Habitat Characteristics Associated with Burrows of Gopher Tortoises and Non-burrow Locations on a Mississippi Military Installation

Katherine E. Edwards, *Wildlife Management Specialist, Fairfax County Police Department—Animal Services Division, 4500 West Ox Rd., Fairfax, VA 22030*

Jeanne C. Jones, *Mississippi State University, Department of Wildlife, Fisheries, and Aquaculture, Box 9690, Mississippi State, MS 39762*

David L. Evans, *Mississippi State University, Department of Forestry, Box 9681, Mississippi State, MS 39762*

Scott D. Roberts, *Mississippi State University, Department of Forestry, Box 9681, Mississippi State, MS 39762*

H. Alexis Londo, *The Ohio State University, School of Environment and Natural Resources, 375 C Kottman Hall, 2021 Coffey Rd., Columbus, OH 43210-1085*

Scott A. Tweddale, *Construction Engineering Research Laboratory, U.S. Army Engineer Research and Development Center, 2902 Newmark Dr., Champaign, IL 61822*

Zhaofei Fan, *Auburn University, School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL 36849*

B. Nicole Hodges, *Mississippi State University, Department of Wildlife, Fisheries, and Aquaculture, Box 9690, Mississippi State, MS 39762*

Abstract: Since the 1987 federal listing as threatened of western populations of gopher tortoises (*Gopherus polyphemus*), tortoise population recovery and habitat restoration efforts have been implemented at Camp Shelby Joint Forces Training Center, Mississippi. We studied plant community and edaphic features around tortoise burrows and at non-occupied locations in 2007. We investigated relationships between burrow presence and habitat characteristics through decision tree and logistic regression analyses. Burrow occurrence was positively related to stem counts of woody plants and species richness of native legumes and negatively related to overstory canopy coverage and maximum tree height. Cross-validation procedures predicted presence of burrows for 91% of observed outcomes. Tortoise burrows were most often found on side slopes of sand ridges where overstory canopy coverage was <60% and conditions were adequate for burrowing, nesting, basking, and establishment of food plants. Our study sites exhibited woody plant coverage >45% at ground and midstory levels and <50% coverage of herbaceous plants. Advancement of these conditions over time can produce suboptimal habitat quality yet tortoises may continue to utilize home burrows due to burrow site fidelity, interspersion of desirable food plants, and suitable soils for burrowing. Advancing shrub and sapling cover on our study sites were potentially related to reduced fire return intervals and burning bans associated with forest damage from the 2005 landfall of Hurricane Katrina. Design and interpretation of tortoise habitat studies should consider many factors, including edaphic and vegetation conditions, history of habitat management, temporal effects on vegetation succession, activity status of burrow, and burrow site fidelity.

Key words: gopher tortoise, endangered species, threatened species, habitat, military lands

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The U.S. Fish and Wildlife Service (USFWS) listed the western population of gopher tortoises (*Gopherus polyphemus*) as threatened under the Endangered Species Act (ESA) in 1987 (Ashton and Ashton 2008). This listing protects tortoises inhabiting areas west of the Mobile and Tombigbee Rivers in southwestern Alabama, southern Mississippi, and southeastern Louisiana. Historically, gopher tortoises inhabited longleaf pine (*Pinus palustris*) and sandhill ecosystems of the Gulf Coastal Plain. These habitats were influenced by frequent, low intensity fires, and were typified by widely-spaced overstory of uneven-aged longleaf pine, interspersed scrub oak communities, and herbaceous communities dominated by native grasses (*Andropogon* spp., *Aristida* spp., *Schizachyrium scoparium*), legumes, and forbs (Guyer and Hermann 1997). In the past century, region-wide reduction of longleaf pine ecosystems from 24 million in the late 1800s to <1.5 million ha by the late 1980s has led to declines in gopher tortoise populations throughout their range (Auffenberg and Franz 1982). In addition to habitat loss and degradation, poaching, disease, depredation, and invasive species impacts have limited population recruitment and resulted in population declines (Auffenberg and Franz 1982, Epperson and Heise 2003, Yager et al. 2007).

Today, populations of gopher tortoises are distributed in relatively small, fragmented habitat patches surrounded by development within the southeastern Coastal Plain (Mushinsky et al. 2006). Many of the remaining viable populations occur on state and federally managed lands, including at least seven Department of Defense (DoD) installations (Hermann et al. 2002). Camp Shelby Joint Forces Training Center (CSJFTC), a Mississippi Army National Guard (MSARNG) installation located in Perry, George, and Forrest counties of southern Mississippi supports tortoise populations within the listed portion of the animal's distributional range. Due to the protected status of gopher tortoises and requirements under the ESA, natural resource and military land managers must design and implement integrative natural resource management and conservation plans that address military training missions and gopher tortoise population recovery (Leonard et al. 2000). Also, approximately 87% of the land used for training at CSJFTS is within the boundaries of DeSoto National Forest, and these lands are utilized by the military under special use permit agreements with the U.S. Forest Service. These special use permit agreements require consideration of tortoise population recovery and management in areas designated as suitable for tortoises (Leonard et al. 2000). Because upland pine and sandhill ecosystems located on DeSoto National Forest have been identified as important for successful population recovery of tortoises within the western region of the Lower Gulf Coastal Plain, conservation and management plans are typically considered high priority and may be developed and implemented cooperatively by multiple agencies including the U.S. Forest Service, USFWS, MSARNG, and the Mississippi Department of Wildlife, Fisheries, and Parks (Leonard et al. 2000). Therefore, assessment of gopher tortoise habitat conditions at CSJFTC is important due to population and habitat monitoring requirements of ESA and multiple agency initiatives. An increased understanding of habitat conditions at tortoise-occupied sites can be utilized in developing integrative plans for accomplishing military training missions and effective conservation and recovery of gopher tortoise populations.

A successful approach for gaining insight into relationships between organisms and their environment is through statistical modeling of associations between species occurrence, habitat conditions, and land use (Debeljak et al. 2002). Therefore, statistical models have become more widely used on public land bases for evaluating species response to habitat characteristics and for assessment of habitat quality (Baskaran et al. 2006). With adequate study designs and sampling intensity, data collected at known locations can be used in modeling efforts to provide insight about un-surveyed areas and habitat management needs (Tweddale et al. 2008). To enhance our understanding of conditions under which gopher tortoises existed on military training sites of CSJTC, we investigated plant community characteristics at tortoise burrow locations and locations without burrows on three disjunct training areas of this MSARNG installation. Our objectives were to estimate and compare differences in vegetation structure and composition among three military training sites inhabited by gopher tortoises, quantify differences in vegetation structure and composition between gopher tortoise burrow locations and non-burrow locations, and investigate relationships burrow occurrence and habitat characteristics measured at burrow and non-burrow locations.

Study Area

The CSJFTC includes lands managed by the Department of the Army (1,360 ha), DoD (2,248 ha), State of Mississippi (3,359 ha), and the U.S. Forest Service (47,348 ha) (Leonard et al. 2000). The study area was located within the Piney Woods subprovince of the Gulf Coastal Plain which was characterized by forested, gently rolling, stream-dissected hills with topographic relief ranging from 6 m to >100 m above sea level (Leonard et al. 2000). Dominant vegetation in this region included upland longleaf pine forests and sandhill communities, mesic flatwoods, pitcher plant (*Sarracenia* spp.) wetlands, and riparian and bottomland forests dominated by oaks (*Quercus* spp.), American beech (*Fagus grandifolia*) and magnolia (*Magnolia* spp.) (Yager et al. 2007). Embedded within forested habitats were ruderal areas, such as powerlines, roadsides, and military training areas, including artillery firing points and impact areas, and small weapons and tank firing ranges (Lee 2009). Soils were predominantly silt-loams, sand-loams, and loams with >80% of the soils of training areas being comprised of highly suitable to suitable soils for gopher tortoises (U.S. NRCS 2012). Upland habitats of the three training areas were characterized by pine forests interspersed with scrub-oak communities located on sandy-loam to sandy soils (Leonard et al. 2000, U.S. NRCS 2012). Training sites of our study were utilized for troop artillery and weapons, bivouacking training. These areas were typically managed with prescribed fire at three-to four-year return intervals; however, at the time of our study's initiation, training sites had not been burned for at least three years due to forest damage and heavy fuel loads, drought conditions, and consequent burning bans that were implemented in south Mississippi following Hurricane Katrina's landfall in August 2005 (Lee 2009). Training sites included in our study were as follows: Mars Hill–463.4 ha; T-44–288.5 ha; and East Area–203.5 ha.

Methods

Plot Selection

Selection of sample points for our study involved a two-tiered approach. First, we selected sample points through use of GIS databases of gopher tortoise distributions and ArcMap programs (Beyer 2004). Following completion of this task, we conducted field surveys to validate locations of gopher tortoise burrows and absence of gopher tortoise burrows in non-burrow locations prior to final inclusion of selected sample points.

During winter 2007, we determined distribution of gopher tortoise burrows using existing databases retained by MSARNG and The Nature Conservancy. These databases were based on surveys that had identified tortoise burrow locations from 2002 through 2006. We selected sample points at known active burrow locations based on these databases and digital imagery prior to field inspections of sample points. All burrows selected for inclusion were located a minimum of 30 m from one another based on daily foraging distances from burrows reported for gopher tortoises (Yager et al. 2007). Databases of active burrow locations indicated that training areas supported variable densities of active gopher tortoise burrows. We included all active burrow locations reported on each of the three training sites which yielded numbers of active burrow sample points per training site as follows: Mars Hill Training Area: 24 active burrows; T-44 Training Area: 18 active burrows; and East Area Training Area: three active burrows. To supplement sample size and address variable burrow occurrence on the three training areas, we selected 15 inactive burrow sites on each site using the afore-indicated selection criteria which produced a sample size of a total of 45 inactive burrows to be included in our burrow sample population. This approach resulted in selection of 90 active and inactive burrows from existing databases prior to field inspection and validation.

From existing databases and digital imagery, we selected 123 non-burrow points within the three training areas. Prior to sample point selection, low topographic elevations such as wetlands, drainages, and lower portions of slopes, were excluded as candidate sample points due to unsuitable soil and hydrological conditions for tortoises (U.S. NRCS 2012). We selected non-burrow locations within eight concentric buffer zones radiating out at 30-m intervals initiating at 60 m from known burrow locations using the buffer operation in ArcMap and Hawth's Tool extension (Beyer 2004). Therefore, all non-burrow locations selected using this approach were a minimum of 60 m from known burrow locations. We used distance criteria within buffers for sample point selection to increase the likelihood of independence of sample points between burrow and non-burrow locations and to avoid potential overlap of occupied and non-occupied locations based on distances of tortoise movement (McRae et al. 1981, Ashton and Ashton 2008).

Following GIS-based sample point selection, we conducted field inspections of burrow and non-burrow locations during May 2007. We inspected non-burrow sample points to validate the absence of tortoise burrows and distance criteria imposed by our design. At burrow sample points, we assessed current activity status of tortoise burrows according to activity categories of active, inactive, or abandoned as described by Guyer and Hermann (1997). We considered burrows active if they had an opening with an outline similar to a tortoise carapace, a soil apron at the burrow entrance relatively free of vegetation, and presence of visible tracks, digging, or plastron markings at burrow soil aprons or entrances (Guyer and Hermann 1997). We classified burrows as inactive if openings were intact but lacked signs of fresh tortoise activity (Auffenberg and Franz 1982, Guyer and Hermann 1997). Following field inspection, we included a total of 90 inactive and active burrows in our sample population as follows: Mars Hill Training Area: 39 burrows; T-44 Training Area: 33 burrows; and East Area Training Area: 18 burrows. Abandoned burrows were not included in our sample population (Auffenberg and Franz 1982).

Habitat Evaluation

We conducted habitat surveys to estimate forest stand and vegetation characteristics at each selected sample point (tortoise burrows: $n = 90$ and non-burrow points: $n = 123$) during June 2007. At all burrow locations, we established one 30-m line-transect that originated 0.5 m from the burrow's entrance and extended in the direction of the burrow opening. For non-burrow locations, we established one 30-m transect from a pre-selected random coordinate and extended it in a randomly selected cardinal direction (Jones and Dorr 2004). Burrow and non-burrow locations and associated transects were recorded geospatially.

Along each transect, we estimated percent coverage of understory and midstory vegetation, bare ground, debris, and leaf litter using methods described by Hays et al. (1981). We grouped vegetation into growth forms and two height regimes: understory vegetation—≤1 m and midstory vegetation—>1 m–6 m (Hays et al. 1981). We identified plants to taxonomic species and grouped plants into herbaceous and woody growth forms. We counted stems of trees and shrubs that intersected each line transect at 0.5 m and 2 m in height using standard carpenter rulers. We measured litter depth (cm) at the midpoint and endpoint of each transect with standard carpenter rulers (Hays et al. 1981). At each burrow and non-burrow sample point, we established 10-m radius plots for estimation of forest stand conditions. Within each plot, we recorded all trees species ≥7.62 cm in diameter-at-breast height (DBH), and we measured DBH to nearest 0.25 cm and total height to nearest 0.30 m of each tree using methods (Avery and Burkhart 1994). Within each plot, we estimated overstory canopy coverage with spherical densitometers at plot center and in eight cardinal directions (Hays et al. 1981).

We acquired baseline geospatial data of roads, streams, boundaries and soil types from MSARNG-GIS coordinator at CSJFTS. We acquired soil descriptions from the Natural Resources Conservation Service (U.S. NRCS) and used these to assign soil texture and drainage classes for all soils polygons (Soil Survey Staff 2007). We used U.S. Geological Survey 10-m DTMs (10 m × 10 m grid cells) from the Mississippi Automated Resource Information System (MARIS) to calculate slope, aspect, and slope curvature (Jensen and Domingue 1988).

Statistical Analysis

We included 54 potential explanatory variables into analyses based on field and GIS-derived data. We tested for normal distribution and homogeneous variance characteristics of data according to methods described by Ott and Longnecker (2001). We used square root transformation to normalize stem count and plant species richness data (Ott and Longnecker 2001). We examined relationships between explanatory variables using Pearson Correlation analysis and excluded one of two collinear variables ($r^2 \geq 0.50$) based on the variable's importance to tortoise habitat quality as reported in current peer-reviewed literature (Myers 1990, SAS Institute, 2002, Kutner et al. 2004, Ashton and Ashton 2008). We used Multivariate Analysis of Variance (MANOVA) to test the following hypotheses: (1) no overall effect of study site on vegetative and topographic characteristics, and (2) no overall effect of plot type (burrow or non-burrow) on vegetative and topographic characteristics (Ott and Longnecker 2001, SAS Institute 2002). Data included in these analyses were based on 79 burrow and 109 non-burrow plots due to omission of plots that lacked matched data for understory and overstory estimation in subplots and exclusion of plots that occurred in drainages or on unsuitable soils (<50 m). Variables included in comparisons of conditions between study areas and burrow and non-burrow locations included mean percent coverage of bare ground, understory herbaceous vegetation, legumes, understory trees and shrubs; species richness of understory herbaceous vegetation, understory trees and shrubs, and legumes; mean number of woody plant stems >1 m – 6 m height/transect; number of overstory pine trees, mean and maximum DBH of overstory trees, maximum height of overstory trees, and percent coverage of overstory canopy in 10-m radius plots, and elevation. If significance was found for the overall model, we tested the univariate main effects for study site. We considered all tests significant at $P \leq 0.05$ and used Wilks Lambda to test for goodness-of-fit (Kutner et al. 2004). We used the Least Square Means procedure to conduct multiple comparisons among study sites and between burrow and non-burrow plots within study sites (Ott and Longnecker 2001, Kutner et al. 2004).

Investigation of relationships between burrow and non-burrow plots and habitat conditions of these plots was a two-step process. We used decision tree analysis as a data reduction technique (De'ath and Fabricius 2000, Lewis 2000). Initially, we examined dependent variables and determined possible splitting criteria (Lewis 2000). Following initial splitting of the data set, we repeated the process independently for observations on each branch of the decision tree. This approach allowed estimation of predictor and response variable associations with χ^2 levels (Lewis 2000). Following this procedure, stepwise logistic regression was performed on predictor variables that were associated with burrow or non-burrow occurrence through decision tree analysis (Hosmer and Lemeshow 1989, SAS Institute 2002). All of the critical variables and interactions between critical variables were evaluated in regression analyses and variable associations were considered significant at $\chi^2 \leq 0.05$ (Hosmer and Lemeshow 1989). We tested the final model through cross validation within our dataset to test accuracy for burrow prediction (Kutner et al. 2004).

Results

Habitat Characteristics of Study Sites

Forest stand conditions of our study sites were typified by a dominance of longleaf pines in the overstory (≥75% frequency of occurrence). Other tree species recorded in the overstory and midstory were loblolly pine (*P. taeda*), red maple (*Acer rubrum*), flowering dogwood (*Cornus florida*), sweetbay magnolia (*Magnolia virginiana*), oaks, black gum (*Nyssa sylvatica*), black cherry (*Prunus serotina*), tulip tree (*Liriodendron tulipifera*), and sweetgum (*Liquidambar styraciflua*). Common midstory shrubs were yaupon (*Ilex vomitoria*), gallberry (*I. glabra, I. coriacea*), wax myrtle (*Morella cerifera*), sweetleaf (*Symplocos tinctoria*), sumac (*Rhus* spp.), and blueberry (*Vaccinium* spp.). Canopy coverage of overstory and midstory typically exceeded 40% on the three training sites (Table 1). Mean percent coverage of herbaceous plant species ranged from >25% to 74% (Table 1). Of the 101 herbaceous plant species detected, common tortoise food plants included bluestems (*Andropogon* spp. and *S. scoparium*), three-awned grasses (*Aristida* spp.), panic grasses (*Panicum* spp. and *Dichanthelium* spp.), beggarticks and trefoils (*Desmodium* spp.), lespedeza (*Lespedeza* spp.), goat's rue (*Tephrosia* spp.), and Asteraceae forbs (*Solidago*, *Aster*, *Pityopsis* spp.). Prickly pear cacti (*Opuntia* spp.) and lichen (*Cladonia* spp.) were present on one study site which exhibited deep sands and sandhill community characteristics.

Table 1. Habitat characteristics of burrow and non-burrow locations of gopher tortoises (*Gopherus polyphemus*) on Camp Shelby Joint Forces Training Center, Mississippi, June 2007.

	T-44				Mars Hill				East Area			
	Burrow		Non-burrow		Burrow		Non-burrow		Burrow		Non-burrow	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Bare ground percent coverage	7.70	2.20	8.00	2.20	3.40	1.10	3.50	0.90	0.50	0.30	0.40	0.30
Debris percent coverage	19.50	1.80	18.60	2.10	42.10	3.20	34.40	3.20	35.30	3.70	23.10	2.10
Understory herbaceous[a] percent coverage	65.00	4.70	73.90	4.70	29.90	3.80	42.70	4.50	25.70	3.90	38.20	5.10
Legume species richness	3.12	0.23	1.85	0.19	1.85	0.21	1.06	0.14	1.67	0.31	1.06	0.18
Understory woody[b] percent coverage	25.60	2.30	19.10	2.80	40.30	3.10	38.30	2.90	50.70	4.90	53.70	4.90
Midstory woody[c] percent coverage	12.20	2.00	5.90	1.80	24.30	2.30	10.50	1.90	15.50	2.50	11.20	1.80
Midstory stem count (intercepting each 20 m line intercept)	20.61	4.52	7.63	3.11	52.67	6.76	22.19	5.39	35.67	8.00	31.94	8.70
Overstory canopy percent coverage	56.19	3.04	62.58	1.72	43.67	3.65	42.03	3.54	16.72	2.77	38.78	3.31
Total basal area (m^2 per plot)	3.84	0.42	5.24	0.44	2.93	0.28	5.78	0.51	4.93	0.57	7.62	0.50
Trees per ha	21.32	2.52	29.99	3.96	51.33	5.50	53.98	6.44	62.84	9.23	50.74	3.79
DBH of pine (m)	0.29	0.02	0.40	0.02	0.16	0.01	0.23	0.02	0.23	0.02	0.31	0.02
Mean tree ht (m)	17.62	0.94	19.58	0.70	11.74	0.74	14.71	0.94	14.58	0.92	17.93	0.58
Maximum tree ht[d] (m)	21.32	1.02	23.63	0.70	15.19	1.01	20.76	1.22	20.09	0.92	25.73	0.74
Elevation (m)	241.40	2.29	217.83	3.34	215.39	3.37	215.90	4.91	167.37	1.61	157.38	2.87

a. Understory Herbaceous–Grasses, grass-like, forb, and legume species of <1 m in ht;[b] Understory Woody- Trees, shrubs, and vine species of <1m in ht;[c] Midstory Woody–Tree and shrub species of 1–6 m in ht;[d] Average maximum tree ht per plot.

Comparisons of Habitat Characteristics between Military Training Sites

One-way MANOVA revealed a significant multivariate main effect for study site (Wilks $\lambda = 0.14$, $F = 19.64$, df = 30,342, $P < 0.001$). Significant univariate main effects were found for species richness and percent coverage of understory herbaceous and woody vegetation, species richness and percent coverage of understory legumes, percent coverage of bare ground, number of woody plant stems in midstory, number of overstory pine trees, mean tree DBH, maximum tree DBH, maximum tree height, percent coverage of overstory canopy, and elevation ($F \geq 6.68$, df = 2,185, $P < 0.002$; Table 1).

Of the three study sites, T-44 exhibited the greatest species richness and percent coverage of herbaceous understory plants and species richness and percent coverage of native legumes (Table 1). The least coverage of understory and midstory woody plants was estimated on T-44 with woody plant coverage (Table 1). Longleaf pine forests of T-44 exhibited >55% overstory canopy coverage and >17 m tree heights. Mean elevations of non-burrow and burrow plots were also greatest on T-44 (>217 m) (Table 1). Mars Hill and East Area exhibited greater coverage of woody plants in the understory than T-44 (Table 1). Number of stems of woody plants in the midstory was greatest on Mars Hill on non-burrow and burrow locations (Table 1).

Comparisons of Habitat Characteristics of Burrow and Non-burrow Plots

One-way MANOVA revealed a significant multivariate main effects for plot type on T-44, Mars Hill, and East Area training areas (Wilks $\lambda > 0.22$, $F > 6.06$, $P < 0.001$). On T-44, significant univariate main effects were as follows: elevation, species richness of understory herbaceous vegetation, species richness of understory woody vegetation, species richness of understory legumes, percent coverage of understory legumes, stem count of woody plants in midstory, mean DBH, maximum tree height, and number of overstory pine trees ($F > 4.14$, df = 1,65, $P < 0.05$). When compared to non-burrow plots, burrow plots of T-44 were located on higher elevations and were characterized by greater species richness of understory herbaceous and woody plants, species richness and percent coverage of legumes, and number of stems and percent coverage of woody plants in midstory (Table 1).

Comparisons of habitat conditions at burrow and non-burrow plots of Mars Hill yielded significant univariate main effects as follows: species richness of understory legumes, percent coverage of understory legumes, stem count of woody plants in midstory, mean DBH, maximum DBH, and tree height ($F > 6.0$, df = 1,68, $P < 0.02$). Burrow plots of Mars Hill were characterized by greater species richness and percent coverage of understory legumes and greater number of woody plant stems in midstory than non-burrow plots (Table 1).

Comparisons of habitat conditions on burrow and non-burrow plots of East Area yielded the following significant univariate main effects: mean DBH, overstory canopy coverage, maximum DBH, tree height, and elevation ($F > 6.02$, df = 1,49, $P < 0.02$; Table 1). On East Area, burrow plots were located on higher level elevations than non-burrow plots. Overstory tree heights and DBH and overstory canopy closure was typically greater on non-burrow plots than burrow plots on East Area (Table 1).

Decision Tree and Logistic Regression Analyses

Decision tree analyses of data from 79 burrow and 109 non-burrow plots yielded five critical variables with relationships to burrow occurrence: maximum height of overstory trees, percent coverage of overstory, stem count of woody plants in midstory, species richness of understory legumes, and GIS-derived elevation. The greatest number of burrow plots (53) was segregated using maximum overstory height value of ≤21.3 m as a criteria resulting in 89 non-burrow plots remaining on the other side of the decision tree (Figure 1). The second node segregated burrow plots with finer resolution based on stem counts of woody plants in midstory. This analysis resulted in identification of 100% of burrow plots that were characterized by maximum overstory heights of ≤21.3 m and a midstory stem counts >46 stems. If conditions

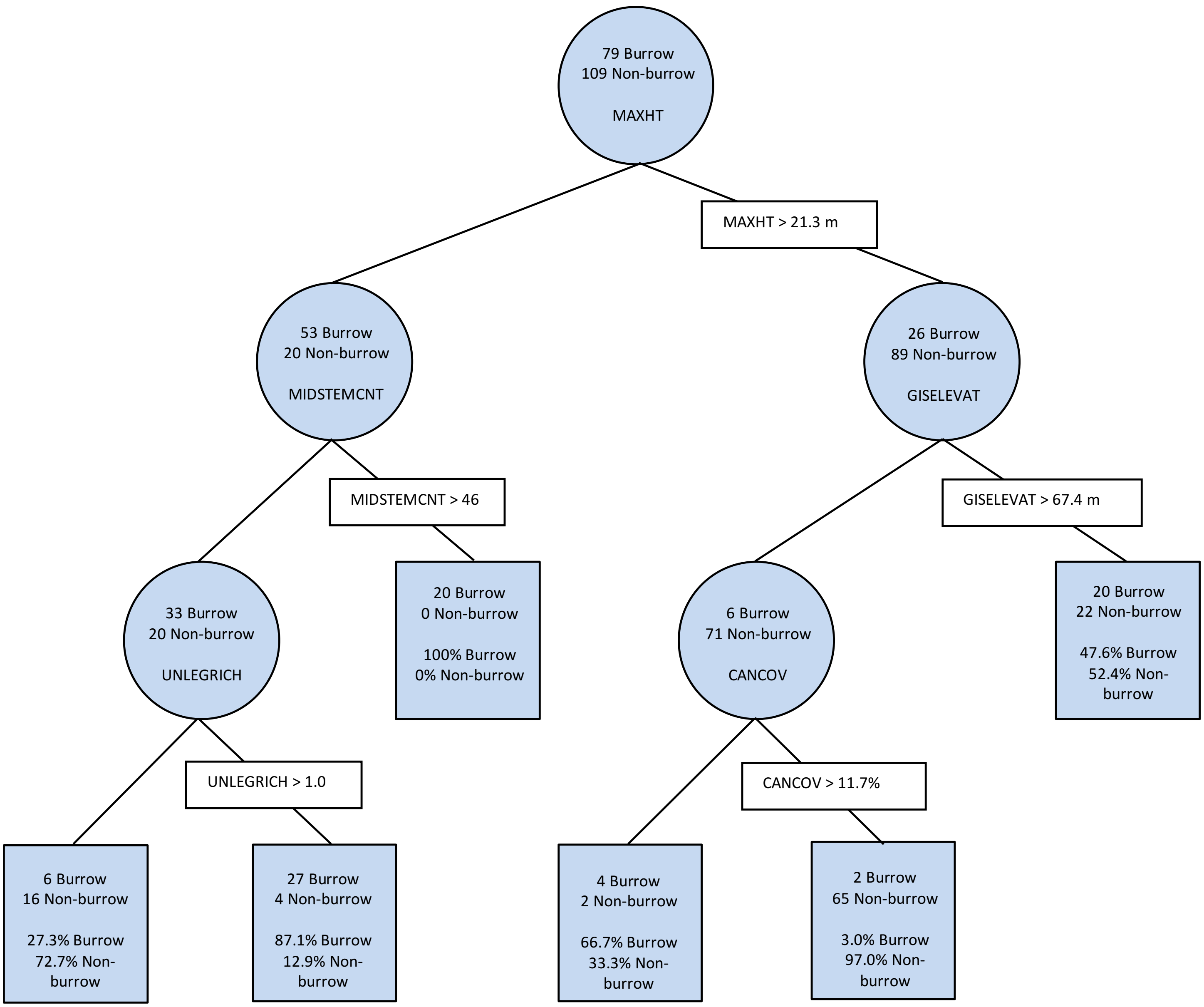

Figure 1. Decision tree for field and GIS variables ($\chi^2 = 0.01$) with probabilities of burrow versus non-burrow plots at terminal nodes for the path set by the decision criteria derived from data collected on Camp Shelby Joint Forces Training Site, Mississippi in summer 2007.

indicated for maximum overstory height of >21.3 m, GIS-derived elevation of ≤67.4 m, and overstory canopy coverage of >11.7% were met, 65 non-burrow plots were successfully identified with a 97.0% probability. Correlation analysis indicated moderate collinearity ($r = 0.42$, $P < 0.001$) between elevation and canopy coverage, but the variables were retained for regression analysis based on degree of correlation and their reported importance in habitat evaluation for gopher tortoises (Ashton and Ashton 2008). From the possible five critical variables and the 26 interaction terms, logistic regression with stepwise variable reduction yielded the following model:

Logit (burrow) = 10.61 – (0.09) Maximum Tree Height in Overstory + (0.85) Total Stem Count of Woody Midstory Plants + (1.69) Species Richness of Understory Legumes – (0.03) GIS-derived Elevation – (0.42) Percent Canopy Coverage of Overstory – (0.01) Maximum Tree Height * Total Stem Count of Midstory Woody Plants + (0.002) Maximum Tree Height in Overstory * Percent Canopy Coverage of Overstory + (0.008) Total Stem Count of Midstory Woody Plants * Percent Canopy Coverage of Overstory + (0.001) GIS-derived Elevation * Percent Canopy Coverage of Overstory.

Within-model cross-validation predicted presence of active and inactive burrows for 90.6% of the observed outcomes.

Discussion

Our findings were similar to other studies that have reported associations between burrows of gopher tortoises and adequate foraging and basking conditions (Guyer and Hermann 1997, Jones and Dorr 2004, Yager et al. 2007, Ashton and Ashton 2008). Our findings also supported those reported by Yager et al. (2007) in that tortoises may often exhibit burrow site fidelity despite advancing woody plant succession. Logistic regression analysis indicated that the strongest predictors of burrow presence were species richness of understory legumes, stem counts of midstory vegetation, and percentage of overstory canopy closure. Our findings of positive associations between burrow occurrence and openness of overstory canopy were similar to studies that reported benefits of open canopy conditions for gopher tortoises (Aresco and Guyer 1999, Boglio et al. 2000, Hermann et al. 2002). Positive association between tortoise burrows and species richness of legumes was in concurrence with other studies that have reported legumes to be valued food plants for tortoises (Garner and Landers 1981, MacDonald and Mushinsky 1988, Mushinsky et al. 2006). Legumes have been reported to be an important food plant due to high palatability and nutritional content including protein, Vitamin A, and minerals including calcium (Garner and Landers 1981). In their study in Georgia, Garner and Landers (1981) reported that legumes were important food plants of gopher tortoises. Nutritional content analyses conducted by Garner and Landers (1981) revealed that native legumes exhibited greater mineral content than did native grasses and selected forb species. On our study sites, leguminous plants of known value to tortoises were detected with the most common species being beggarticks (66% of plots), goat's rue (33% of plots), lespedezas (31% of plots), vetches (*Vicia* spp.; 17% of plots), and milk peas (*Galactia* spp.; 9% of plots; MacDonald and Mushinsky 1988, Mushinsky et al. 2003). Collectively, native legumes were detected ≥20% frequency of occurrence on transects of gopher tortoise burrows, and native legumes persisted on one training sites that exhibited >45% coverage of midstory shrubs and trees. Relationships of burrow occupancy to species richness of understory legumes suggested that food plant quality might be important in allowing tortoises to persist in habitats with advancing woody plant coverage. Presence of legumes on sandy soils of two training areas despite woody plant coverage in midstory may explain our findings of positive associations between stem counts of woody plants and tortoise burrows, a finding that does not concur with many studies on tortoise habitat quality (Jones and Dorr 2004, Yager et al. 2007, Ashton and Ashton 2008).

Our findings related to associations between elevation and tortoise burrows warrant discussion and consideration of burrow locations on the three training sites and our sampling design. Our MANOVA results indicated that burrows were associated with higher elevations than non-burrow locations on two of the three training sites, and this finding is consistent with other studies (Jones and Dorr 2007, Ashton and Ashton 2008). However, logistic regression analysis indicated a negative association between burrow occurrence and elevation. At least one of our study sites exhibited a greater number of non-burrow locations than burrow locations at elevations of >200 m. Sandhill plant communities and deep sands on ridgetops and side slopes of ridges typified this study site. On this study site, most (>75%) active and inactive burrows were located on side slopes of ridges (185 m to 230 m). We hypothesize that tortoises of this site utilized side slopes for burrow construction due to the availability of deep sand substrates in these locations. Our findings are in concurrence with others who reported that tortoises tend to construct their burrows on upper side slopes of ridges with deep sand soil types (Auffenberg and Franz 1982). In addition to being more suitable for burrow construction, well-drained sandy soils are typically more xeric and exhibit greater fire frequencies that stimulate pyric plant communities that benefit tortoises (Yager et al. 2007, Ashton and Ashton 2008). Also, because we excluded drainages and low-lying elevations (<50 m) to avoid unsuitable soils and hydrological conditions for tortoises, we did not evaluate tortoise burrow location as related to the entire range in elevations on study sites. We selected burrow locations from GIS databases and selected non-burrow locations within designated buffers in vicinities of tortoise-occupied areas. As a result of this study design, elevation of sample points for burrow and non-burrow locations of our study ranged from 132 m to 267 m. Interpretation of our model should consider this study design strategy. We submit that soil suitability classes as described by USFWS and U.S. NRCS (2012) should be considered in addition to site elevation within the northwestern distributional range when assessing site suitability for tortoises, because these suitability rankings have been developed through reference to long term studies of tortoise occupancy, recruitment, and habitat quality (USFWS and U.S. NRCS 2012).

One challenge of our study was the variability in habitat conditions and tortoise densities of our three training area study sites. Among the three surveyed areas, T-44 had the greatest proportion of active burrows per study area (0.06 burrows/ha). This area had been actively managed for gopher tortoise conservation since federal listing in 1987 (Yager et al. 2007). Past management included application of growing and dormant season prescribed fire at three- to four-year return intervals, control of invasive species, and silvicultural management of forests (Yager et al. 2007). Sample points in this area were typically located at higher elevations and exhibited greater coverage of herbaceous ground cover plants than the other study sites. Percent coverage of legumes, forbs, and grasses usually exceeded 65% on both burrow and non-burrow plots. This study site also exhibited a greater species richness and coverage of leguminous food plants than other sites. Greater abundance and coverage of herbaceous ground cover and less woody plant coverage at ground and midstory levels were potentially related to history of prescribed fire management on T-44. These ground cover characteristics have been reported as good foraging conditions for gopher tortoises and are common in open canopy, longleaf pine forests managed with two- to three-year fire return intervals (Auffenberg and Franz 1982, Yager et al. 2007).

Numbers of active burrows were similar between T-44 and Mars Hill (0.05 burrows/ha). However, habitat conditions varied between the two sites with Mars Hill exhibiting greater coverage of midstory trees and shrubs (>24%) and greater debris coverage (≥42%). Also, coverage of woody plant midstory and debris was greater on burrow plots than non-burrow plots. Percent coverage of herbaceous ground cover on both plot types was ≤43% that was less than food plant coverage recommended for tortoises. For example, studies conducted on industrial timberlands and public lands reported that gopher tortoises typically utilized habitats with open overstory canopy (<60% canopy closure), abundant herbaceous understory (>50% coverage), and sparse midstory shrub cover (McRae et al. 1981, Jones and Dorr 2004, Yager et al 2007). In addition to vegetation conditions, Jones and Dorr (2004) reported that edaphic factors, such as elevation and deep sandy soils, were related to occurrence of active burrows on industrial timberlands in south Alabama and Mississippi. Although our study sites were typified by dominant coverage of suitable soils for gopher tortoises, detailed investigations of updated digital NRCS soil surveys revealed that >40% of Mars Hill had Wadley fine sands, highly suitable soils for gopher tortoises (USFWS and U.S. NRCS 2012). Therefore, this training site was typified by a mosaic of suitable and highly suitable soils, which are characterized by coarse well-drained sands of ≥1 m in depth, edaphic conditions that represent optimal conditions for burrowing and nesting (USFWS and U.S. NRCS 2012). Soils and past fire history of this site created sandhill plant communities characterized by high quality, drought tolerant food plants, such as legumes (*Rhynchosia*, *Stylosanthes*, beggartick and trefoil, lespedezas, forbs (Family Asteraceae), prickly pear cacti, and soft-mast producing shrubs and vines (blueberry and *Licania michauxii*; Garner and Landers 1981, MacDonald and Mushinsky 1988). Tortoises occupying this site may have remained on site due to interspersion of high quality food plants and highly suitable burrowing conditions despite greater stem densities of woody plants. Also, site fidelity to home burrows reported by Yager et al. (2007) may have also played a role in that tortoises remained in their home burrow complexes despite percent coverage and stem densities of woody plants surrounding the burrow. Yager et al. (2007) found that gopher tortoises exhibited site fidelity to their burrows and did not relocate from habitats with less desirable vegetation cover type to adjacent habitats in which prescribed burning had improved food plant availability. Because tortoises may remain at home burrow systems, show selectivity for deep sandy soils for burrow construction, and sun-exposed soil surfaces for basking, nesting, and foraging, a combination of edaphic and plant community conditions probably influenced distribution gopher tortoise burrows on Mars Hill.

Habitat conditions found on East Area were the least favorable for supporting gopher tortoises, and initial burrow searches revealed that this area had the fewest number of active burrows (0.01 burrows/ha). This area had significantly greater coverage of understory trees and shrubs (≤1m height) than T-44 and Mars Hill and 83% of burrow plots surveyed within East Area were inactive burrows. Woody understory coverage exceeded 50% on burrow and non-burrow plots and coverage of herbaceous vegetation averaged 26% at burrow locations. East Area plots also supported the least species richness and percent coverage of legumes compared to other study sites. Of the three study sites, East Area had the least history of prescribed fire and silvicultural management for tortoises. Advancing woody plant succession and less availability of tortoise food plants on East Area indicated a need for habitat management if tortoise habitat quality is of importance (Russell et al. 1999, Yager et al. 2007).

At the time of our study, habitat conditions for tortoises at East Area were considered suboptimal, and these conditions may have been related to catastrophic events of 2005. Our study was conducted two years following Hurricane Katrina's 2005 landfall. At the time of our 2007 study, habitats of our study sites were exhibiting a dominance of shrub and sapling cover of <1 m in height. This advanced woody plant succession was detected surrounding burrows of gopher tortoises and non-burrow locations and was potentially related to burning bans implemented after Hurricane Katrina's landfall. In the three years following Hurricane Katrina, hazardous fuel loads followed by abnormally low rainfall levels during 2006–2007 caused burning bans to be implemented for hurricane impact zones in south Mississippi (Lee 2009, U.S. Drought Monitor Archives 2010). We suggest that coverage and densities of midstory and woody plants detected in our study were a result of burning bans and subsequent lapses in prescribed burning on training sites from 2005 through 2007. Because fire suppression over five to seven years has been shown to render habitat unsuitable for tortoises, implementation of prescribed burning should be prioritized on sites with advancing woody plant succession (Aresco and Guyer 1999). Over time without regular prescribed fire application, shrub and sapling cover may exclude sunlight penetration to ground surface reducing quality of nesting, basking, and foraging conditions. Under these conditions, tortoises may abandon occupied sites as habitat quality continues to decline (Aresco and Guyer 1999, Jones and Dorr 2004). Without habitat management in occupied areas, gopher tortoises of military training sites may relocate to anthropogenically-maintained and intensely-utilized ruderal areas, such as road and utility rights-of-way, tank trails, troop staging areas, and artillery firing points and impact areas (Yager et al. 2007). This movement and relocation typically poses challenges in military training and tortoise conservation due to increases in tortoise mortality rates and recruitment failures due to exposure to traffic, poaching, collection, and depredation by native and non-native predators (Epperson and Heise 2003, Yager et al. 2007).

Implications

Our study documented the conditions in which tortoises existed on three military training areas in summer 2007. Plant community and tortoise densities were variable on our study sites; however, greatest numbers of active and inactive burrows were detected on two study sites that exhibited open overstory canopy conditions, greatest species richness of herbaceous legumes, and interspersion of deep sandy soils for burrow construction. We also found that tortoise burrows were associated with increasing woody plant stem densities that is in contrast to many other studies. However, we suggest that advancing woody plant colonization in understory and midstory may have been due to reduced implementation of prescribed burning following Hurricane Katrina's 2005 landfall (Lee 2009). On at least one training area, habitat quality for tortoises was poor, and this area exhibited the least number of active burrows. The best forest stand and forage plant cover was detected on the training area that was managed for tortoises through prescribed fire and other silvicultural measures. Because of advancing woody plant colonization on two training sites, we suggest that our models cannot be used as predictors for habitat quality for gopher tortoises due to the occurrence of tortoise burrows in sub-optimal conditions. Our models revealed current conditions at burrow and non-burrow locations and provided quantitative data that could be utilized in planning and implementing remedial habitat management measures for tortoises on these areas. Following recovery from Hurricane Katrina's impacts, implementation of prescribed burning has been used to enhance coverage of food plants on training sites.

Rarity of active burrows on training areas presented challenges in the design of our study. Because of the scarcity of active burrows on one study site, we selected unequal numbers of active burrows from each training site. Also, we included inactive burrows that exhibited no recent signs of recent, visible tortoise activity in our sample population. Inclusion of inactive burrows may have biased our findings due to the possibility that the occupant had abandoned these burrows. Unequal sample sizes between training areas and between plot types may also have influenced our findings. However, we encountered challenges in locating sufficient numbers of active tortoise burrows on training areas within our study design criteria for addressing independence of sample points. Also, we found that selection of active burrows based on GIS databases of recent (<5 years) tortoise surveys was not adequate for determining a sample population without follow-up field investigations. We suggest that selection of sample burrow populations through existing databases should be followed by field surveys to validate activity status of tortoise burrows. If distance criteria are necessary for addressing independence of burrow and non-burrow sample points, researchers should conduct field surveys in adequate time to incorporate field reconnaissance information into the study design prior to initiation of the targeted study. Additionally, our study involved three training sites at CSJFTS with one summer of data collection. This sampling intensity level possibly influenced the power of inference of our study's findings and may be an impediment to extrapolation of our findings to areas outside of CSJFTS. We submit that our study could have been strengthened by inclusion of additional training sites, collection of data over multiple growing seasons, scoping of burrows to ensure tortoise occupancy, and incorporation of soil suitability classes into sample point selection.

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