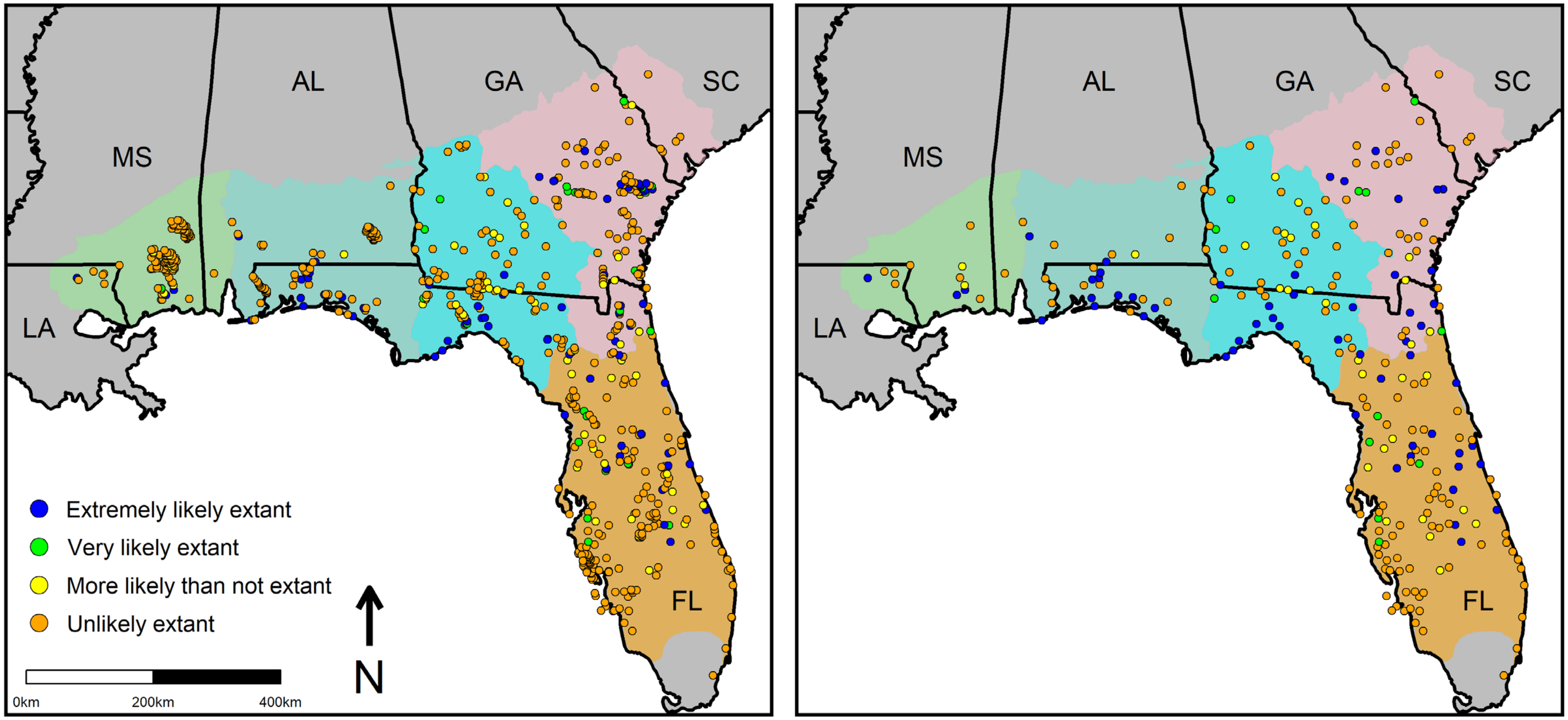


Figure 5. Persistence probabilities (P_p) of gopher tortoise (*Gopherus polyphemus*) local populations (left) and landscape populations (right) predicted by a future scenario of less habitat management with medium stressor (Table 2) projected 80 years into the future. Symbols are colored by persistence probability categories: Extremely Likely Extant (P_p > 95.0%), Very Likely Extant (P_p = 80.0–94.9%), More Likely Than Not Extant (P_p = 50.0–79.9%), and Unlikely Extant (P_p < 50.0%; i.e., extirpated). See Table 2 for descriptions of scenarios and their parameters.

Appendix 1. Demographic estimates for gopher tortoises (*Gopherus polyphemus*) identified during a literature review and used in the construction of a female-only population model. Parameters are: fecundity (F); nest survival (NS); probability of viable eggs (i.e., hatching success; VE); survival of hatchlings (φ^h), juveniles (φ^j), and adult females (φ^a); and maturity age for females (MA).

Parameter	Locality	Estimate	Reference
F	Okeeheelee County Park, FL	8.2	Ashton et al. 2007
F	Archbold Biological Station, FL	6.5	Ashton et al. 2007
F	Archbold Biological Station, FL	8.7	White et al. 2018
F	Archbold Biological Station, FL	8.1	White et al. 2018
F	South of Tampa, FL	7.6	Godley 1989
F	USF's Ecological Research Area, Tampa, FL	7.1	Mushinksy et al. 1994
F	Boyd Hill Nature Preserve, FL	8.3	Goessling and Heinrich, unpubl. data
F	North of Tampa, FL	4.8	Macdonald 1996
F	North of Tampa, FL	5.8	Small and Macdonald 2001
F	North of Tampa, FL	8.0	Small and Macdonald 2001
F	Cape Canaveral, FL	7.5	Demuth 2001
F	Gainesville, FL	5.8	Diemer-Berish et al. 2012
F	Gainesville, FL	4.7	Iverson 1980
F	Ordway Preserve, Gainesville, FL	5.8	Smith 1995
F	Jacksonville, FL	5.0	Butler and Hull 1996

F	Jacksonville, FL	5.0	Hallinan 1923
F	Branan Field Wildlife and Environmental Area, FL	5.0	Perez-Heydrich et al. 2012
F	Mobile County, AL	4.6	Marshall 1987
F	Ben's Creek WMA, LA	5.5	Smith et al. 1997
F	Silver Lake WMA, GA	7.0	Landers et al. 1980
F	The Wade Tract, GA	5.9	Radzio et al. 2017
F	Joseph W. Jones Ecological Research Center, GA	6.8	L. Smith, unpubl. Data
F	Marion County WMA, FL	5.6	Smith et al. 1997
F	Camp Shelby, MS	4.8	Epperson and Heise 2003
F	Camp Shelby, MS	5.3	J. Watkins (pers. comm.) in Butler and Hull 1996
F	Camp Shelby, MS	5.0	C. Jones and T. Mann (pers. comm.) in Butler and Hull 1996
F	Camp Shelby, MS	4.1	M. Hinderliter, unpubl. data
F	Camp Shelby, MS	4.9	J. Lee, unpubl. data
F	Fort Stewart, GA	6.5	Rostal and Jones 2002
F	St. Catherines Island, GA	8.2	Quin et al. 2016, p. 14
F	Reed Bingham State Park, GA	7.4	Quin et al. 2016, p. 14
F	Yuchi WMA, GA	6.7	Quin et al. 2016, p. 14
F	South Carolina	3.80	Wright 1982
F	George L. Smith State Park, GA	4.50	Rostal and Jones 2002
F	Alabama	4.29	Folt et al. submitted

NS	Joseph W. Jones Ecological Research Center, GA	0.35	Smith et al. 2013
VE	Archbold Biological Station, FL	0.78	White et al. 2018
VE	Ordway Preserve, Gainesville, FL	0.83	Smith 1995
VE	Jacksonville, FL	0.82	Butler and Hull 1996
VE	Branan Field Wildlife and Environmental Area, FL	0.90	Perez-Heydrich et al. 2012
VE	Silver Lake WMA, GA	0.86	Landers et al. 1980
VE	The Wade Tract, GA	0.73	Radzio et al. 2017
VE	St. Catherines Island, GA	0.90	Quin et al. 2016, p. 14
VE	Reed Bingham State Park, GA	0.93	Quin et al. 2016, p. 14
VE	Yuchi WMA, GA	0.93	Quin et al. 2016, p. 14
φ^h	Meta-analysis of three localities	0.13	Perez-Heydrich et al. 2012
φj	Archbold Biological Station, FL	0.83	Meshaka et al. 2019, p. 98
φj	Archbold Biological Station, FL	0.74	Howell et al. 2020
φj	Joseph W. Jones Ecological Research Center, GA	0.70	Tuberville et al. 2014
φj	St. Catherines Island, GA	0.84	Tuberville et al. 2008, p. 2694
φj	Conecuh National Forest, AL	0.82	Tuberville et al. 2014
φj	Conecuh National Forest, AL	0.67	Folt et al. 2021
φ^j	Conecuh National Forest, AL	0.69	Folt et al. 2021
φ^j	Conecuh National Forest, AL	0.79	Folt et al. 2021
φ^j	Conecuh National Forest, AL	0.70	Folt et al. 2021

φ^j	Conecuh National Forest, AL	0.72	Folt et al. 2021
φ^j	Conecuh National Forest, AL	0.72	Folt et al. 2021
φ^a	Archbold Biological Station, FL	0.92	Meshaka et al. 2019, p. 98
φ^a	Archbold Biological Station, FL	0.93	Howell et al. 2020
φ^a	Gainesville, FL	0.95	Ozgul et al. 2009
φ^a	Joseph W. Jones Ecological Research Center, GA	0.96	Tuberville et al. 2014
φ^a	St. Catherines Island, GA	0.98	Tuberville et al. 2008, p. 2694
φ^a	Conecuh National Forest, AL	0.98	Tuberville et al. 2014
φ^a	Conecuh National Forest, AL	0.97	Folt et al. 2021
φ^a	Conecuh National Forest, AL	0.63	Folt et al. 2021
φ^a	Conecuh National Forest, AL	0.96	Folt et al. 2021
φ^a	Conecuh National Forest, AL	0.96	Folt et al. 2021
φ^a	Conecuh National Forest, AL	0.65	Folt et al. 2021
φ^a	Conecuh National Forest, AL	0.90	Folt et al. 2021
MA	Silver Lake WMA, GA	20	Landers et al. 1982
MA	Conecuh National Forest, AL	16	Folt et al. 2021
MA	Gainesville, FL	16	Diemer and Moore 1994
MA	Gainesville, FL	12.5	Iverson 1980
MA	Tampa, FL	13	Linley 1986
MA	Tampa, FL	9	Mushinsky et al. 1994, p. 123

MA	Tampa, FL	15	Godley 1989
MA	Archbold Biological Station, FL	11.5	Meshaka et al. 2019, p. 98
MA	Jupiter, FL	8	Sano 2014
MA	Sanibel Island, FL	14	McLaughlin 1990

Appendix 2. Simulated population projections for gopher tortoises populations in each of the five genetic representation units (Gaillard et al. 2017). Six scenarios of predicted future change were projected 80 years into the future; results are summarized by the initial number, future predicted number, and population growth rate (λ) for the total population size, number of local populations, and number of metapopulations in each genetic unit. See Table 2 for descriptions of scenarios and parameters.

Scenarios	Total population size			Number of local populations			Number of metapopulations		
	Initial	Future	λ	Current	Future	λ	Initial	Future	λ
Unit 1									
Low stressors	1571	1151	0.73 (0.22–3.55)	102	23	0.23 (0.18–0.27)	13	6	0.46 (0.46–0.46)
Medium stressors	1573	1066	0.68 (0.22–3.50)	102	23	0.23 (0.18–0.27)	13	6	0.46 (0.46–0.54)
High stressors	1572	990	0.63 (0.22–3.86)	102	23	0.23 (0.18–0.26)	13	6	0.46 (0.46–0.54)
More management	1572	1066	0.68 (0.21–4.01)	102	23	0.23 (0.19–0.27)	13	6	0.46 (0.44–0.54)
Less management	1573	1026	0.65 (0.22–3.79)	102	22	0.22 (0.18–0.26)	13	6	0.46 (0.46–0.54)
Much less management	1572	947	0.60 (0.22–3.42)	102	22	0.22 (0.18–0.26)	13	6	0.46 (0.46–0.54)
Unit 2									
Low stressors	2896	7316	2.53 (1.49–4.08)	81	21	0.26 (0.21–0.30)	29	16	0.55 (0.48–0.66)
Medium stressors	2896	7022	2.42 (1.24–3.94)	81	19	0.23 (0.20–0.27)	29	15	0.52 (0.45–0.59)
High stressors	2894	6868	2.37 (1.50–4.04)	81	19	0.23 (0.20–0.28)	29	14	0.48 (0.45–0.59)
More management	2896	7086	2.45 (1.39–3.95)	81	20	0.25 (0.21–0.28)	29	15	0.52 (0.45–0.59)
Less management	2898	7007	2.42 (1.58–4.10)	81	20	0.25 (0.20–0.28)	29	15	0.52 (0.45–0.59)

Much less management	2898	7084	2.44 (1.44–3.92)	81	19	0.23 (0.20–0.27)	29	14	0.48 (0.45–0.52)
Unit 3									
Low stressors	19432	9468	0.49 (0.31–1.08)	110	42	0.38 (0.34–0.44)	55	29	0.52 (0.36–0.73)
Medium stressors	19428	9125	0.47 (0.31–1.04)	110	42	0.38 (0.34–0.44)	55	27	0.49 (0.32–0.68)
High stressors	19419	9406	0.48 (0.30–1.02)	110	42	0.38 (0.34–0.44)	55	28	0.50 (0.35–0.72)
More management	19426	9338	0.48 (0.30–1.11)	110	43	0.39 (0.35–0.45)	55	29	0.53 (0.38–0.76)
Less management	19430	9224	0.47 (0.31–1.06)	110	42	0.38 (0.33–0.43)	55	28	0.51 (0.35–0.75)
Much less management	19432	9332	0.48 (0.31–1.03)	110	41	0.37 (0.33–0.43)	55	27	0.48 (0.35–0.70)
Unit 4									
Low stressors	14032	13793	0.98 (0.55–2.20)	123	50	0.37 (0.33–0.43)	46	21	0.46 (0.35–0.65)
Medium stressors	14030	13368	0.95 (0.55–2.28)	123	50	0.39 (0.35–0.45)	46	22	0.48 (0.37–0.64)
High stressors	14040	12013	0.86 (0.42–1.98)	123	48	0.41 (0.37–0.46)	46	20	0.43 (0.35–0.62)
More management	14036	13325	0.95 (0.54–2.11)	123	51	0.40 (0.36–0.44)	46	22	0.48 (0.35–0.66)
Less management	14034	13109	0.93 (0.54–2.09)	123	49	0.41 (0.37–0.46)	46	22	0.48 (0.35–0.67)
Much less management	14039	13118	0.93 (0.56–2.11)	123	49	0.39 (0.35–0.43)	46	20	0.43 (0.36–0.63)
Unit 5									
Low stressors	32684	19120	0.58 (0.25–1.70)	210	62	0.30 (0.27–0.32)	103	41	0.40 (0.30–0.52)
Medium stressors	32666	17786	0.54 (0.24–1.65)	210	60	0.29 (0.26–0.31)	103	43	0.41 (0.27–0.53)

High stressors	32653	18102	0.55 (0.25–1.66)	210	60	0.29 (0.26–0.32)	103	39	0.38 (0.25–0.58)
More management	32655	18300	0.56 (0.24–1.64)	210	60	0.29 (0.26–0.31)	103	41	0.40 (0.26–0.57)
Less management	32662	16836	0.52 (0.23–1.71)	210	60	0.29 (0.25–0.32)	103	37	0.36 (0.27–0.54)
Much less management	32666	18038	0.55 (0.24–1.59)	210	58	0.28 (0.25–0.30)	103	40	0.38 (0.27–0.51)

Appendix 3. Simulated population projections for gopher tortoises in each of the six states within which the gopher tortoise occurs. Six scenarios of predicted future change were projected 80 years into the future; results are summarized by the initial number, future predicted number, and population growth rate (λ) for the total population size, number of local populations, and number of metapopulations in each state. See Table 2 for descriptions of scenarios and parameters.

Scenarios	Total population size			Number of local populations			Number of metapopulations		
	Initial	Future	λ	Initial	Future	λ	Initial	Future	λ
Alabama									
Low stressors	2318	3638	1.57 (0.98–2.49)	54	7	0.13 (0.09–0.19)	14	6	0.43 (0.29–0.43)
Medium stressors	2318	3709	1.60 (0.81–2.51)	54	7	0.13 (0.09–0.19)	14	5	0.36 (0.29–0.43)
High stressors	2316	3642	1.57 (1.13–2.70)	54	7	0.13 (0.09–0.19)	14	6	0.39 (0.29–0.43)
More management	2318	3752	1.62 (0.96–2.54)	54	8	0.15 (0.09–0.19)	14	6	0.43 (0.29–0.43)
Less management	2320	3633	1.57 (1.18–2.71)	54	7	0.13 (0.09–0.19)	14	5	0.36 (0.29–0.43)
Much less management	2320	3737	1.61 (1.02–2.53)	54	7	0.13 (0.07–0.17)	14	5	0.36 (0.29–0.43)
Florida									
Low stressors	44037	34536	0.78 (0.40–1.95)	314	108	0.34 (0.32–0.37)	152	74	0.48 (0.38–0.62)
Medium stressors	44022	32286	0.73 (0.39–1.87)	314	105	0.33 (0.31–0.36)	152	69	0.45 (0.36–0.59)
High stressors	44004	31798	0.72 (0.38–1.83)	314	103	0.33 (0.31–0.35)	152	70	0.46 (0.35–0.62)
More management	44009	33094	0.75 (0.39–1.90)	314	106	0.34 (0.31–0.36)	152	70	0.46 (0.34–0.63)

Less management	44020	31470	0.71 (0.38–1.91)	314	105	0.33 (0.31–0.36)	152	71	0.47 (0.36–0.61)
Much less management	44022	32924	0.75 (0.40–1.83)	314	102	0.32 (0.30–0.35)	152	68	0.45 (0.34–0.59)
Georgia									
Low stressors	22183	11510	0.52 (0.28–1.23)	151	59	0.39 (0.34–0.43)	63	27	0.43 (0.35–0.65)
Medium stressors	22176	11290	0.51 (0.27–1.32)	151	59	0.39 (0.35–0.43)	63	27	0.43 (0.32–0.63)
High stressors	22181	10934	0.49 (0.22–1.21)	151	58	0.38 (0.34–0.42)	63	30	0.48 (0.32–0.59)
More management	22180	11186	0.50 (0.27–1.21)	151	59	0.39 (0.35–0.44)	63	27	0.43 (0.33–0.63)
Less management	22178	11060	0.50 (0.27–1.22)	151	57	0.38 (0.33–0.42)	63	28	0.44 (0.33–0.63)
Much less management	22188	10897	0.49 (0.27–1.18)	151	57	0.38 (0.34–0.42)	63	27	0.43 (0.32–0.60)
Louisiana									
Low stressors	24	246	10.25 (8.00–14.29)	7	1	0.14 (0.14–0.29)	5	1	0.20 (0.20–0.20)
Medium stressors	24	244	10.17 (7.88–13.79)	7	1	0.14 (0.14–0.29)	5	1	0.20 (0.20–0.20)
High stressors	24	242	10.08 (7.71–14.21)	7	1	0.14 (0.14–0.29)	5	1	0.20 (0.20–0.20)
More management	24	248	10.33 (7.63–14.83)	7	1	0.14 (0.14–0.29)	5	1	0.20 (0.20–0.20)
Less management	24	244	10.17 (8.08–15.63)	7	1	0.14 (0.14–0.29)	5	1	0.20 (0.20–0.40)
Much less management	24	246	10.25 (8.21–15.42)	7	1	0.14 (0.14–0.29)	5	1	0.20 (0.20–0.20)
Mississippi									
Low stressors	1514	902	0.60 (0.10–3.45)	94	22	0.23 (0.18–0.28)	7	5	0.71 (0.71–0.71)

Medium stressors	1516	820	0.54 (0.10–3.41)	94	22	0.23 (0.18–0.28)	7	5	0.71 (0.71–0.71)
High stressors	1515	746	0.49 (0.10–3.77)	94	21	0.22 (0.18–0.28)	7	5	0.71 (0.71–0.71)
More management	1515	816	0.54 (0.10–3.92)	94	22	0.23 (0.19–0.29)	7	5	0.71 (0.57–0.71)
Less management	1516	780	0.51 (0.10–3.69)	94	21	0.22 (0.18–0.28)	7	5	0.71 (0.71–0.71)
Much less management	1516	698	0.46 (0.10–3.30)	94	21	0.22 (0.17–0.27)	7	5	0.71 (0.71–0.71)
South Carolina									
Low stressors	538	16	0.03 (0.02–0.15)	6	1	0.17 (0–0.50)	4	0	0 (0–0.50)
Medium stressors	538	17	0.03 (0.02–0.14)	6	1	0.17 (0–0.50)	4	0	0 (0–1.00)
High stressors	538	16	0.03 (0.02–0.16)	6	1	0.17 (0–0.50)	4	0	0 (0–0.75)
More management	538	18	0.03 (0.02–0.17)	6	1	0.17 (0–0.50)	4	1	0.25 (0–0.75)
Less management	538	16	0.03 (0.02–0.18)	6	1	0.17 (0–0.50)	4	1	0.25 (0–1.00)
Much less management	538	17	0.03 (0.02–0.16)	6	1	0.17 (0–0.50)	4	0	0 (0–0.75)