

**MODELING GOPHER TORTOISE (*GOPHERUS POLYPHEMUS*) HABITAT IN A
FIRE-DEPENDENT ECOSYSTEM IN NORTH FLORIDA**

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DEDICATION

This paper is dedicated to my father, my inspiration, my best friend and my hero, Clovis Peter Legleu III (1938-2010).



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ABSTRACT

Gopher tortoise (*Gopherus polyphemus*) populations have declined with longleaf pine (*Pinus palustris*) ecosystems across their historic range. The influence of gopher tortoise burrows on co-inhabiting plants and animals necessitates an understanding of how landscape features and management practices influence gopher tortoise presence, absence, and abandonment. In this study, naïve gopher tortoise burrow encounter rates from a line transect distance sampling (LTDS) pilot study were used for two methods of modeling gopher tortoise habitat.

In Chapter 1, naïve encounter rates were tested for linear correlation to a HSI model created from three ranked geographic information system (GIS) landscape variables. Initial results showed a positive linear correlation (all $P < 0.0001$, $0.55 < r < 0.70$) but a second test using only transects with observed burrows resulted in the loss of all correlations (all $P > 0.05$, r values ranged from 0.17 to 0.42). However, logistic regression analysis revealed the HSI model was able to predict burrow presence along transects ($P = 0.0003$).

In Chapter 2, microhabitat variables and five GIS landscape variables were reduced into seven correlated principal components (PCs). According to a generalized linear (logit) model three PCs were significantly associated to active and abandoned burrows. Active burrows were positively associated to: 1) sandhill habitats, longleaf pine canopy, Lakeland soils, high elevations, xeric oak midstory, and wiregrass (*Aristida beyrichiana*) presence (overall $P = 0.003$; active $P = 0.008$); and 2) grassland habitats, little to no canopy, and increased herbaceous ground cover (overall $P = 0.0042$; active $P = 0.0052$). Active burrows were negatively associated to mesic flatwoods, Scranton soils, mixed pine canopy, high basal areas, and increased percent tree canopy (overall $P = 0.003$; Active $P = 0.008$). Abandoned burrows were positively associated to xeric hammocks, xeric hardwood canopy, mesic hardwoods midstory, increased canopy cover,

increased litter ground cover, and increased mean years between burns (overall $P = 0.0448$; abandoned $P = 0.0137$). The relationship between fire suppression and burrow abandonment is widely accepted but poorly documented, and the poor resolution of this fire layer accentuates the importance of this detected relationship.

CHAPTER 1. A GIS BASED HABITAT SUITABILITY INDEX MODEL FOR GOPHER TORTOISES AT ST. MARKS NATIONAL WILDLIFE REFUGE, FLORIDA

INTRODUCTION

The longleaf pine (*Pinus palustris*) ecosystem of the southeastern United States is a community rich with rare and endemic plant and animal species. It is home to specialized inhabitants such as the gopher tortoise (*Gopherus polyphemus*), which is federally threatened in the western portion of its range and was recently added to the U.S. Fish and Wildlife Service's (USFWS) candidate species list in the eastern portion of its range (Federal Register, 2011). Gopher tortoise burrows are an integral part of this community as they provide refuge to over 300 species of vertebrate and invertebrate species including the federally Threatened eastern indigo snake (*Drymarchon corais couperi*), and both the Florida pine snake (*Pituophis melanoleucus mugitus*) and the gopher frog (*Rana capito*) (Hubbard, 1983; Franz, 1984; Franz, 1986; Jackson and Milstrev, 1989; Lips, 1991; Witz *et al.*, 1990; Witz *et al.*, 1991) which are listed as Species of Special Concern by the Florida Fish and Wildlife Commission (FFWCC, 2008). Gopher tortoises also play other important roles in their community by acting as seed dispersers (Auffenberg, 1969; Landers 1980) and creating heterogeneous local habitats through burrow excavation that influence plant community structure (Kalisz and Stone, 1984).

According to Noss *et al.* (1995), the longleaf pine ecosystem is critically endangered. Pre-European settlement longleaf pine forests dominated between 60,000,000 and 92,000,000 acres of the Atlantic and Gulf Coastal Plains (Wahlenburg, 1946; Frost, 1993; Ware *et al.*, 1993; Noss *et al.*, 1995) while most recent estimates of remaining longleaf pine forests are less than 3,000,000 acres (Dennington and Farrar, 1983; Landers *et al.*, 1995; Engstrom *et al.*, 1996), with old-growth longleaf pine forests covering only 12,590 acres representing only 0.004% of

remaining longleaf forests, and 0.00014% of pre-settlement longleaf forests (Varner and Kush, 2004).

St. Marks NWR is located in the Big Bend region of Florida, south of Tallahassee, and is situated within the historic range of longleaf pine forests (U.S. Fish and Wildlife Service, 2006). Gopher tortoises are currently distributed across the western half of the refuge in xeric upland habitats but recent concerns have arisen over potential habitat degradation from hardwood encroachment, insufficient fire return intervals, and the long term consequences of historic trapping of gopher tortoises as a food source in the surrounding community (M. Keys, St. Marks NWR, pers. comm.). The recent gopher tortoise status update suggested management goals be aimed at removing or alleviating current threats to the gopher tortoise in hopes of eliminating the need for listing under the Endangered Species Act (Federal Register, 2011). Specific recommendations included restoring degraded habitat and maintaining suitable habitat on public lands by way of mechanical vegetation removal and short fire return intervals, eliminating legal harvests of burrow inhabitants (*i.e.* rattlesnake roundups), screening for diseases, and protecting nests from predation in populations identified at high risk (Federal Register, 2011). Additional emphasis was placed on using advances in GIS to model potential gopher tortoise habitat, and to additionally collect information regarding local population numbers and the impacts and effectiveness of management activities.

In 1979, a survey estimated there to be 5,589 acres of suitable gopher tortoise habitat on St. Marks NWR, with a density of one tortoise per 2.74 acres and a total population size of 2,500 individuals (Logan, 1981). In 1988, another survey estimated there to be 1,811 acres of gopher tortoise habitat with 2,765 active, 2,890 inactive, and 1,438 abandoned burrows but gave no estimate of actual density or population size (McCoy and Mushinsky, 1995). More recent non-

strategic surveys were implemented by St. Marks NWR, who surveyed 1,670 acres of recently burned units from November 2005 to April 2006. They observed 58 tortoises via camera scope, and counted 128 active, 133 inactive, and 13 abandoned burrows (M. Keys, St. Marks NWR, pers. comm.). However, there have not been any strategic surveys attempted on the refuge in over two decades.

Line Transect Distance Sampling (LTDS) (Buckland *et al.*, 2001) is a commonly-used method of obtaining gopher tortoise population estimates because of its efficiency and accuracy, and because repeated surveys allows conservation professionals to detect population trends over time (Carthy *et al.*, 2005; Meyer *et al.*, 2008; Nomani *et al.*, 2008). One caveat of LTDS is defining potentially suitable habitat, referred to as the sampling frame, then conducting a pilot survey within that sampling frame to determine the naïve rate (termed so because detection probabilities for different habitats were not determined) of tortoise encounters per distance surveyed. This naïve rate is used to determine which areas of the sampling frame have encounter rates high enough to be included in the final survey (Buckland *et al.*, 2001). Because pilot surveys are conducted across the entire sampling frame, they provide burrow encounter rates (from here on out referred to as encounter rates) across multiple strata rather than just in areas of high burrow densities. These encounter rates can be applied to test Habitat Suitability Index (HSI) models, designed by the U.S. Fish and Wildlife Service (1981) to ‘represent the capacity of a given habitat to support a selected fish or wildlife species.’ To create an HSI model, various species-specific habitat variables are ranked from 0 (unsuitable) to 1.0 (most suitable). Geometric means are used to calculate the final HSI value, which is assumed to have a linear relationship with carrying capacity (U.S. Fish and Wildlife Service, 1981).

This study evaluates whether a HSI model based on ranked GIS landscape variables can predict habitat quality based on burrow encounter rates from a LTDS pilot study. I hypothesize that the GIS data and the HSI model will show a positive correlation to burrow observations and the model will be capable of distinguishing suitable from unsuitable gopher tortoise habitat.

METHODS

Study Area

The following description of the study area was provided by USFWS (2006). St. Marks NWR is located in the Big Bend region of Florida south of Tallahassee. It is characterized by a mild, subtropical climate with mean summer temperatures of 27.2 degrees Celsius and mean winter temperatures of 12.2 degrees Celsius, as reported in Tallahassee (31.7 km north) and average rainfall is 139.7 cm (measured annually from a rain gauge situated on the refuge). The refuge occurs in the Woodville Karst Plain of the Gulf Coastal Lowlands physiographic province, which consists of a layer of Pleistocene sands (no more than 9 meters deep) over limestone. The refuge boundaries extend over 69 kilometers of coastal salt marshes that border hardwood swamps, hardwood hammocks, and upland pine communities. Minor elevational changes, fire history, current fire management practices, historic timber harvest and current timber management practices are the driving factors of the vegetative communities. Nearly 28% of the refuge is occupied by pine-dominated uplands from four Florida Natural Area Inventory natural community types: mesic flatwoods, scrubby flatwoods, wet flatwoods, and sandhills. These areas generally have pine-dominated overstories; most commonly longleaf (*Pinus palustris*), slash (*Pinus elliottii*), pond (*Pinus serotina*), and loblolly (*Pinus taeda*). Woody midstory is characterized by various species of scrub oaks, hollies, oaks, and blueberry among

others. The common understory species include wiregrass (*Aristida beyrichiana*), Florida dropseed (*Sporobolus junceus*), blueberries (*Vaccinium* spp.), huckleberries (*Gaylussacia* spp.), and saw palmetto (*Serenoa repens*). The other major communities on the refuge and their respective coverage include: hardwood swamp forest and hydric hammock (24%); salt marsh (29%); and fresh lakes, marshes, and impoundment (10%). The remaining 9% represents infrequent vegetative assemblages including mesic hammock, maritime hammock, and human altered habitats.

Sampling Frame

St. Marks NWR encompasses a large diversity of habitats with highly variable environmental characteristics, not all of which are suitable for gopher tortoises. To focus efforts to areas potentially suitable for gopher tortoises, two GIS based landscape features (habitat type and soil type) were imported into ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, CA, USA).

Habitat type was incorporated using a shapefile (Environmental Systems Research Institute; ESRI) that was created by St. Marks NWR from the 1989 Wildlife Management Plan for the Forested Uplands of St. Marks NWR, in which stand boundaries were traced onto non-geographically referenced aerial photos in 2006 and are continually updated and refined by St. Marks NWR. These boundaries were converted into habitat polygons in ArcGIS 9.3 and classified according to the Florida Natural Area Inventory (FNAI) Guide to the Natural Communities of Florida (2010). Seven of these natural community types (habitat types) were selected as potentially suitable for gopher tortoises based on previous occupancy, distribution, and abundance research (Auffenberg and Iverson, 1979; Auffenberg and Franz, 1982; Diemer, 1986; Cox *et al.*, 1987; Breininger *et al.*, 1994) as well as professional experience and

observations of St. Marks NWR personnel. The seven habitat type polygons (Sandhill, Sandhill Plantation, Xeric Hammock, Scrubby Flatwoods, Mesic Flatwoods, Mesic Flatwoods Plantation, and Grassland) were selected and merged into a single polygon shapefile (Table 1.1).

Soil type was incorporated from 2006 Natural Resource Conservation Service shapefiles. Gopher tortoises are predominantly found in well drained, sandy soils, and similarly tend to avoid areas with high clay content (Auffenburg and Franz, 1982; Baskaran *et al.*, 2006; Campbell and Christman, 1982; Cox *et al.*, 1987; Diemer, 1986; Garner and Landers, 1981; Jones and Dorr, 2004). According to Auffenberg and Iverson (1979) groundwater levels likely influence gopher tortoise distributions and densities in coastal areas. Therefore, 14 of the 24 soil types found on the refuge having an average depth to water table in Wakulla County greater than 0.2 meters (Allan, 1991) were selected (Table 1.2). Leon soil type has a DWT less than 0.2 meters but was requested to be included by refuge personnel because of observations of gopher tortoise burrows in that soil series. All 14 soil types included have sandy components and range from being poorly drained to excessively drained (Allan, 1991). These 14 soil types were also selected and merged into a single polygon shapefile.

In ArcGIS, the previous soil and habitat polygons were overlaid so that the final study area consisted of only suitable habitat positioned over suitable soil types (Analysis Tools, Clip Feature). The final study area polygon covered 51.5 km² (12,733 acres) which is 18% of the 283 km² (69,996 acres) the refuge occupies and included all seven habitat types, Quartzipsamment and Udorthens soils were removed because they were not positioned over suitable habitat type, which reduced the number of suitable soil types from 14 to 12. However, Chiefland, Hurricane, Mandarin, and Otela soils all had less than one tenth of an acre represented over the final study area.

Table 1.1 List of seven potentially suitable habitat types included in the Habitat Suitability Index (HSI) model, ranked ordinally from most suitable to least suitable.

Habitat Type	Rank
Sandhill	7
Grassland	6
Xeric Hammock	5
Scrubby Flatwoods	4
Sandhill Plantation	3
Mesic Flatwoods	2
Mesic Flatwoods Plantation	1

Table 1.2 List of 14 potentially suitable soils included in the Habitat Suitability Index (HSI) model and associated average Depth to Water Table for Wakulla County, Florida (Allan, 1991).

Soil Type	Average DWT (meters)
Alpin	2.1
Chiefland	1.5
Hurricane	0.8
Lakeland	2.1
Leon	0.2
Lutterloh	0.8
Mandarin	0.8
Moriah	0.7
Ortega	1.3
Otela	1.4
Quartzipsamment	0.8
Ridgewood	0.8
Scranton	0.3
Udorthens	0.8

Rather than using randomly placed transects, based on recommendations from St. Marks NWR personnel, a systematic grid of lines was used to determine transect placement because of the assumption that this method would increase coverage of the refuge from random locations. This systematic grid consisted of parallel lines running east and west and spaced 1000 meters apart were overlain so that transects were only situated over the previously described study area polygon (Analysis Tools, Clip; Fig. 1.1). Each line was divided into transects designed to contain

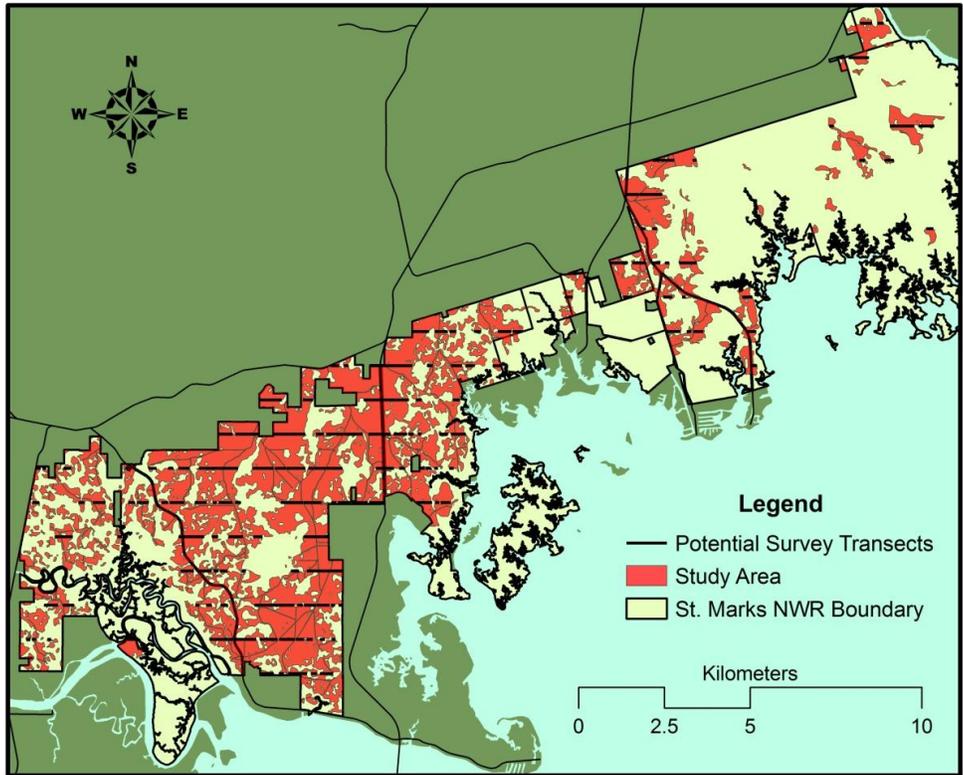


Figure 1.1 Study area sampling frame at St. Marks National Wildlife Refuge and potential survey transects.

only one habitat type. However, inaccuracies of the GIS habitat layer and complications from habitat transition zones resulted in some transects containing multiple habitat types. Transects were also separated by roads because on St. Marks NWR roads are also compartment boundaries and are thus subject to different management activities such as burn prescriptions. The mosaic nature of habitats on the refuge caused there to be numerous transects that were isolated and small; therefore all transects less than 100 meters long were excluded. This resulted in 48.1 km of potential transects ranging from 100 to 995 meters in length. Additionally, transects were replicated 100 meters to the north (if possible) to permit a second transect when returning from the first transect thereby doubling the total length of potential transects to 96.2 km. Transects were assigned random numbers from which they were surveyed in sequential order; however

some transects were prioritized by request of St. Marks NWR personnel. No attempts were made to estimate the probability of burrow detection among different habitat types; therefore burrow observations and associated rates are considered to be naïve encounter rates.

Burrow Data

I conducted burrow surveys by walking at a slow pace along the centerline of transects and searching for burrows during day light hours from April through August of 2010. According to the Florida Climate Center at Florida State University, the average monthly temperatures in nearby Tallahassee during these months ranged from 19.8 to 29.2 degrees Celsius, and the cumulative rainfall was 82 cm. While surveying, I made every effort to remain on, or maintain a clear visual of the transect centerline at all times to ensure all burrows on the centerline were detected. If obstructions were encountered that were impassable, then I generated a stopping point and restarted on the other side of the obstruction. I collected relevant data following recommendations by Smith *et al.* (2009) using a handheld Trimble® GeoXT™ GeoExplorer®3000 series to record field data and GIS locations. Upon sighting a burrow, I generated a geographic location and assigned a unique burrow identification number. Next, I assessed burrow activity status based on external characteristics described by Meyer *et al.* (2008) as: 1) active, if there were obvious signs of burrow use (footprints and/or scat) and maintenance with little or no debris at the burrow entrance, or there was no sign of current use but there was some maintenance with little or no debris at the burrow entrance; 2) inactive, if some debris was present at the burrow entrance and the burrow entrance was still intact; or 3) abandoned, if large amounts of debris was present at the burrow entrance and in the tunnel, or the burrow appeared to be used by other animals, or was partially collapsed. I determined occupancy by sending an Amazing Machinery push cable video kit down each burrow until a tortoise was observed

(occupied), the end of the burrow was reached (unoccupied), or I was physically unable to maneuver the scope any further (undetermined). Supplemental data collected included burrow diameter at 50 cm inside the opening using burrow calipers to estimate the age class of the constructor (Alford, 1980; Smith, 1992), burrow length (measured using the burrow scope), commensal species, and any extra comments. I later used ArcGIS to determine both the linear and perpendicular distance of burrows from transects.

Habitat Suitability Index (HSI) Model

Three GIS based variables were incorporated into this HSI model; habitat type, soil type, and elevation. I used the same habitat and soil layers that were described previously for use in determining the sampling frame. Each of the seven included habitat types were ranked ordinally from most suitable to least suitable according to a compilation of previous density estimates provided by Ashton and Aston (2008) and professional experience of refuge personnel (Table 1.1). Soil suitability was based on each soil type's average depth to water table (DWT) for Wakulla County (Allan, 1991) with the highest DWT of 2.1 meters being most suitable and the lowest DWT of 0.2 meters being least suitable (Table 1.2). Elevation was incorporated using a 0.2 meters Digital Elevation Model (DEM) obtained from 2009 Light Detection and Ranging (LiDAR) data provided by the Florida Division of Emergency Management. Elevation across the refuge ranges from 0 to 11.6 meters with 11.6 being most suitable and zero being unsuitable.

Suitability values for the three GIS were converted to a 0 to 1.0 scale, and in ArcGIS polygons shapefiles were converted to raster files so each pixel had a suitability value that ranged from 0 to 1.0 for each of the three variables. Next, ArcGIS was used to determine the HSI value at each pixel using the formula $HSI = (\text{habitat} \times \text{soil} \times \text{elevation})^{1/3}$ where if any one of the included variables equals 0 then the resulting HSI value equals zero, thereby requiring that all

variables be greater than one to have a suitability greater than zero (Spatial Analyst, Raster Calculator).

Transects spanned multiple pixels and thus contained a range of HSI values. To determine the HSI value for each transect, a buffer was created around each transect to extract the calculated HSI values (Analysis Tools, Buffer). The size of the buffer was determined by plotting the cumulative sum of active, inactive and total number of burrows against the distance from the transect line (Fig. 1.2). Examination of these plots showed that a 10 meter buffer would include 83% (n=48) of active burrows, 77% (n=47) of inactive burrows, 90% (n=57) of inactive burrows, 83% (n=15) of collapsed burrows (n=15) and 73% (n=167) of all burrows. A 10 meter buffer was therefore created around each transect, and all active and inactive burrows within the transect buffers were selected. Abandoned and collapsed burrows were not selected because the purpose of this model was to predict gopher tortoise presence, and the presence of these burrows without the presence of active or inactive burrows may indicate poor or declining habitat quality. Next, ArcGIS was used to extract the mean HSI value and the sum HSI value of each transect within the 10 meter buffer (Spatial Analyst, Zonal Statistics). Both mean and sum HSI values were considered in analysis because some information can be lost using means whereas summing all HSI values within buffered transects assured that all values were accounted.

Statistical Analysis

All data were analyzed using SAS (version 9.2). Because transects were replicated and not of equal lengths, the weighted mean of each transect (weighted by length) for average HSI, sum HSI, average depth to water table, average habitat value, average elevation, number of active burrows, number of inactive burrows, and total number of burrows was calculated. These

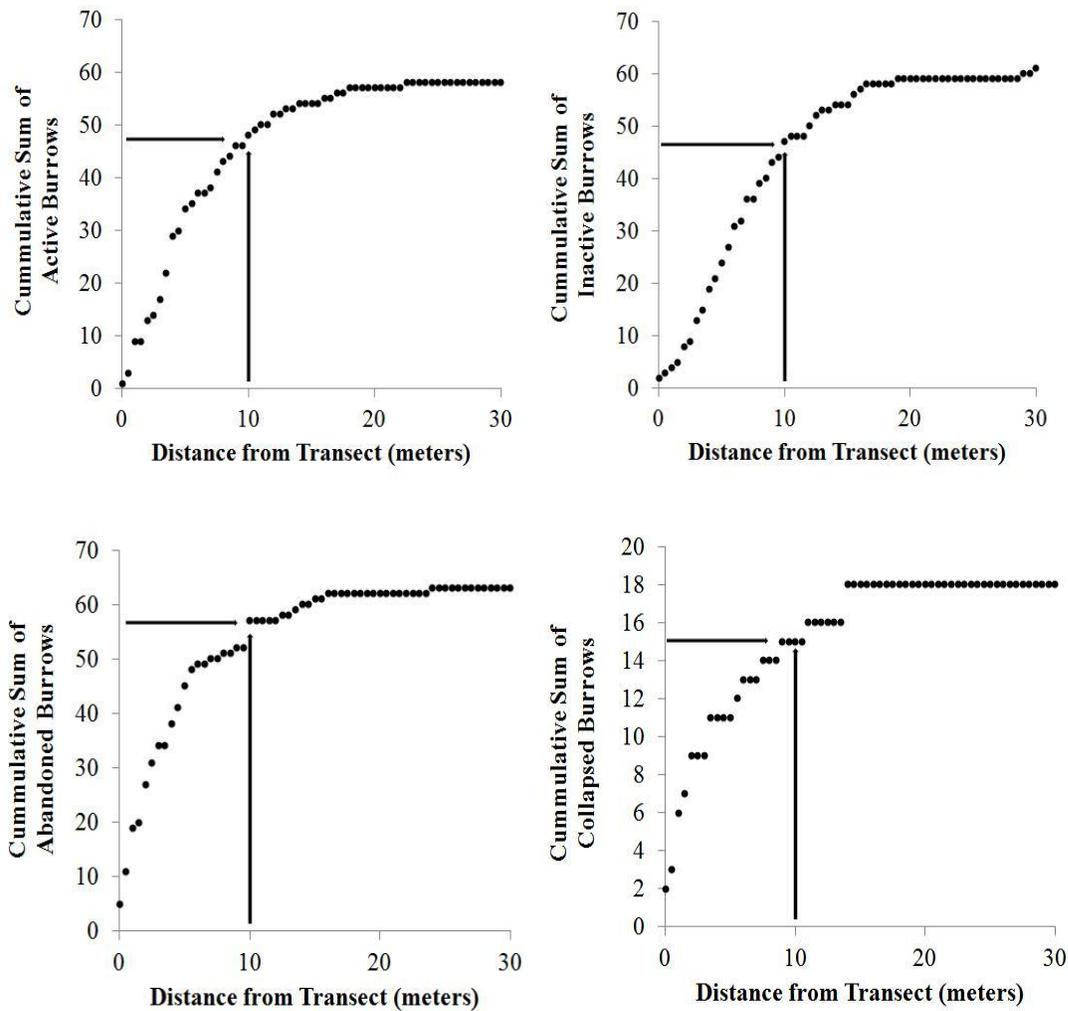


Figure 1.2 Cumulative sum of observed burrows plotted against burrow distance from transect line. Arrows point to the number of burrows within 10 meters that were included in analysis.

mean values for n=59 transects were used for all further analysis. Distribution of both average HSI and sum HSI was tested by Shapiro–Wilk test and box plot. Non-parametric Spearman’s rank-order correlation coefficient (Siegel and Castellan, 1988) was used to determine if HSI values (average and sum) were correlated with number of burrows (active, inactive, and total). This is a common test developed for use when data are not normally distributed or violate other assumptions of parametric testing. It requires that data be ranked ordinally and tests whether or not one variable increases or decreases with another (Siegel and Castellan, 1988). Two separate

tests were performed; the first included all transects and the second used only transects with observed burrows. The null hypothesis for both tests was there would be no correlation between number of burrows (active, inactive and total) and HSI values (average and sum), and the alternative hypothesis for both tests was that number of burrows would show a positive correlation with both HSI values. Scatterplots of both HSI values and values of the three input variables against burrow encounter rates along transects were used to visually evaluate results from the correlation analysis.

Further analysis was conducted by performing a logistic regression analysis to determine if the HSI model was capable of predicting which transects would have burrows present by using burrow presence and absence along transects as a binomial response variables. Additionally, covert linear predictors were used to estimate probabilities of burrow presence with HSI values. Finally, a non-linear mixed model was used to determine if individual components of the HSI model (habitat, soil, and elevation) were individually statistically significant to the presence or absence of burrows along transects.

RESULTS

A total of 59 transects were surveyed. Of those, 57 transects were replicated once and two transects were inadvertently replicated twice (total transects = 120), summing to 40.5 kilometers (42% of potential transect length); 201 burrows were detected along transects of which 59 were active, 61 were inactive, 63 were abandoned, and 18 were collapsed. Of the 59 active burrows, 20 were occupied, 33 were unoccupied, and 6 were undetermined. Of the 61 inactive burrows, two were occupied, 50 were unoccupied, and nine were undetermined. No

tortoises were observed in abandoned or collapsed burrows. The final naïve occupancy rate was 22% for active and inactive burrows.

The correlation coefficients were examined at two separate levels for a positive relationship using a one tailed test; first using a significance level of 0.05 with a critical value of 0.235 (referred to as liberal criteria), and then using a significance level of 0.0005 with a critical value of 0.456 (referred to as conservative criteria). The second criterion was used because it was protective against multiple comparisons. Active, inactive and total burrows were positively correlated with average HSI and sum HSI. All P values were < 0.0001 and r values ranged from 0.55 to 0.70 and therefore met with even the conservative criteria (Table 1.3). The highest correlation was between average HSI and total burrows ($r = 0.70$) with the lowest correlation being between average HSI and active burrows ($r = 0.55$). The correlation coefficients of the three input variables (DWT, habitat, and elevation) used to create the HSI model individually were also examined. All three variables were significantly correlated to all burrows categories using the liberal criteria, but the correlation between habitat and active burrows ($P = 0.002$; $r = 0.40$) as well as the correlation between elevation and active burrows ($P = 0.003$; $r = 0.38$) was lost using the conservative criteria.

Examination of scatter plots of total burrows, active burrows and inactive burrows against sum HSI and average HSI values (Fig. 1.3) showed conflicting results in that there was not a positive relationship after all. These plots revealed that the detected correlations likely resulted because 39 of the 59 transects (66%) had zero observed burrows.

Another Spearman test was performed using only transects with observed active and inactive burrows ($n = 20$). For sum HSI and average HSI, all P values were > 0.05 and r values

Table 1.3 Correlation coefficients (r values) from non-parametric Spearman's rank-order correlation test for number of active and inactive burrows against Habitat Suitability Index (HSI) values using n=59 transects (all P < 0.001).

Input Variable	Active	Inactive	Total
DWT	0.57	0.56	0.66
Habitat	0.40	0.52	0.57
Elevation	0.37	0.48	0.52
Average HSI	0.55	0.61	0.70
Sum HSI	0.55	0.57	0.64

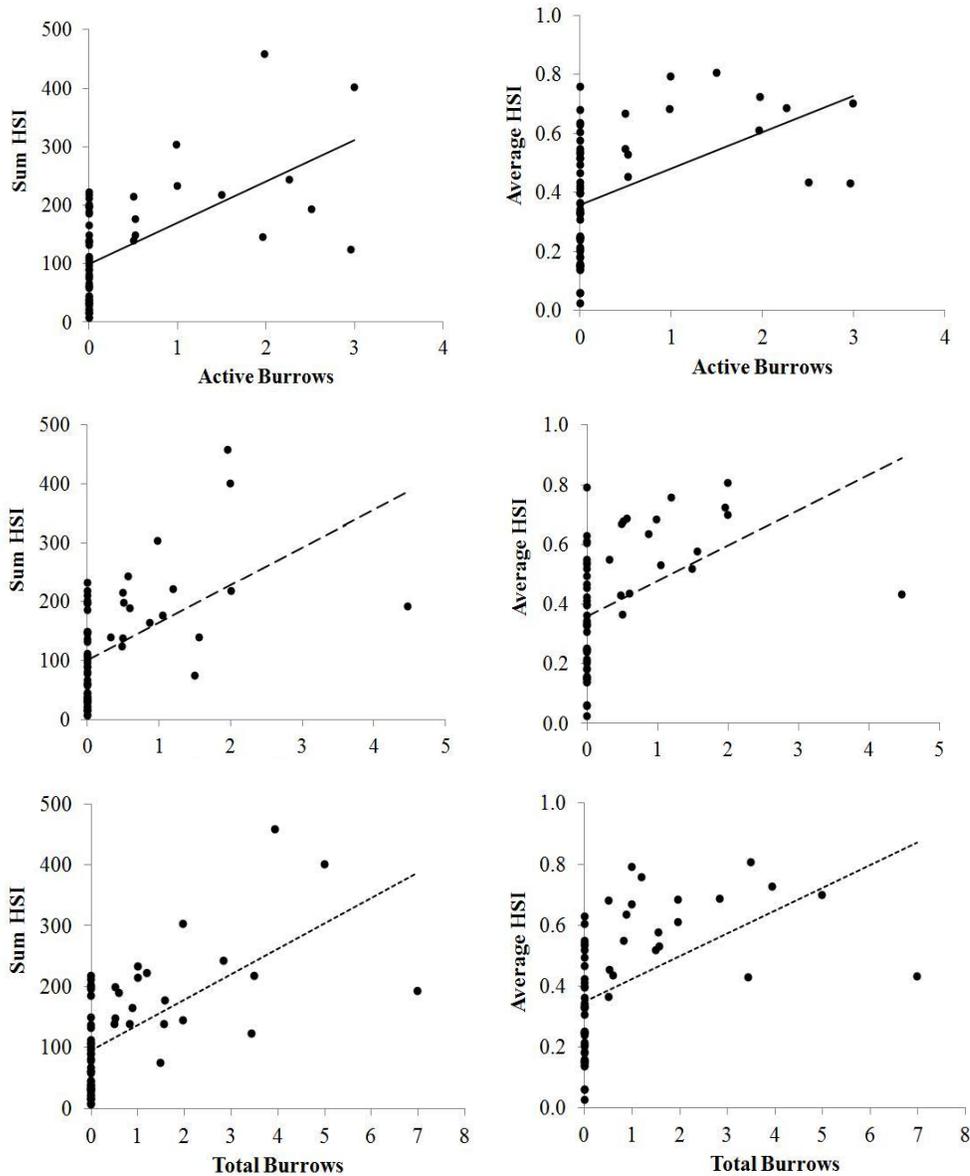


Figure 1.3 Scatter plots of active, inactive, and total burrows against average and sum Habitat Suitability Index (HSI) values and associated linear correlation lines for n=59 transects

values for any of the included variables. However, examination of the correlation coefficients using the liberal criteria showed the correlations between sum HSI and active burrows was above the critical value ($r = 0.41$) but had a P value > 0.05 ($P = 0.071$). Similarly, sum HSI and total burrows had a correlation coefficient greater than the critical value ($r = 0.42$) and also had a P value > 0.05 ($P = 0.06$). The scatter plots of total burrows, active burrows and inactive burrows against sum HSI and average HSI values for $n = 20$ transects is depicted in Fig. 1.4.

Examination of the three input variables used to create the HSI model (DWT, habitat, and elevation) ranged from 0.17 to 0.42 (Table 1.4). Examining the correlation coefficients using the conservative criteria showed no significant correlations between number of burrow and HSI values for any of the included variables. However, examination of the correlation coefficients using the liberal criteria showed the correlations between sum HSI and active burrows was above the critical value ($r = 0.41$) but had a P value > 0.05 ($P = 0.071$). Similarly, sum HSI and total burrows had a correlation coefficient greater than the critical value ($r = 0.42$) and also had a P value > 0.05 ($P = 0.06$). The scatter plots of total burrows, active burrows and inactive burrows against sum HSI and average HSI values for $n = 20$ transects is depicted in Fig. 1.4.

Examination of the three input variables used to create the HSI model (DWT, habitat, and elevation) showed that no correlations existed using the conservative criteria, but when using the liberal criteria DWT and active burrows were positively correlated ($P = 0.04$; $r = 0.46$), however the scatter plot did not show a clear increase in active burrows with an increase in DWT (Fig. 1.5). Burrows were only detected on transects with an average DWT of 0.7 meters and greater. Similarly, burrows were not detected on transects with an average habitat value less than 0.49 or on transects with an average elevation less than 2.7 meters (Fig. 1.5).

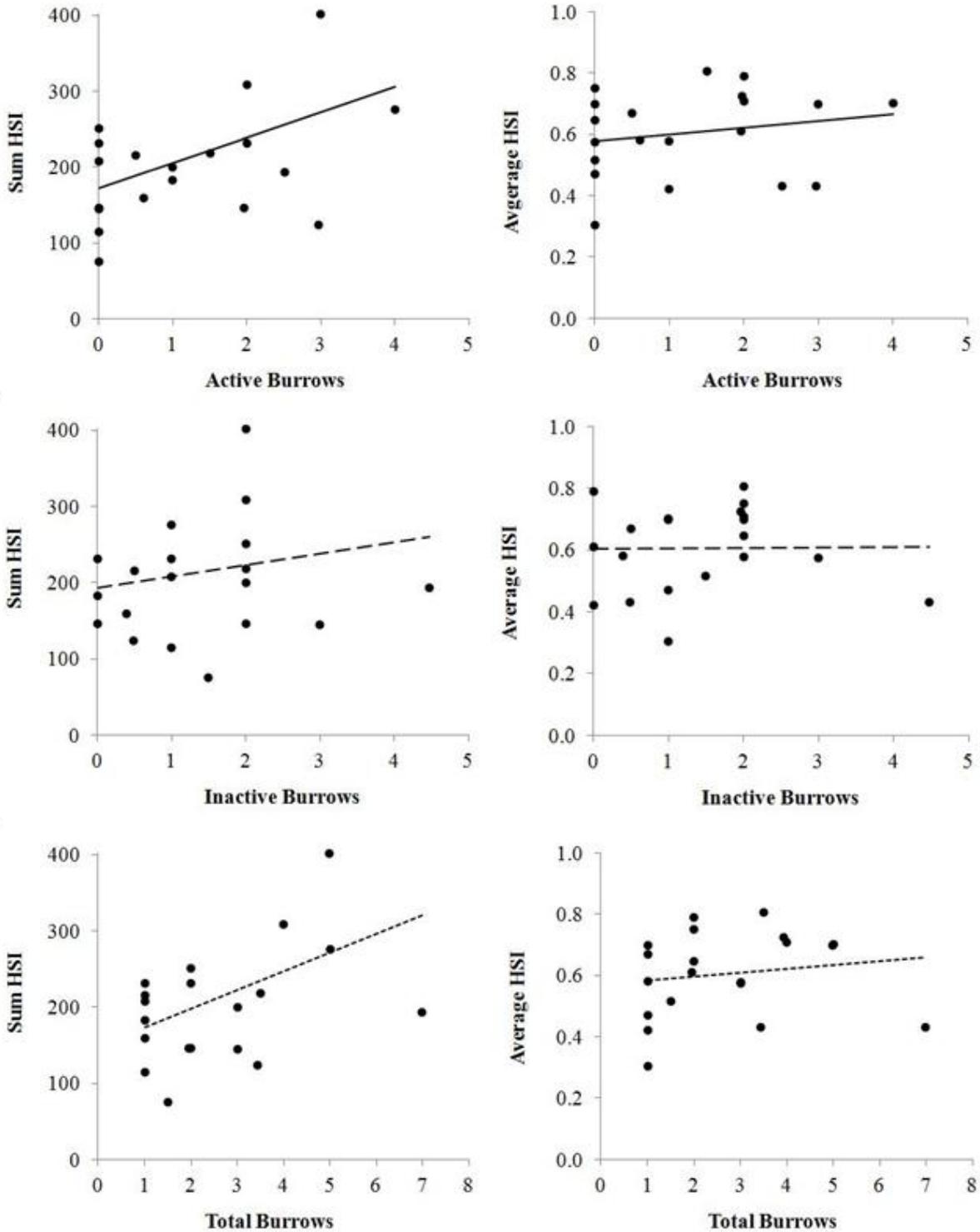


Figure 1.4 Scatter plots of active, inactive, and total burrows against average and sum Habitat Suitability Index (HSI) values and associated simple linear correlation lines for n=20 transects.

Table 1.4 Correlation coefficients (r values) from non-parametric Spearman's rank-order correlation test for active and inactive burrows against Habitat Suitability Index (HSI) values using n=20 transects. Associated P values are in parentheses.

Input Variable	Active	Inactive	Total
DWT	0.46 (P = 0.04)	-0.02 (P = 0.91)	0.37 (P = 0.11)
Habitat	-0.25 (P = 0.28)	0.25 (P = 0.28)	-0.04 (P = 0.85)
Elevation	0.06 (P = 0.79)	0.22 (P = 0.35)	0.27 (P = 0.25)
Average HSI	0.25 (P = 0.30)	0.46(P = 0.46)	0.36 (P = 0.12)
Sum HSI	0.41 (P = 0.07)	0.16 (P = 0.48)	0.42 (P = 0.06)

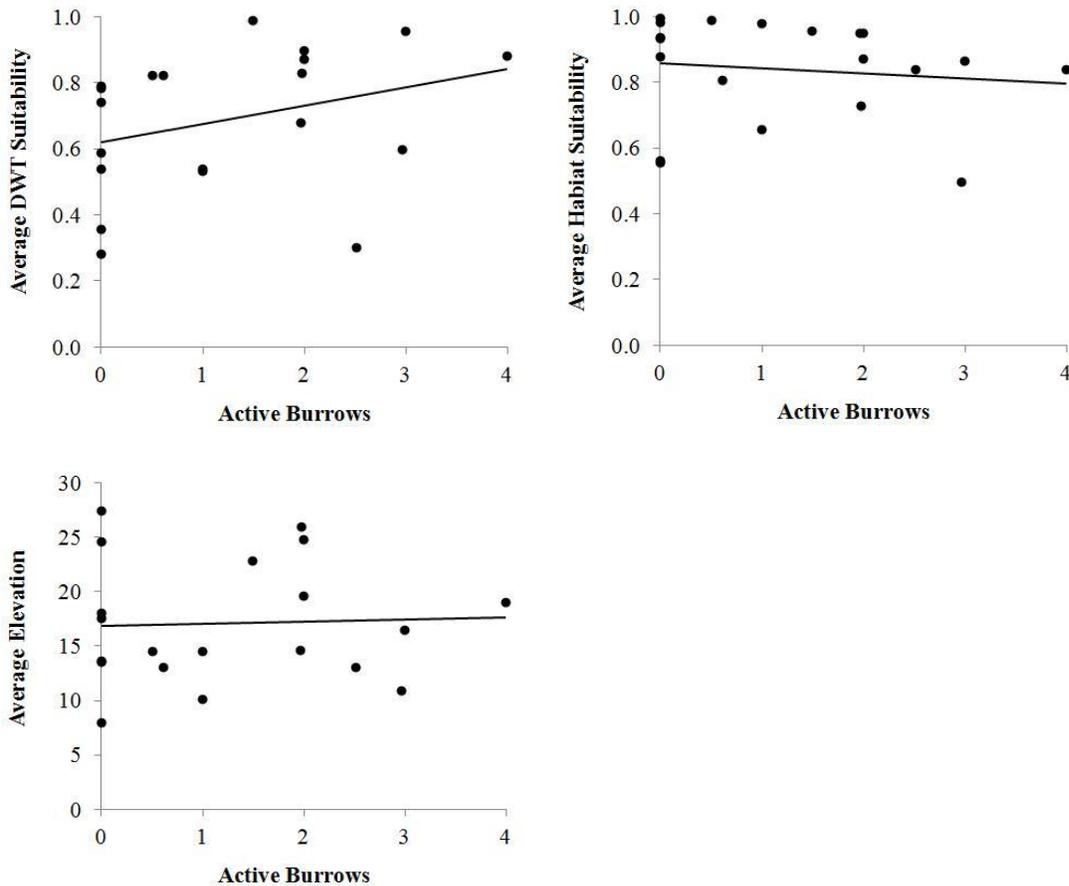


Figure 1.5 Scatter plot of active burrows against average depth to water table, habitat suitability values, and average elevation and associated linear correlation lines for n=20 transects.

Logistic regression analysis showed that there was relationship between the HSI model and the presence and absence of burrows along transects (estimate = 0.024; standard error = 0.0006, $df = 57$, $F = 14.7$, $P = 0.0003$). Following anti-logit, every one unit increase in the HSI model (HSI value of 0.1), increased the probability of burrow presence along transects by 5%, and thus the HSI model at best explains 50% of the probability of burrow presence. However, results from the non-linear mixed model analysis showed that none of the HSI components (soil, habitat, elevation) were individually statistically significant to the presence or absence of burrows along transects (all P values > 0.05)

DISCUSSION

The decision to include transects without burrows or to exclude these transects had a profound influence on results, suggesting that the HSI model was sensitive to the presence or absence of burrows. Removal of transects with zero observed burrows resulted in the loss of all significant correlations using the stricter conservative criteria for statistical significance. Using a more liberal criteria to determine statistical significance, a correlation did exist, but also demonstrated evidence that a type I error may have occurred, and, hence, the correlation coefficients were likely false positives. The correlation between the three variables (DWT, habitat and elevation) used to create the HSI model and burrow numbers (active, inactive, and total) was also examined and prior to removal of transects with zero burrows, all variables were significantly correlated with all burrow categories. However, after removal only DWT retained a correlation with active burrows but inspection of the scatter plot did not show a clear increase in number of burrows with DWT. Therefore, the relationship between the overall HSI model with burrow presence was clear but DWT was not clear.

Even though the HSI model did not show a linear relationship as intended by the U.S. Fish and Wildlife Service (1981), results from the logistic regression show that the HSI model is able to distinguish between areas where there should be active and inactive gopher tortoise burrows from areas where there should not be, but burrow numbers do not increase as HSI values increase, nor do they increase as any one of the HSI variables increase. According to the non-linear mixed model analysis, none of the HSI components were individually statistically significant to burrow presence. Controversially, the results from the correlation analysis showed that DWT was correlated with active burrows; however the scatter plot of this data implied a weak correlation. DWT was used to quantify soil suitability for gopher tortoises but the data used was based on the results of a survey completed more than 20 years ago that was averaged across the entire county. Because neither active nor inactive burrows were located on transects with an average DWT less than 0.73 meters, it can be assumed that this variable does play some part in soil suitability however, the weak correlation may have resulted because the DWT values used were based on the average DWT for the county, and therefore were not accurate at each transect. In addition to inaccurate DWT values, there are other properties that play a role in soil suitability that were not quantified that may be important for burrow construction such as water permeability, moisture content, soil texture and particle size, clay content, erosion factors, as well as chemical and mineralogical properties. Baskaran *et al.* (2006) found that percent clay content in the top soil layer was the most significant variable related to the probability of finding active burrows. Similarly, Jones and Dorr (2004) and Landers and Speake (1980) determined that the presence of active burrows was positively related to sand content and depth (mostly sandy soils > 1m in depth). Even though these results did not show a clear correlation with DWT, soil has been held as an important component for burrow construction in much of the

gopher tortoise literature (Landers and Speake, 1980; Auffenburg and Franz, 1982; Campbell and Christman, 1982; Lohofener, 1982; Diemer, 1986; Cox *et al.*, 1987; Jones and Dorr, 2004; Baskaran *et al.*, 2006) and the weak correlation was likely a result of methodological error.

Habitat had the strongest correlation with inactive and total burrows when all 59 transects were included. Active burrows were also correlated with habitat, but was not strong enough to be retained using the conservative measure of significance, when all transects were included. Habitat suitability was assigned using an equal interval ranking of habitats from most suitable to least suitable, which may not accurately reflect the actual suitability of habitats because 'habitat type' is a broad definition used to classify natural community assemblages (Florida Natural Area Inventory (FNAI), (2010) that may not accurately reflect the complex nature of tortoise-habitat systems. Additionally, the shapefiles used did not reflect detailed habitat components such as species composition, canopy cover, and herbaceous ground cover that may influence suitability (Auffenburg and Franz, 1982; Diemer, 1986; Cox *et al.*, 1987; Jones and Dorr, 2004; Baskaran *et al.*, 2006). However, examination of the raw data indicated that neither active nor inactive burrows were observed on transects with an average habitat value less than 0.49, which may be evidence of some influence on suitability. According to the habitat ranking scale used, habitats with values greater than 0.49 include Sandhills, Sandhill Plantations, Grasslands, and Xeric Hammocks and exclude Scrubby Flatwoods, Mesic Flatwoods, and Mesic Flatwoods Plantations. Even though the ranking was not indicative of increased suitability, the absence of active and inactive burrows in the excluded habitat types may indicate some degree of unsuitability in the surveyed areas.

Like the other variables, elevation was correlated with active, inactive, and total burrows only when all transects were included with the strongest correlation being with total burrows.

Yet again, all correlations were lost when transects with zero burrows were removed. Active burrows were not detected on transects with an average elevation less than 3.3 meters, and inactive burrows were not detected on transects with an average elevation less than 2.7 meters. Elevation was the only variable in the HSI model that did need to be assigned numeric rankings and therefore was not susceptible to ranking errors. It was also the most current and accurate input variable used and therefore lack of correlation did not likely result from human error. The only error may have occurred by averaging across transects, which in the case of extreme topographic relief would have lost any dimensional relationship between burrows and elevation. Jones and Dorr (2004) found that elevation could be used to predict the presence of active burrows, but only in combination with other environmental conditions. Subsequently, elevation alone is not enough to predict presence of active or inactive gopher tortoise burrows, but rather should potentially be viewed as a limiting factor.

CONCLUSIONS AND RECOMMENDATIONS

Habitat Suitability Index (HSI) models were created by the U.S. Fish and Wildlife Service (1981) to be used in conjunction with Habitat Evaluation Procedures (HEP) to ‘represent the capacity of a given habitat to support a selected fish or wildlife species.’ The HSI values from this model did not show a linear relationship with burrow activity, however it was capable of predicting the presence and absence of active gopher tortoise burrows along transects. The relationship between an organism and its environment is complicated at best, and is even more complex when dealing with a specialized species that has experienced population declines from human exploitation, habitat reduction, fragmentation and degradation. The simplistic nature of this HSI model was not only inadequate for predicting active burrow encounter rates, it was only

capable of explaining up to 50% of the probability of active burrow presence suggesting either more or better data are needed . In addition to using potentially incorrect values to quantify suitability, there are other variables not accounted for that likely play a large role in habitat suitability such as mean years between burns, species composition, canopy cover, and herbaceous ground cover (Auffenberg and Iverson, 1979; Auffenberg and Franz, 1982; Landers, 1980; Diemer, 1986; Breininger *et al.*, 1994; Mushinsky and McCoy, 1994; Smith *et al.*, 1997; Aresco and Guyer, 1999; Jones and Dorr, 2004; Tuberville *et al.*, 2007).

Absence of burrows from an area does not indicate the area is not suitable. This method of modeling habitat suitability assumes suitability is directly reflected by the presence of active and inactive burrows which may not be accurate when gopher tortoises have relatively large annual home ranges of up to 1.1 hectares and exhibit more movement (2-5 miles to breed and forage) than would be expected for a slow moving tortoise (Cox *et al.*, 1987; McRae *et al.*, 1981; MacDonald and Mushinsky, 1988; Diemer, 1992; Eubanks *et al.*, 2003; Ashton and Ashton, 2008). Furthermore, there is a long history in the surrounding communities of collecting gopher tortoises as a food resource, and the absence of gopher tortoise burrows in some areas could be a reflection of a population below carrying capacity. The absence of burrows in seemingly suitable habitat could also result because from the area being compromised in ways not easily observed such as by toxins and pollutants. Additionally, the social structure of gopher tortoise pods may influence the location of individual burrows resulting in a clumped distribution across the landscape and thereby leaving some potentially suitable areas seemingly unoccupied (Auffenberg and Iverson, 1979; Ross, 1980; Auffenberg and Franz, 1982; McRae *et al.*, 1981).

Evaluating gopher tortoise habitat suitability using this HSI model may not be the most appropriate tool considering the complex relationship of the gopher tortoise with its environment

and more complex models that include both macrohabitat and microhabitat variables may be more appropriate. Other variables that may be useful for future model evaluation include mean years between burns, disturbance, canopy cover, herbaceous ground cover, shrub cover, depth of sandy soils, and species composition (Auffenberg and Iverson, 1979; Auffenberg and Franz, 1982; Landers, 1980; Landers and Speake, 1980; Diemer, 1986; Mushinsky and McCoy, 1994; Smith *et al.*, 1997; Aresco and Guyer, 1999; Jones and Dorr, 2004; Tuberville *et al.*, 2007). Chapter 2 describes how these variables (excluding disturbance and depth of sandy soils) were used in a multivariate model of gopher tortoise habitat.

CHAPTER 2. A MULTIVARIATE MODEL RELATING THREE GOPHER TORTOISE BURROW CATEGORIES TO HABITAT VARIABLES AT ST. MARKS NATIONAL WILDLIFE REFUGE, FLORIDA

INTRODUCTION

The dramatic decline of the longleaf pine forests of the southeastern United States has caused many of its specialized inhabitants such as the gopher tortoise (*Gopherus polyphemus*) to disappear across large portions of their historic range. The gopher tortoise only receives federal protection in the eastern portion of its range, and even though the recent finding of the U.S. Fish and Wildlife Service (USFWS) concluded that the gopher tortoise is in need of protection and regulatory actions through listing under the Endangered Species Act, there are other priorities that prohibit their ability to complete the exhaustive task of doing so (Federal Register, 2011). As a result, conservation agencies were urged to take actions in preventing any further declines of this ecologically beneficial animal.

One step in preventing population declines lies in having a defensible estimate of the population size. As many agencies are facing the daunting task of estimating the numbers of gopher tortoise over very large tracts of land, many have chosen to utilize a method known as Line Transect Distance Sampling (LTDS) which is thought by the gopher tortoise conservation community to provide the most efficient and precise estimate available aside from a complete count (Meyer *et. al.*, 2008; Nomani *et. al.*, 2008; Smith *et. al.*, 2009; Stober and Smith, 2010). However, complete counts are financially unrealistic. Additionally, with repeated surveys, LTDS enables conservationists to monitor population trends over time, which is necessary for measuring effectiveness of conservation efforts. Furthermore, conservation efforts can be greatly enhanced if monitoring efforts are supplemented with knowledge of the specific environmental characteristics associated with gopher tortoise presence, absence and

abandonment. Therefore, to adhere to requests from the recent status update by the U.S. Fish and Wildlife Service (Federal Register, 2011), biologists at St. Marks National Wildlife Refuge planned a LTDS survey and coordinated with researchers at Louisiana State University to measure habitat variables during the pilot study of the LTDS survey to predict the absence and occurrence of active and abandoned gopher tortoise burrows. This study evaluated whether burrow observations along transects from a LTDS pilot study could be used to model the probability of occurrence for three gopher tortoise burrow categories (active, abandoned, and none) when used in combination with two types of habitat data: 1) microhabitat variables collected at predefined intervals along transects; and 2) easily obtainable Geographic Information Systems (GIS) based macrohabitat variables.

METHODS

From May to August of 2009, 120 transects containing 404 plots that summed to 48.1 km were surveyed. For details, see chapter one METHODS for Study Area, Sampling frame, and Burrow Data.

Plot Data

Plot data were collected at 100 meter intervals along each transect (also using the handheld Trimble® GeoXT™ GeoExplorer® 3000 series) following similar protocol as the Red-cockaded Woodpecker (RCW) foraging habitat matrix application for ArcMap created by Intergraph Corporation (http://www.fws.gov/rcwrecovery/matrix_download.html). . At each plot, the observed habitat type was documented and the dominant canopy species was assessed and classified into one of the following categories: 1) longleaf pine (*Pinus palustris*); 2) slash pine (*Pinus elliottii*); 3) xeric hardwoods (included sand live oak (*Quercus geminate*), sand post

oak (*Quercus stellata* var. *margaretta*), turkey oak (*Quercus laevis*) or bluejack oak (*Quercus incana*); 4) mesic hardwoods (including water oak (*Quercus nigra*), laurel oak (*Quercus laurifolia*) and other tree species common to the mesic hammock natural communities); 5) other; or 6) none for sites without canopy species. Transects were assigned habitat type and dominant canopy species based on the category that occurred most frequently along each transect, however for dominant canopy species, if there was an equal number of classifications along a transect, a mixed category was assigned. Basal area of the center point for each plot was determined using a 10-factor prism. Four separate categories of basal area were assessed; total basal area, longleaf pine basal area, other pine tree basal area, and basal area of trees with a diameter breast height (DBH) greater than 25 cm. All four basal area categories were averaged separately across each transect. Five canopy cover readings were taken at each plot using a densitometer (Lemmon, 1957); one at the center and one each at 10 meters north, south, east, and west. The five readings were averaged for each plot, then plot averages were averaged across each transect. The final transect canopy cover average is referred to as % canopy cover. Dominant arboreal midstory species within a 0.1 acre plot (11.3 meter radius) was classified as one of the following: no arboreal midstory, pine saplings, sand live oak, sand post oak, turkey and/or bluejack oak, or other hardwoods. Each transect was given a separate category for each dominant arboreal midstory classification based on the presence or absence of each category (e.s., consider a transect having six total plots, two having pine saplings as the dominant midstory species and four having sand live oak as the dominant midstory species; pine saplings and sand live oak would be assigned a values of one and all other arboreal midstory variables would be assigned a values of zero). This method was selected to reduce computational difficulties. The same concept was applied to dominant shrubby midstory species with the following categories: 1) no

shrubby midstory, 2) palmetto (*Serenoa repens*), 3) oak (*Quercus*) species, 4) gallberry (*Ilex glabra*), 5) huckleberry (*Gaylussacia dumosa*), 6) staggerbush (*Lyonia*) species, 7) blueberry (*Vaccinium*) species, and 8) dead and/or burned (and therefore not identifiable). Percent groundcover within a 0.01 acre plot (3.4 meter radius) was assessed for each of the following categories: herbaceous plants, woody plants, ferns, palmetto, debris/litter, and bare ground. Percentages were grouped into one of the following categories: 0%, 1-5%, 6-25%, 26-50%, 51-75%, 76-95%, or 96-100% and was averaged across each transect. Lastly, wiregrass (*Aristida beyrichiana*), presence or absence was determined at each plot, and each transect was given a wiregrass value based on the percentage of plots where wiregrass was present.

GIS Data

Five GIS-based variables were incorporated: habitat type, soil type, elevation, percent tree canopy, and mean fire frequency. The same habitat and soil type layers that were described in Chapter 1 for use in the Habitat Suitability Index (HSI) model and in determining the sampling frame were used but as categorical variables and accordingly assigned to transects. To incorporate elevation, a 1.5 meter (horizontal pixel size) Digital Elevation Model (DEM) was obtained from 2009 Light Detection and Ranging (LiDAR) data provided by the Florida Division of Emergency Management (horizontal accuracy was 1.2 meters and vertical accuracy was 1.8 meters). The fourth GIS layer incorporated was the National Land Cover Database (NLCD) 2001 Percent Tree Canopy (Version 1.0; Homer *et al.*, 2004). Huang *et al.* (2001) developed a method of determining tree canopy density by modeling the relationship between tree canopy density and Landsat 7 ETM+ imagery, using 1 meter digital orthophoto quadrangles as reference data. This method was used to create a national tree canopy density dataset at a 30 meter resolution as part of the Multi-Resolution Land Characteristics 2000 project and can be acquired online from the

NLCD website (http://www.mrlc.gov/nlcd01_data.php). Mean fire frequency was incorporated as a raster shapefile created by St. Marks NWR (M. Keys, St. Marks NWR, pers. comm.), in which the total number of prescribed fires was counted for burn compartment shapefiles from 1998 to 2011. These years were selected because of inconsistent burn records for the previous years. Mean years between burns was calculated as the total number of burns per total days (between 1/1/1998 to 8/11/2011). These three variables (elevation, percent tree canopy, and mean fire frequency) were in raster format; following procedures from Chapter 1, the average raster values within a 10 meter buffer around each transects was extracted using ArcGIS and used for data analysis.

Analysis

Data Management

Area covered, number of transects and distance surveyed by soil and habitat type are shown in Table 2.6. To reduce variation within transects, each of the original 120 transects described in Chapter 1 were divided into transects with a single soil type which resulted in 226 total transects. Soil types having no burrow observations or those represented by less than five transects were removed from analysis thus reducing 226 transects to 184 transects totaling to 35.8 km in the final analysis. Transects were assigned one of the three following activity statuses: active, abandoned, or none. Transects were considered ‘active’ if at least one active or inactive burrow was observed, regardless of whether abandoned or collapsed burrows were present. ‘Abandoned’ transects contained only abandoned or collapsed burrows. If no burrow was detected, then transects were classified as ‘none.’ To account for differing transect lengths, a burrow encounter rate was determined for each transect by dividing the number of burrows observed by the total transect length in kilometers. For ‘active’ transects, only the number of

active and inactive burrows were used to determine this rate. Thus each transect was given either an 'active rate' or an 'abandoned rate' based on transect activity status, while transects classified as 'none' were accordingly assigned zero.

Statistical Analysis

Principal component analysis (PCA; PROC FACTOR, SAS version 9.2) was used to reduce the large number of input variables into correlated groups or principal components (PCs). All variable, including potentially redundant and categorical variables, were retained in the PCA following recommendations by Khattree and Naik (2000), Garigal *et. al.*, (2000), and Stevens (2000). Varimax rotation (Kaiser, 1958) was applied to the resulting PCs to better correlate the data. The interpretation of the output was cutoff at correlations less than $|0.3|$ or $|30\%|$ between the absolute values of the original variable and its corresponding principal component. The number of components retained was determined by inspection of the scree plot (Cattell, 1966) which visually depicts the amount of variation explained with each additional PC. Initial inspection of the data suggested that dominant shrubby midstory species and mean years between burns were correlated; therefore, four PCAs were constructed for further investigation. The first PCA treated all habitat variables equally and included all variables in the PCA. The second PCA excluded fire return because this variable was of specific management interest. The third PCA excluded both mean years between burns and potentially redundant fire related variables (dominant shrubby midstory species). Lastly, the fourth PCA included fire return but excluded potentially redundant fire related variables. After inspecting the information provided by each PCA through the Kaiser-Guttman (eigenvalues; 1958) and Cattell (scree plot; 1966) criteria, I concluded that the fourth PCA presented the data in the most informative and logical

format and therefore mean years between burns was included and dominant shrubby midstory species was removed for further analysis.

Three separate response variables; ‘active rate’, ‘abandoned rate’ and ‘none’ (based on the previously described ‘burrow rate’) were tested for significant association with resulting PCs using a generalized linear mixed model (GLMM; PROC GLIMMIX, SAS version 9.2), with a logit link and binomial probability distribution, thereby, modeling a multcategory logit model with PCs as fixed effects and transects as random effects (Littel *et al.*, 2006; Agresti, 2007). Alternative link functions and probability distributions were evaluated by chi-square/degree of freedom fit statistic. Although the data were zero-rich, the above tests of overdispersion did not suggest the need for zero-inflated analyses. Statistical significance was determined using a P value of 0.05 and all reported PC scores are in number of standard deviations from the mean.

Linear predictors of burrow probabilities were generated, so that each of the 184 transects received three separate probabilities (one each for active burrows, abandoned burrows and no burrows). These probabilities were plotted against PC scores (each representing one standard deviation from the mean for each variables correlated within PC) to observe how probabilities change in relation to changing variable values. These plots depict how active, inactive, and no burrow probabilities change between opposing positive and negative PC associated variables, which are better understood as opposing habitat types. Fitted polynomial regression lines were added to these plots to observe data trends; however these lines do not represent model estimated probabilities for any specific observation.

Statistically significant associations with PC assembled variables do not inherently mean that all correlated variables within a PC are important to burrow activity, abandonment or absence. Furthermore, one cannot assume that the absence of a variable from statistically

significant PCs infers it has no influence on burrow activity, abandonment or absence. Therefore, linear predictors of probability rates and polynomial regression lines of these predictors relative to PC scores were also plotted for individual variables. It is important to note that probabilities were not tested for statistical significance against individual variables, but these trend lines do provided a framework for deducing which variables within statistically significant PCs and which individual variables (not included in statistically significant PCs) exhibited biological (not statistical) significance to burrow probability rates.

RESULTS

Of 184 transects, 35 were 'active', 31 were 'abandoned' and 118 were 'none'. A total of 201 burrows were detected of which 59 were active, 61 were inactive, 63 were abandoned, and 18 were collapsed. Of the 59 active burrows, 20 were occupied, 33 were unoccupied, and 6 were undetermined. Of the 61 inactive burrows, two were occupied, 50 were unoccupied, and nine were undetermined. No tortoises were observed in abandoned or collapsed burrows. The final naïve occupancy rate was 22% for active and inactive burrows. On active transects, the average active burrow rate was 5.7 burrows/km, the average inactive burrow rate was 5.4 burrows/km, and the combined rate was 5.5 burrows/km. On abandoned transects, the average abandoned burrow rate was 6.4 burrows/km, the average collapsed burrow rate was 2.1 burrows/km, and the combined rate was 4.2 burrows/km. Table 2.1 shows the minimum, maximum and mean values for elevation, mean years between burns, percent tree canopy, percent canopy cover, and the four basal area categories.

Table 2.1 Minimum, maximum and mean values for elevation, mean years between burns, percent tree canopy, percent canopy cover, and four basal area categories. DBH abbreviates diameter breast height and DBH > 25cm Basal Area represents trees with a DBH greater than 25 cm.

Variable	Minimum	Maximum	Mean
Elevation (meters)	1.5	10.4	4.3
Years Between Burns	2.3	6.8	3.1
Percent Tree Canopy	0	92	44
Percent Canopy Cover	0	86	37
Total Basal Area (m ² /acre)	0	46	20
Longleaf Pine Basal Area (m ² /acre)	0	46	12
Other Pine Basal Area (m ² /acre)	0	46	4
DBH > 25cm Basal Area (m ² /acre)	0	30	10

Principal Component Analysis

The 13 principal components (PCs) with Eigenvalues >1 explained 74% of the variability in the data (Table 2.2). Most variation (55.4%) was captured by the first seven PCs and little information was gained, at the expense of greater complexity, when the remaining PCs were included.

PC 1 characterized habitat variables correlated with Lakeland soils versus those correlated with Scranton soils (Table 2.3); this PC will be referred to as Lakeland vs. Scranton PC. Statistically significant variables correlated with Lakeland soils included Sandhill habitats with longleaf pine as the dominant canopy species, a dominant arboreal midstory composed of turkey and /or bluejack oak, with wiregrass present, and increased elevation. Attributes correlated with Scranton soils include Mesic Flatwoods habitat with mixed longleaf pine and slash pine as the dominant canopy species, high total basal area, and high basal area of other pine trees, increased % tree canopy, and an arboreal midstory dominated by other hardwoods.

PC 2 exemplified habitat variables correlated with mesic flatwoods plantations (MFP) versus those correlated with Sandhill habitats and will be referred to as MFP vs. Sandhill PC

Table 2.2 Eigenvalues of the correlation matrix for habitat and GIS variables following principal component analysis. Retained Principal Components (PCs) are in **bold**.

PC	Eigenvalue	Proportion	Cumulative
1	6.54	0.15	0.15
2	4.50	0.11	0.26
3	3.83	0.09	0.35
4	2.73	0.06	0.41
5	2.38	0.06	0.46
6	2.13	0.05	0.51
7	1.72	0.04	0.55
8	1.60	0.04	0.59
9	1.52	0.04	0.63
10	1.42	0.03	0.66
11	1.37	0.03	0.69
12	1.10	0.04	0.72
13	1.03	0.02	0.74

Table 2.3 Correlations following rotation by Varimax for all variables in Principal Components (PCs) 1 through 7 (x100) and percent variance explained by each. Significant variables |30| are marked in **bold** and with an asterisk (*).

Variables	PC1	PC2	PC3	PC4	PC5	PC6	PC7
SOIL TYPE							
Lakeland	-35*	-17	-10	-15	-38*	-20	-3
Leon	27	58*	-5	12	-7	-10	-21
Ortega	-21	-22	-14	23	-5	19	-36*
Ridgewood	-8	-2	11	-10	47*	-2	41*
Scranton	56*	2	18	-10	-15	7	11
HABITAT							
GIS Grassland	-2	-5	94*	-3	-3	0	1
OBS Grassland	-2	-5	94*	-3	-3	0	1
GIS Mesic flatwoods PL	-17	87*	-1	-15	3	4	4
OBS Mesic flatwoods PL	-18	87*	-1	-15	3	9	-1
GIS Mesic flatwoods	87*	0	-9	-18	0	-8	0
OBS Mesic flatwoods	89*	3	-9	-18	-6	-5	9
GIS Sandhill	-51*	-33*	-21	-11	-37*	-46*	-14
OBS Sandhill	-52*	-34*	-22	-26	-31*	-48*	-6
GIS Sandhill PL	-10	-8	0	-3	1	85*	-21
GIS Scrubby flatwoods	1	-2	-6	28	63*	-2	-3
OBS Scrubby flatwoods	-2	-7	-11	-14	61*	-1	20
GIS Xeric hardwoods	-16	-3	-3	39*	9	0	45*
OBS Xeric hardwoods	-4	-4	3	64*	12	2	3
DOMINANT CANOPY							
Mixed pines	37*	5	-6	-1	8	0	8

Table 2.3 Continued

Longleaf pines	-35*	-58*	-36*	-36*	1	13	-1
Xeric hardwoods	-9	4	0	70*	3	-14	-5
None	2	-3	82*	-3	14	-3	-4
BASAL AREA							
Total BA	7	14	-43*	23	-40*	50*	32*
Trees >10" BA	36*	6	-30	-11	-39*	-4	50*
Longleaf pine BA	-14	-36*	-30	-23	-21	60*	27
Other pine BA	39*	74*	-5	5	-22	-6	10
CANOPY COVER							
Canopy cover (Densimeter)	-10	-10	-40*	61*	-38*	13	13
% Tree Canopy	43*	35*	-26	25	-17	23	33*
DOMINANT ARBOREAL MIDSTORY							
None	19	53*	-1	29	-4	23	28
Turkey/Bluejack Oak	-35*	-35*	-23	0	10	11	-21
Sand post oak	-7	-9	-5	4	-23	-1	13
Sand live oak	-7	-16	20	37*	43*	-18	4
Other hardwoods	33*	5	28	33*	-39*	6	11
Pine saplings	7	10	-11	-32*	-19	-10	-11
GOUND COVER							
Herbaceous plants	-19	-11	35*	-47*	-8	-21	-9
Ferns	10	-14	-9	23	1	-1	46*
Woody plants	17	25	5	-8	15	-5	52*
Palmetto	14	47*	-12	2	18	-9	9
Litter	-4	-11	-37*	46*	-17	11	-24
Bare ground	-27	-16	-13	-19	13	-29	-52*
WIREGRASS PRESENCE							
	-39*	-23	-46*	-28	29	-15	-8
ELEVATION							
	-51*	-17	-4	-18	-33*	19	11
FIRE RETURN INTERVAL							
	7	2	1	64*	38*	-6	11
Proportion variance explained	15.2%	10.5%	8.9%	6.4%	5.5%	5.0%	4.0%

(Table 2.3). Important variables correlated with MFP included Leon soils, high basal area of other pines, increased % tree canopy, no arboreal midstory and high % palmetto ground cover. Important attributes correlated with Sandhill habitats included longleaf pine as the dominant canopy species, high basal area of longleaf pines, and turkey oak and / or bluejack oak as the dominant arboreal midstory species.

PC 3 described habitat attributes correlated with Grassland habitats versus those areas with longleaf pine as the dominant canopy species and will be referred to as Grassland vs. Longleaf PC (Table 2.3). Important attributes correlated with Grassland habitats included no canopy cover, and high % herbaceous ground cover. Areas with longleaf pine as the dominant canopy species were statistically correlated with high total basal area, increased % canopy cover (densiometer), high % litter ground cover, and wiregrass presence.

PC 4 represented Xeric Hammock habitats versus areas with longleaf as the dominant canopy species and will be referred to as Xeric vs. Longleaf PC (Table 2.3). Xeric Hammock habitats were significantly correlated with xeric hardwoods as the dominant canopy species, increased % canopy cover (densiometer), sand live oak and other hardwoods as the dominant arboreal midstory species, high % litter ground cover, and increased mean years between burns. Areas with longleaf as the dominant canopy species were significantly correlated with having saplings as the dominant arboreal midstory species, and high % herbaceous ground cover.

PC 5 characterized Ridgewood soils versus Lakeland soils and will be referred to as Ridgewood vs. Lakeland PC (Table 2.3). Ridgewood soils were significantly correlated with Scrubby Flatwoods habitats, sand live oak as the dominant arboreal midstory species, and increased mean years between burns. Alternatively, Lakeland soils were significantly correlated with Sandhill habitats, high total basal area, high basal area of trees with a DBH greater than 25 cm, increased % canopy cover (densiometer), other hardwoods as the dominant arboreal midstory species, and high elevations.

PC 6 exemplified Sandhill plantation (SP) habitats versus Sandhill habitats and will be referred to as SP vs. Sandhill PC (Table 2.3). Significant correlations for SP include high total

basal area, and high longleaf pine basal area. Sandhill habitats had no other significant correlation within this principal component.

PC 7 signified Ridgewood soils versus Ortega soils and will now be referred to as Ridgewood vs. Ortega PC (Table 2.3). Ridgewood soils were significantly correlated with Xeric hardwood habitats, high total basal area, high basal area of trees with a DBH greater than 25 cm, increased % tree canopy, high % fern ground cover, and high % woody plant ground cover. Ortega soils were only significantly correlated with high % bare ground cover.

Generalized Linear (Logit) Model

Results of the GLMM analysis indicated that Lakeland vs. Scranton PC, Grassland vs. Longleaf PC, and Xeric vs. Longleaf PC were all statistically significantly associated to burrow probabilities (Tables 2.4 and 2.5). The other four PCs did not show any significant associations to burrow probability rates. Linear predictors of burrow probability rates and associated polynomial regression lines plotted against PC scores (in standard deviations) for each of the three significantly associated PCs appear in Fig. 2.1.

Lakeland vs. Scranton PC

Active burrow probability rates were positively associated to the variables correlated to Lakeland soils and were also negatively associated to the variables correlated to Scranton soils (overall P value = 0.003; Active P value = 0.008; Abandoned P value = 0.546). Inspection of the polynomial regression line (Fig. 2.1) showed that as PC scores decreased and became more like those related to Lakeland soil assemblages, the probability of active burrows increased from 0.16 (at PC score = 0) to 0.40 (at PC score = -1.3). On the other hand, as PC scores increased and became more like habitat variables correlated to Scranton soils, active burrow probabilities decreased from 0.16 (at PC score = 0) to 0.0 (at PC score = 1.8). The polynomial regression line

Table 2.4 Generalized Linear Mixed Model (GLMM) Test of fixed effect for association of 7 Principal Components (PCs) to burrow probabilities (numerator degrees of freedom = 2, and denominator degrees of freedom = 168).

Principal Component	F value	Pr > F
Scranton vs. Lakeland PC	3.7	0.027
MFP vs. Sandhill PC	1.8	0.163
Grassland vs. Longleaf PC	5.7	0.004
Xeric vs. Longleaf PC	3.2	0.045
Ridgewood vs. Lakeland PC	0.5	0.632
SP vs. Sandhill PC	2.3	0.108
Ridgewood vs. Ortega PC	2.2	0.110

Table 2.5 Parameter estimates of the Generalized Linear Mixed Model analysis referenced against no burrows present (i.e. more or less likely to find a burrow in an active or abandoned state given habitat conditions). Statistically significant parameters are in **bold**. PC abbreviates Principal Component

Parameter	Status	B estimate \pm SE	P-value
Intercept	Abandoned	0.18 \pm 0.23	<0.0001
	Active	0.13 \pm 0.29	<0.0001
Scranton vs. Lakeland PC	Abandoned	0.87 \pm 0.18	0.5455
	Active	0.21 \pm 0.37	0.0080
MFP vs. Sandhill PC	Abandoned	1.21 \pm 0.16	0.3186
	Active	0.46 \pm 0.33	0.1214
Grassland vs. longleaf PC	Abandoned	0.26 \pm 0.43	0.0836
	Active	1.78 \pm 0.17	0.0052
Xeric vs. longleaf PC	Abandoned	1.63 \pm 0.16	0.0137
	Active	1.03 \pm 0.20	0.9211
Ridgewood vs. Lakeland PC	Abandoned	1.01 \pm 0.17	0.9742
	Active	0.76 \pm 0.22	0.3455
SP vs. Sandhill PC	Abandoned	1.33 \pm 0.16	0.1313
	Active	0.75 \pm 0.20	0.2462
Ridgewood vs. Ortega PC	Abandoned	0.74 \pm 0.18	0.1635
	Active	0.64 \pm 0.20	0.0745

for the probability of no burrows was nearly linear, increasing steadily from 0.50 (PC score = - 1.3) to 0.92 (PC score = 2.8).

Lakeland was the only soil type to have a statistically significant positive association to active burrow probabilities. The total number of transects surveyed are shown in Table 2.6, and

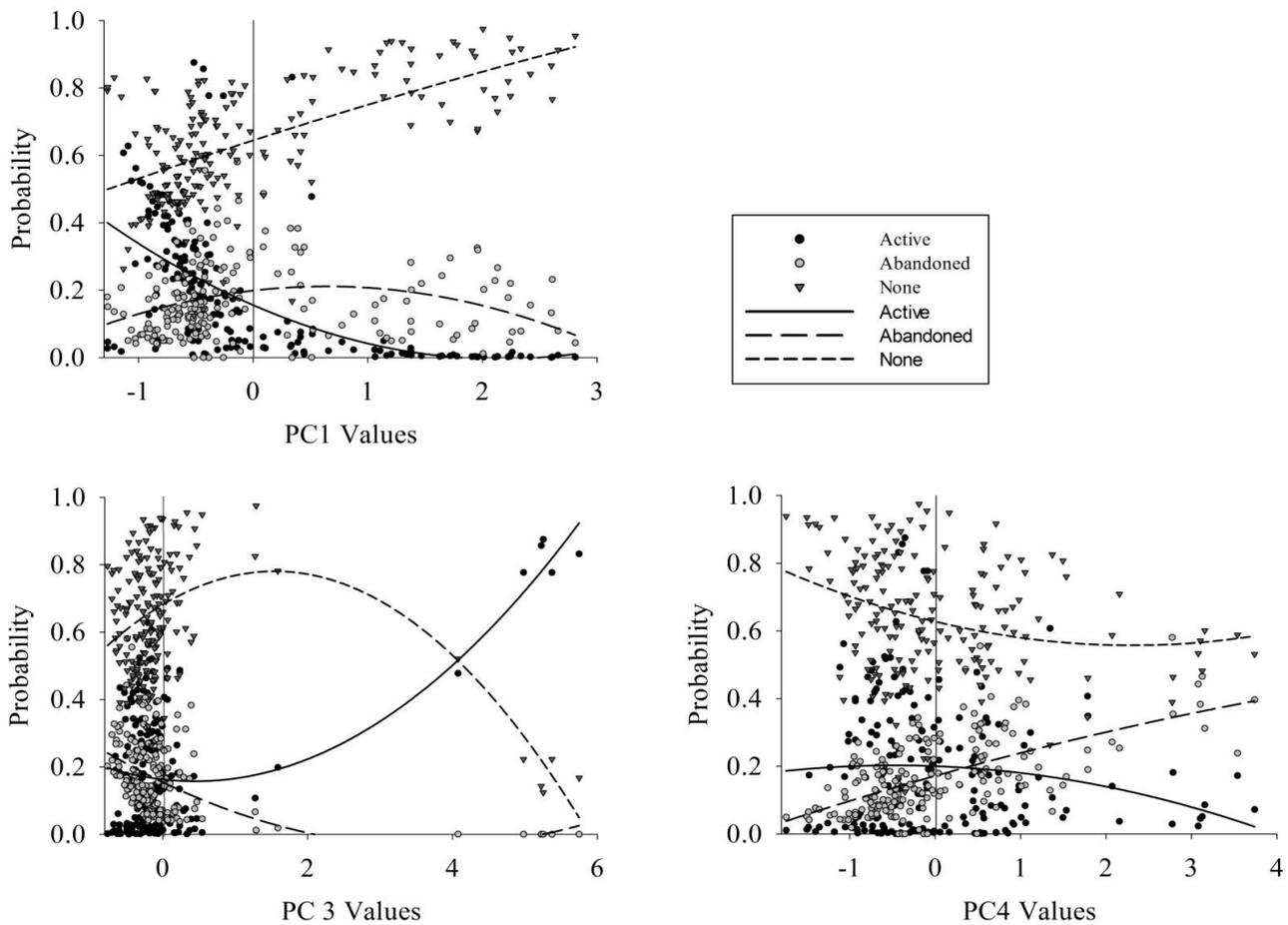


Figure 2.1 Scatter plot of active, inactive, and no burrow probability rates against Principal Component (PC) values (in standard deviations) for PC1 (Lakeland vs. Scranton PC), PC3 (Grassland vs. Longleaf PC), and PC4 (Xeric vs. Longleaf PC).

the number of active and abandoned burrows observed for Lakeland soils, Sandhill habitats, and on transects with longleaf pine as the dominant canopy species are shown in Tables 2.7 through 2.9. There was no observable relationship between active burrow probabilities and transects with midstories dominated by turkey and/or bluejack oak; active burrow probabilities ranged from 0 to 0.63 for the 77 transects with turkey and/or bluejack oak, and ranged from 0 to 0.89 for the 107 transects without turkey and/or bluejack oak. There was also no observable relationship between active burrow probabilities and wiregrass; wiregrass was absent on 25 transects that had

Table 2.6 Area covered, number of transects and distance surveyed by soil and habitat type. Pl. abbreviates plantation.

Variable	Area (km ²)	#Transects	Distance (km)
SOIL			
Scranton	10.9	21	2.9
Ridgewood	14.4	66	13.2
Ortega	8.3	52	10.3
Leon	5.4	16	3.2
Lakeland	4.2	29	6.5
HABITAT			
Grassland	0.9	6	1.1
Sandhill	15.0	77	16.2
Sandhill Pl.	3.6	12	4.4
Mesic Flatwoods	24.4	43	9.1
Mesic Flatwoods Pl.	3.8	11	3.1
Scrubby Flatwoods	1.7	2	1.8
Xeric Hammock	3.1	5	3.7

Table 2.7 Raw total number of four burrow categories observed within soil and habitat types. Burrow rate (burrows per kilometer) are shown in parenthesis.

Variable	Active	Inactive	Abandoned	Collapsed	Total
SOIL					
Scranton	0 (0.0)	1 (0.3)	1 (0.3)	0 (0.0)	2 (0.7)
Ridgewood	7 (0.5)	15 (1.1)	25 (1.9)	5 (0.4)	52 (3.9)
Ortega	17 (1.7)	16 (1.6)	10 (1.0)	6 (0.6)	49 (4.8)
Leon	0 (0.0)	1 (0.3)	15 (4.7)	2 (0.6)	18 (5.6)
Lakeland	33 (5.1)	26 (4.0)	10 (1.5)	4 (0.6)	73 (11.2)
Pottsburg	0 (0.0)	0 (0.0)	2 (4.0)	0 (0.0)	2 (4.0)
Alpin	2 (10.0)	2 (10.0)	0 (0.0)	1 (5.0)	5 (25.0)
TOTAL	59 (1.6)	61 (1.7)	63 (1.7)	18 (0.5)	201 (5.5)
HABITAT					
Grassland	5 (4.5)	9 (8.2)	3 (2.7)	0 (0.0)	17 (15.5)
Sandhill	41 (2.5)	39 (2.4)	15 (0.9)	9 (0.6)	104 (6.4)
Sandhill Pl.	10 (2.3)	3 (0.7)	12 (2.7)	5 (1.1)	30 (6.8)
Mesic Flatwoods	0 (0.0)	1 (0.1)	22 (2.4)	3 (0.3)	26 (2.9)
Mesic Flatwoods Pl.	0 (0.0)	0 (0.0)	4 (1.3)	0 (0.0)	4 (1.3)
Scrubby Flatwoods	0 (0.0)	1 (0.6)	3 (1.7)	1 (0.6)	5 (2.8)
Xeric Hammock	3 (0.8)	8 (2.2)	4 (1.1)	0 (0.0)	15 (4.1)
TOTAL	59 (1.5)	61 (1.5)	63 (1.6)	18 (0.5)	201 (5.1)

Table 2.8 Number of four burrow categories observed by soil and habitat type after removal of transects on soil types with no burrow observations and transects on soil types represented by less than 5 observations for multivariate analysis. Burrow rate (burrows per kilometer) are shown in parenthesis.

Variable	Active	Inactive	Abandoned	Collapsed	Total
SOIL					
Scranton	0 (0.0)	1 (0.3)	0 (0.0)	0 (0.0)	1 (0.3)
Ridgewood	6 (0.5)	14 (1.1)	15 (1.1)	5 (0.4)	40 (3.0)
Ortega	12 (1.2)	8 (0.8)	8 (0.8)	5 (0.5)	33 (3.2)
Leon	0 (0.0)	0 (0.0)	13 (4.1)	2 (0.6)	15 (4.7)
Lakeland	22 (3.4)	15 (2.3)	9 (1.4)	2 (0.3)	48 (7.4)
TOTAL	40 (1.1)	38 (1.1)	45 (1.2)	14 (0.4)	137 (3.8)
HABITAT					
Grassland	5 (4.5)	9 (8.2)	3 (2.7)	0 (0.0)	17 (15.5)
Sandhill	25 (1.5)	26 (1.6)	12 (0.7)	5 (0.3)	68 (4.2)
Sandhill Pl.	8 (1.8)	1 (0.2)	8 (1.8)	4 (0.9)	21 (4.8)
Mesic Flatwoods	0 (0.0)	0 (0.0)	14 (1.5)	3 (0.3)	17 (1.9)
Mesic Flatwoods Pl.	0 (0.0)	0 (0.0)	3 (1.0)	0 (0.0)	3 (1.0)
Scrubby Flatwoods	1 (0.6)	1 (0.6)	1 (0.6)	1 (0.6)	4 (2.2)
Xeric Hammock	1 (0.3)	1 (0.3)	4 (1.1)	1 (0.3)	7 (1.9)
TOTAL	40 (1.0)	38 (1.0)	45 (1.1)	14 (0.4)	137 (3.5)

Table 2.9 Transect distance (km) and number of active and abandoned burrows observed on transects by dominant canopy species.

Dominant Canopy Species	Transect Distance	Active	Abandoned
Longleaf Pine	26.7	58	37
Mixed Pines	1.4	3	4
Slash Pine	4.8	1	9
Xeric Hardwoods	1.6	3	6
None	1.3	13	3

active burrow probabilities ranging from 0 to 0.88, and wiregrass was present on one or more plots along 159 transects that had active burrow probabilities ranging from 0 to 0.63. Active burrows were located on transects having average elevations that ranged from 2.7 to 9.8 meters. The scatter plot of elevation against active burrow probabilities (Fig. 2.2) showed that active burrow probabilities varied greatly with elevation, however it did revealed that a cluster of five

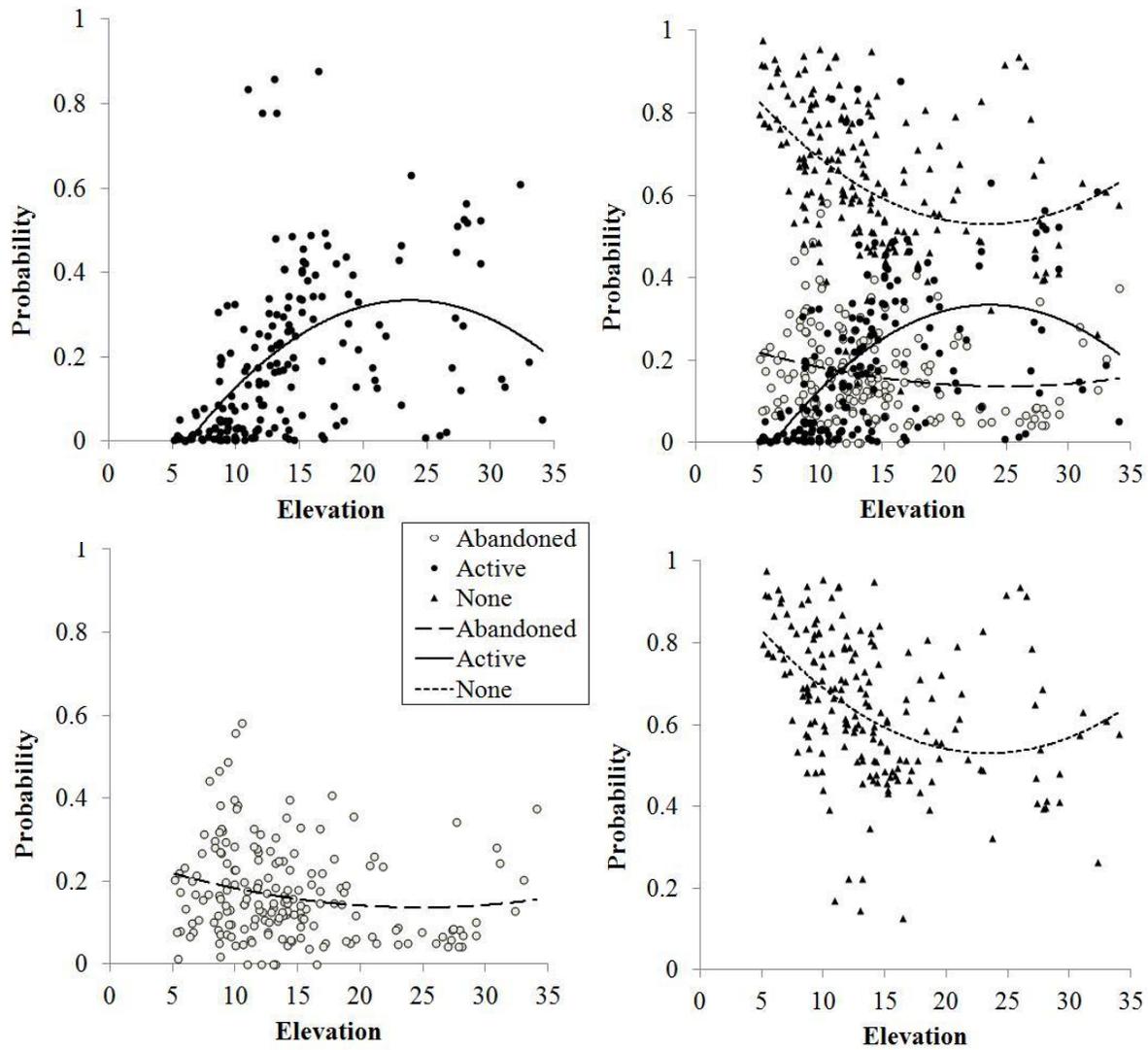


Figure 2.2 Scatter plots of burrow probabilities and associations with fitted polynomial regression lines against elevation.

transects situated at elevations between 3.4 and 5.2 meters had the highest active burrow probabilities that ranged from 0.78 to 0.88.

Mesic Flatwoods habitats over Scranton soils had a negative association to active burrow probabilities. Active burrow probabilities decreased as the basal area of other pine trees (slash

pine) increased (Fig. 2.3); with the exception of one transect, when the basal area of other pine trees was greater than 6 m²/acre then probabilities were higher for abandoned burrows (which were not significantly associated to this PC) than active burrows. Furthermore, active burrow probabilities decreased as the basal area of trees with a DBH greater than 25 cm increased, and according to the polynomial regression line active burrow probabilities fell below abandoned burrow probabilities when trees with a DBH greater than 25 cm was greater than 12 m²/acre (Fig. 2.4). As % tree canopy increased from 0% to 86%, active burrow probabilities decreased (Fig. 2.5). Inspection of the polynomial regression line showed that when % tree canopy was less than 8%, active burrow probabilities were greater than no burrow probabilities; and when % tree canopy was less than 42%, active burrow probabilities were greater than abandoned burrow probabilities, but abandoned burrow probabilities were not significantly associated to this PC. There was no observable relationship between active burrow probabilities and transects with midstories dominated by other hardwood species; active burrow probabilities ranged from 0 to 0.83 for the 23 transects with other hardwood species, and ranged from 0 to 0.88 for the 161 transects without other hardwood species.

Grassland vs. Longleaf PC

Active burrow probabilities were positively associated with variables correlated to Grassland but were not negatively associated with variables correlated to Longleaf (overall P value = 0.0042; Active P value = 0.0052; Abandoned P value = 0.0836). According to the polynomial regression line (Fig. 2.1), as PC scores increased and became more like variables related to Grassland habitats, the probability of active burrows increased dramatically from around 0.16 (at PC score = 0) to 0.92 (at PC score = + 5.9). The polynomial regression line showed the probability of no burrows started at 0.68 (at PC = 0), increased to 0.78 (when PC

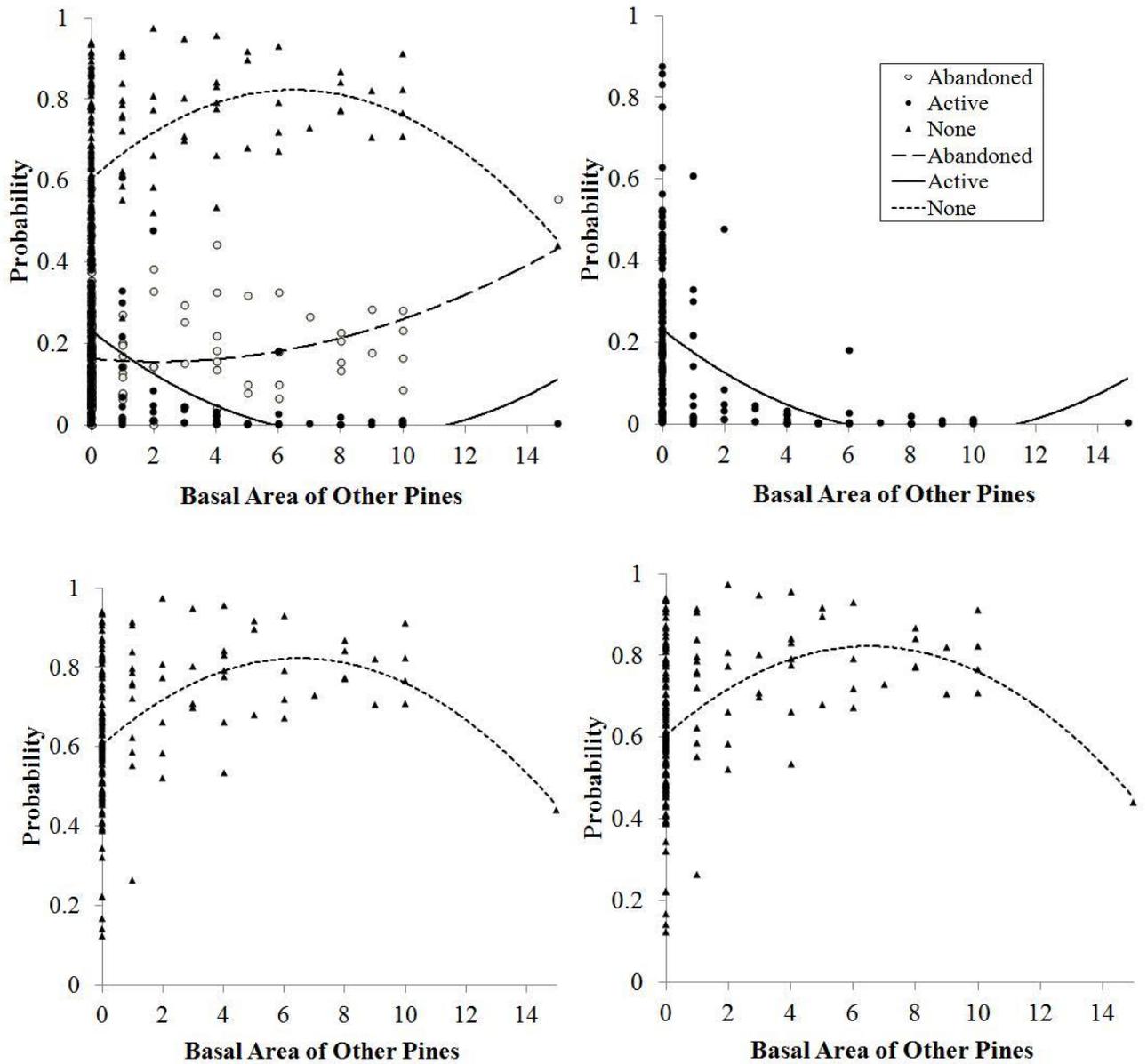


Figure 2.3 Scatter plots of burrow probabilities and associations with fitted polynomial regression lines against the basal area of other pines.

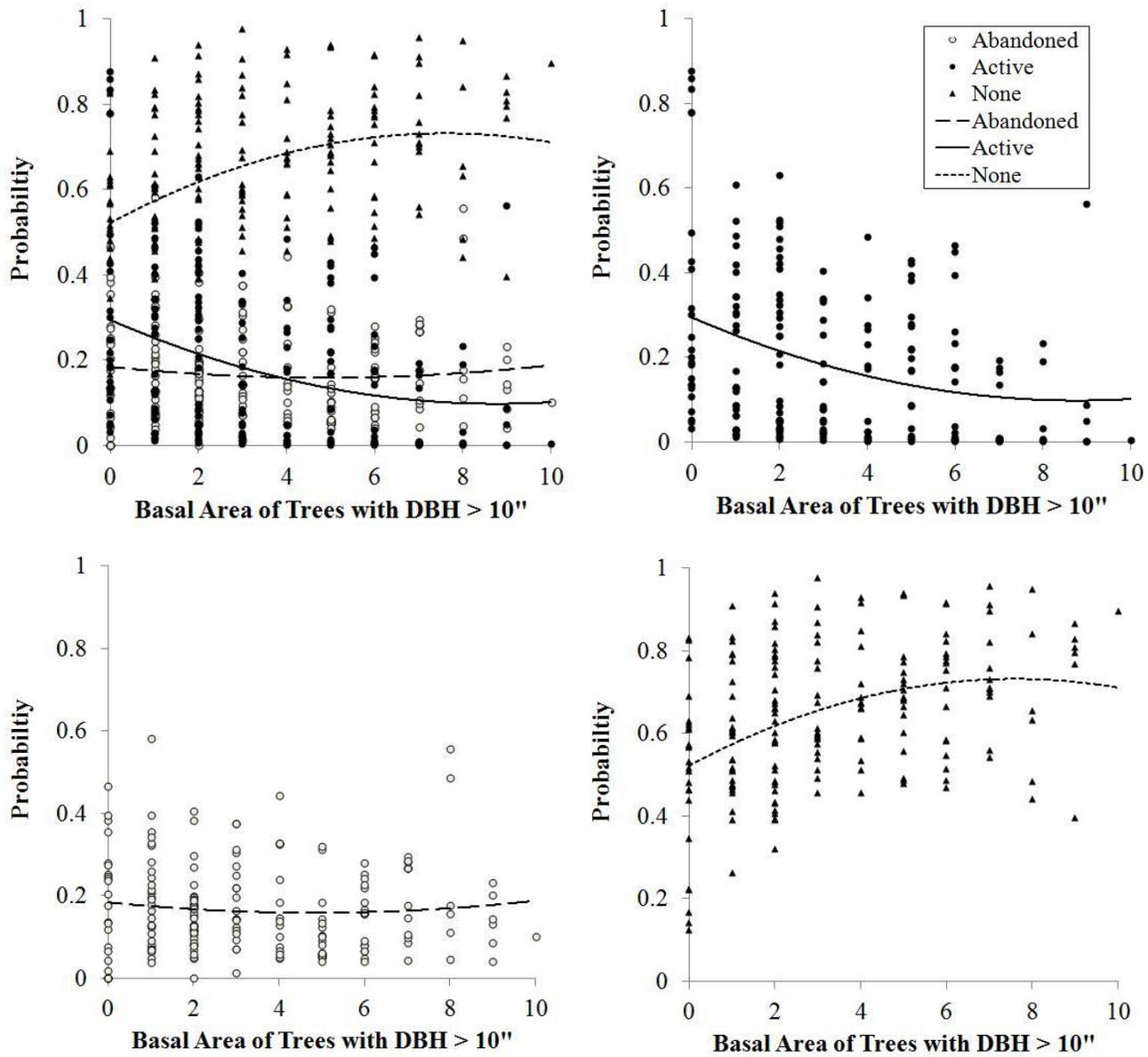


Figure 2.4 Scatter plots of burrow probabilities and associations with fitted polynomial regression lines against the basal area of trees with a DBH greater than 10 inches.

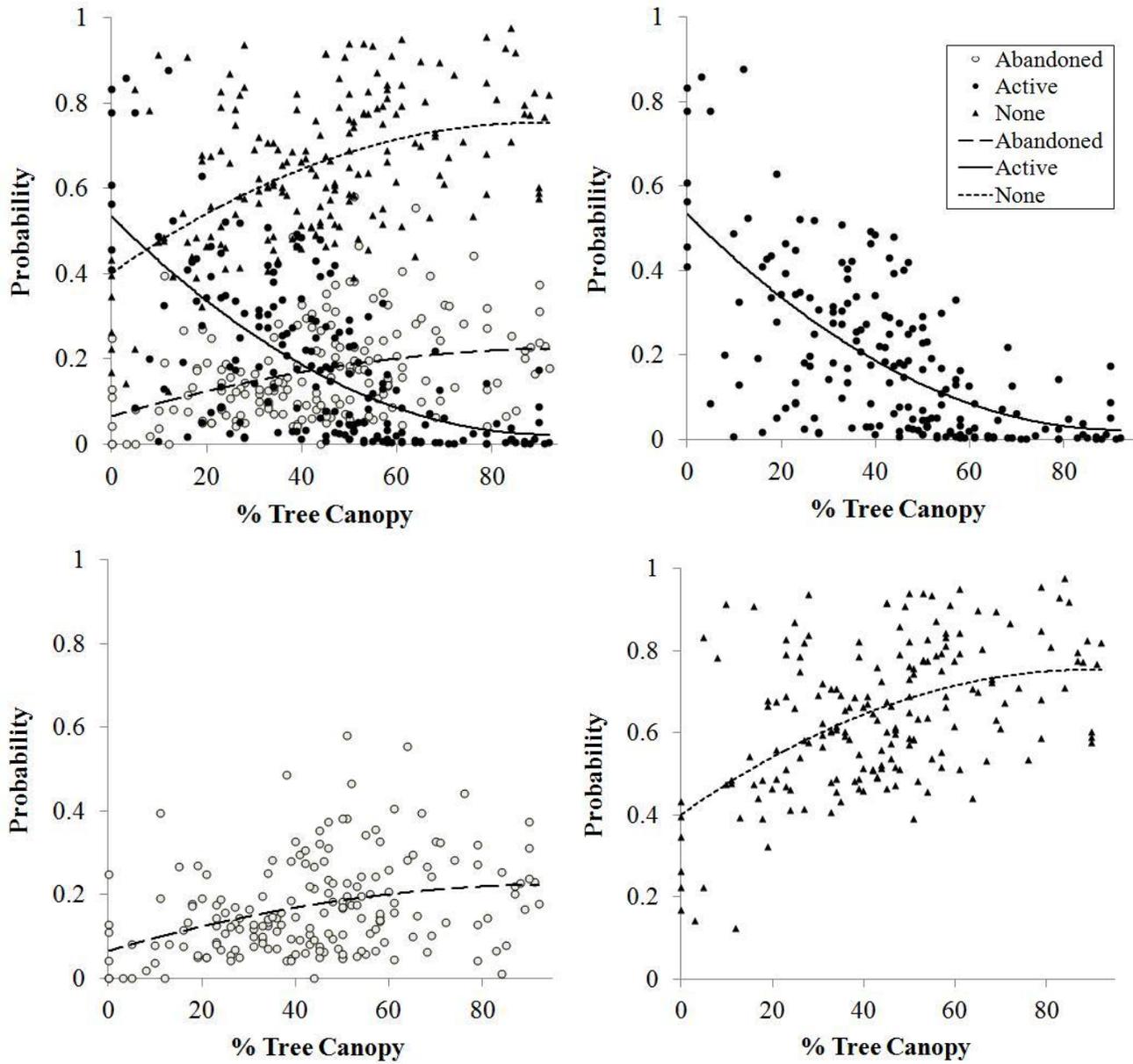


Figure 2.5 Scatter plots of burrow probabilities and associations with fitted polynomial regression lines against percent tree canopy.

scores were between 1.2 and 1.8) and dropped to 0.04 (at PC score = 5.8). Examination of the scatter plot (Fig. 2.1) showed that most of the data were concentrated between PC scores of -1 and 1, and there were few observations as PC scores increased beyond 1, which indicated the extreme increase and decrease of these polynomial regression lines was likely influenced by unusual values.

The polynomial regression line suggested that active burrow probabilities increased with increasing % herbaceous ground cover (Fig. 2.6); where herbaceous ground cover surpassed Tables 2.6 through 2.9 show the total number of transects surveyed and the number of active and abandoned burrows observed in Grassland habitats, and on transects with no dominant canopy 19%, active burrow probabilities were higher than abandoned, and where herbaceous ground cover exceeded 78%, active burrow probabilities were higher than no burrow probabilities. However, the large amount of variation exhibited by the scatter plot for active and no burrow probabilities suggested a questionable relationship but abandoned burrow probabilities clearly decreased with increasing % herbaceous ground cover.

Xeric vs. Longleaf PC

Abandoned burrow probabilities were positively associated to variables correlated to Xeric habitats and negatively associated to variables correlated to Longleaf habitats (overall P value = 0.0448; Active P value = 0.9211; Abandoned P value = 0.0137). The polynomial regression lines for the probability of abandoned burrows (Fig. 2.1) showed that as PC scores increased and became more like those correlated to Xeric Hammock habitats, abandoned burrow probabilities increased from 0.17 (at PC score = 0) to 0.40 (at PC score = 3.7). Alternatively, as PC scores decreased and became more like those correlated with Longleaf habitats, the probability of abandoned burrows decreased from 1.7 (at PC score = 0) to 0.04 (at PC score = -

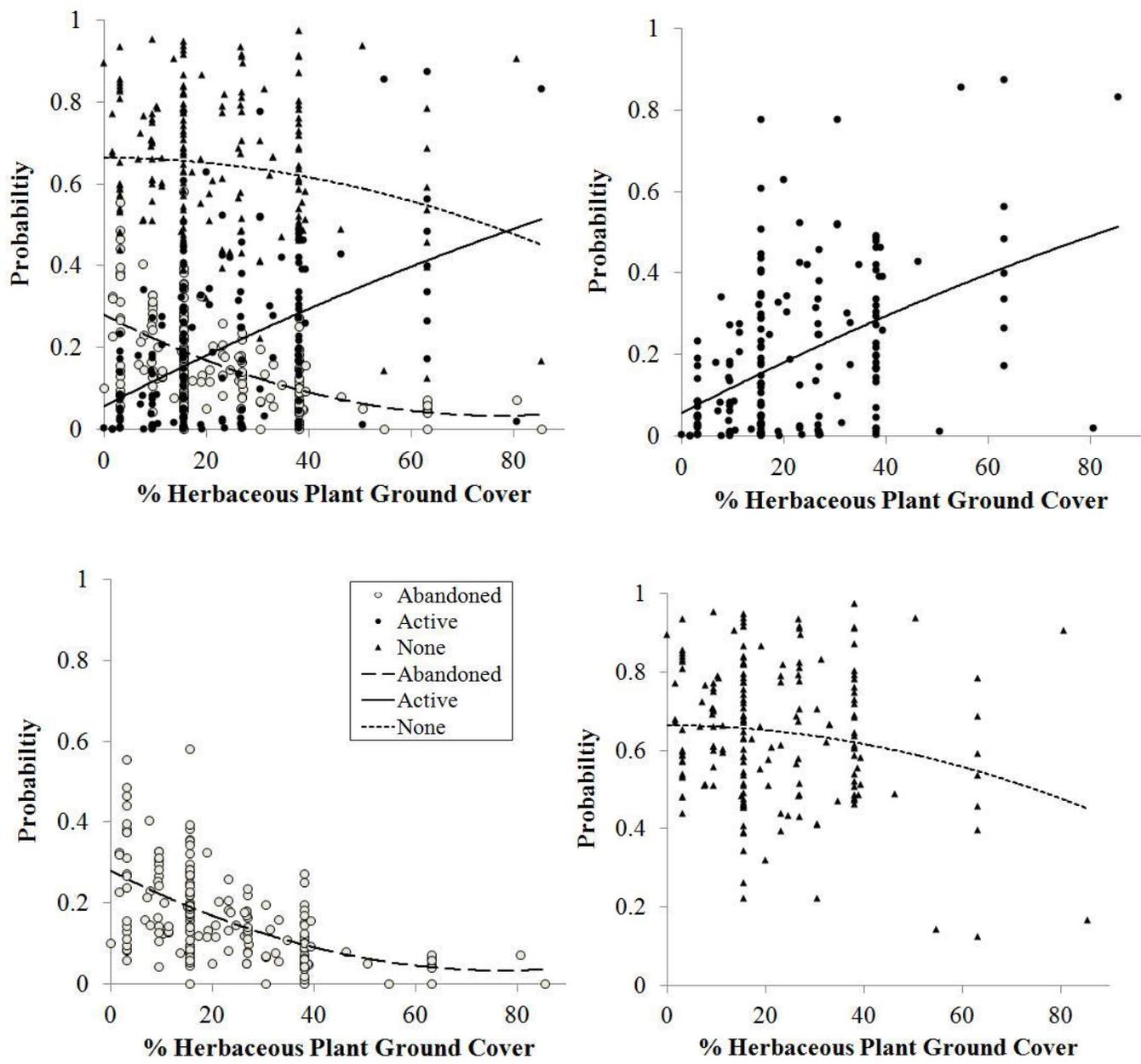


Figure 2.6 Scatter plots of burrow probabilities and associations with fitted polynomial regression lines against percent herbaceous ground cover.

PC score = 3.7).

Tables 2.6 through 2.9 shows the total number of transects surveyed and the number of active and abandoned burrows observed in Xeric Hammock habitats, and on transects with xeric hardwoods as the dominant canopy species. Percent canopy cover (measured by a densiometer) ranged from 0 to 86%. Abandoned burrow probabilities clearly increased as % canopy cover increased but there was no observable relationship with active or no burrow probabilities (Fig. 2.7). Sand live oak was present as a dominant midstory species on 46 transects that had abandoned burrow probabilities ranging from 0 to 0.58, and was absent on 138 transects that had abandoned burrow probabilities ranging from 0 to 0.569. Other hardwoods were present as a dominant midstory species on 23 transects that had abandoned burrow probabilities ranging from 0 to 0.35, and was absent on 161 transects that had abandoned burrow probabilities ranging from 0 to 0.58. Percent litter ground cover ranged from 0% to 90% (Fig. 2.8) and abandoned burrow probabilities increased as % litter cover increased. According to the polynomial regression line, when litter ground cover was greater than 48%, there were higher probabilities of abandoned burrows than active burrows.

Mean years between burns ranged from every 2.3 to every 6.8 years. The polynomial regression line (Fig. 2.9) suggests that abandoned burrow probabilities increased as mean years between burns increased, but the scatter plot does not illustrate a clear increase. However, the scatter plot suggests that mean years between burns may have more of an influence on active burrows probabilities than abandoned burrow probabilities. Furthermore, the polynomial regression lines suggest that when mean years between burns is greater than 3.3 years, abandoned burrow probabilities surpass active burrow probabilities.

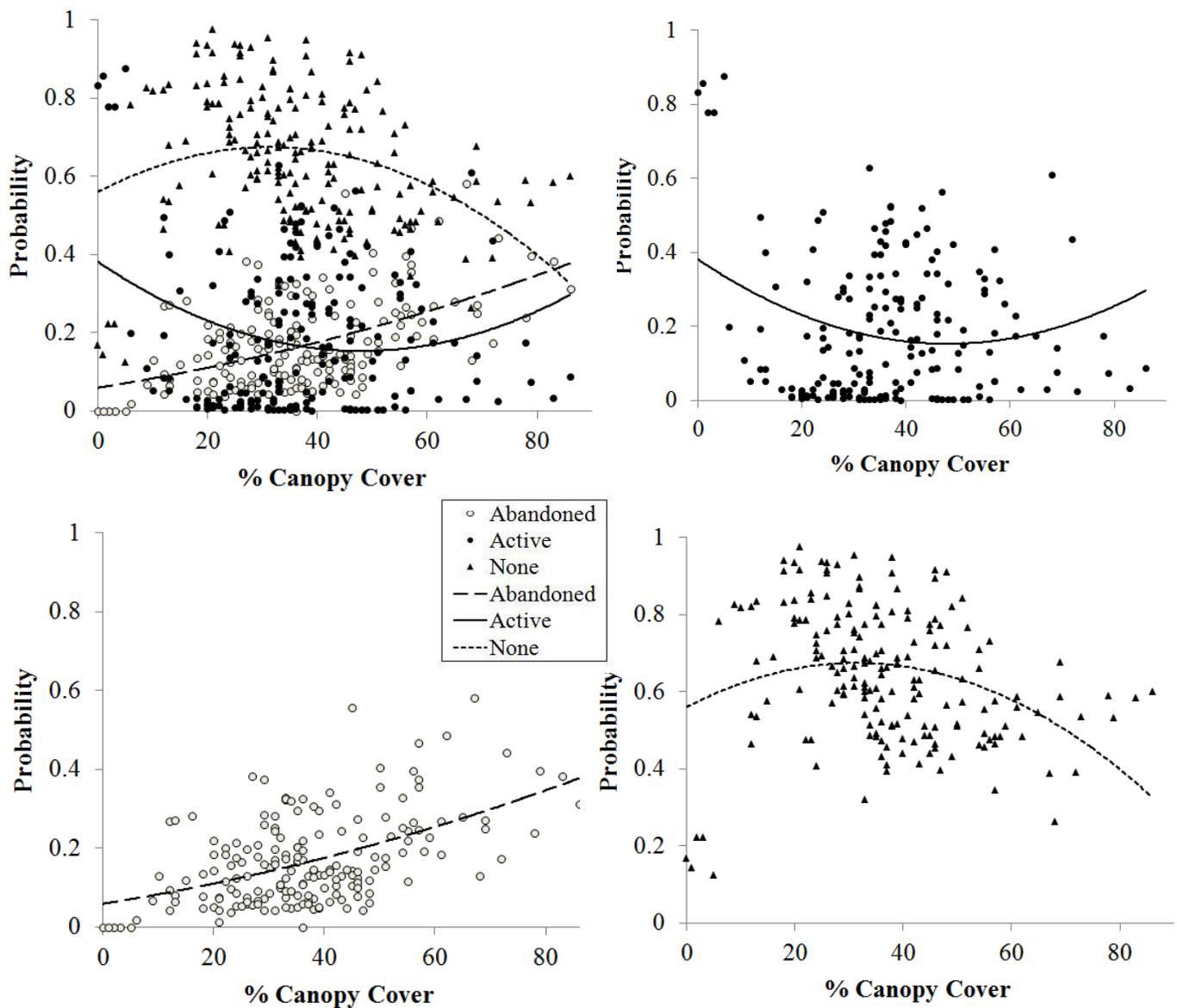


Figure 2.7 Scatter plots of burrow probabilities and associations with fitted polynomial regression lines against percent canopy cover.

Abandoned burrow probabilities were negatively associated with variables correlated to Longleaf. Tables 2.6 through 2.9 shows the total number of transects surveyed and the number of active and abandoned burrows observed having longleaf pine as the dominant canopy species. Like all other arboreal midstory variables, presence or absence of pine saplings as a dominant

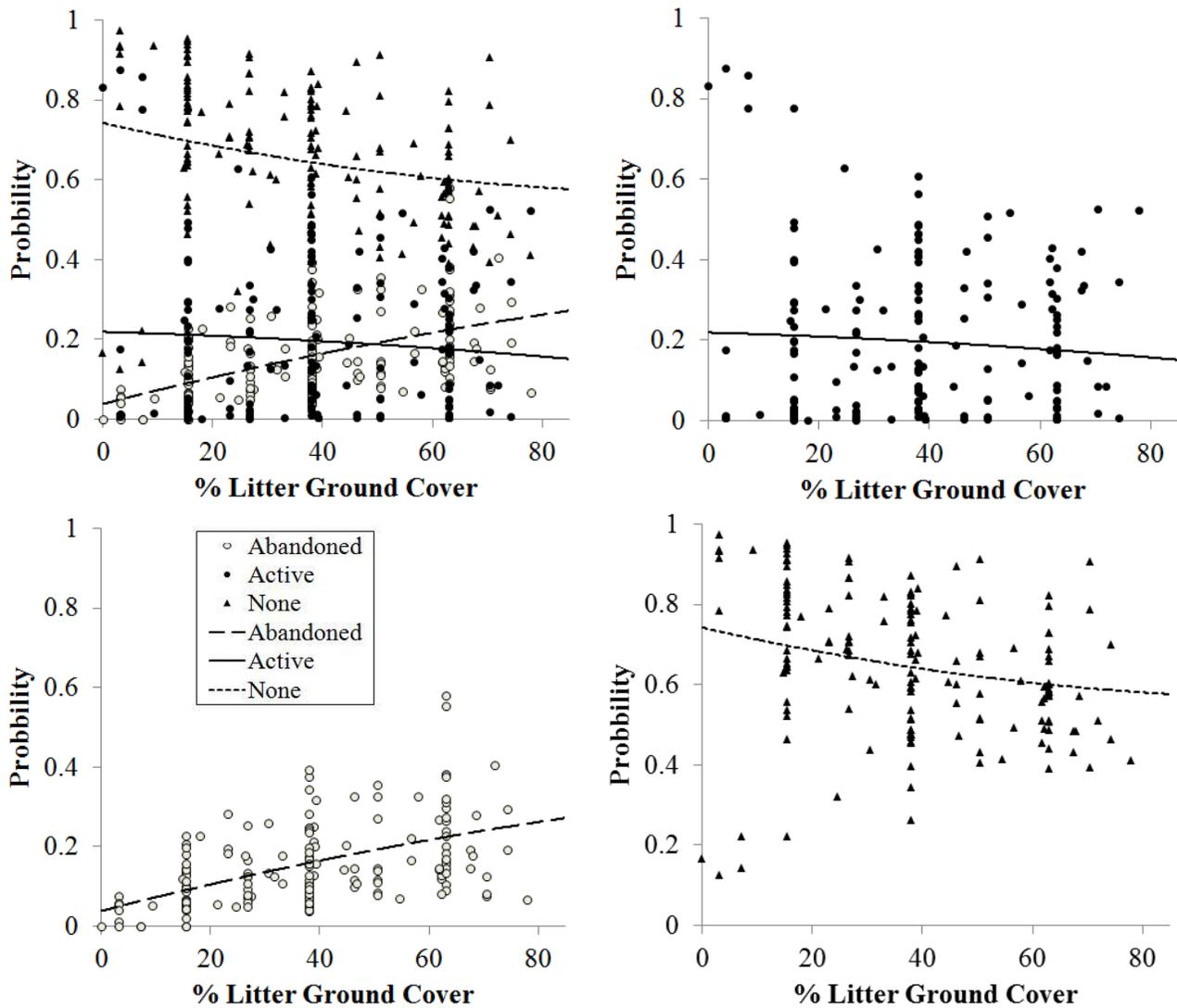


Figure 2.8 Scatter plots of burrow probabilities and associations with fitted polynomial regression lines against percent litter ground cover.

arboreal midstory species did not seem to influence burrow probabilities. Pine saplings were present as a dominant midstory species on 63 transects that had abandoned burrow probabilities ranging from 0.02 to 0.41, and was absent from 121 transects that had abandoned burrow probabilities ranging from 0 to 0.58.

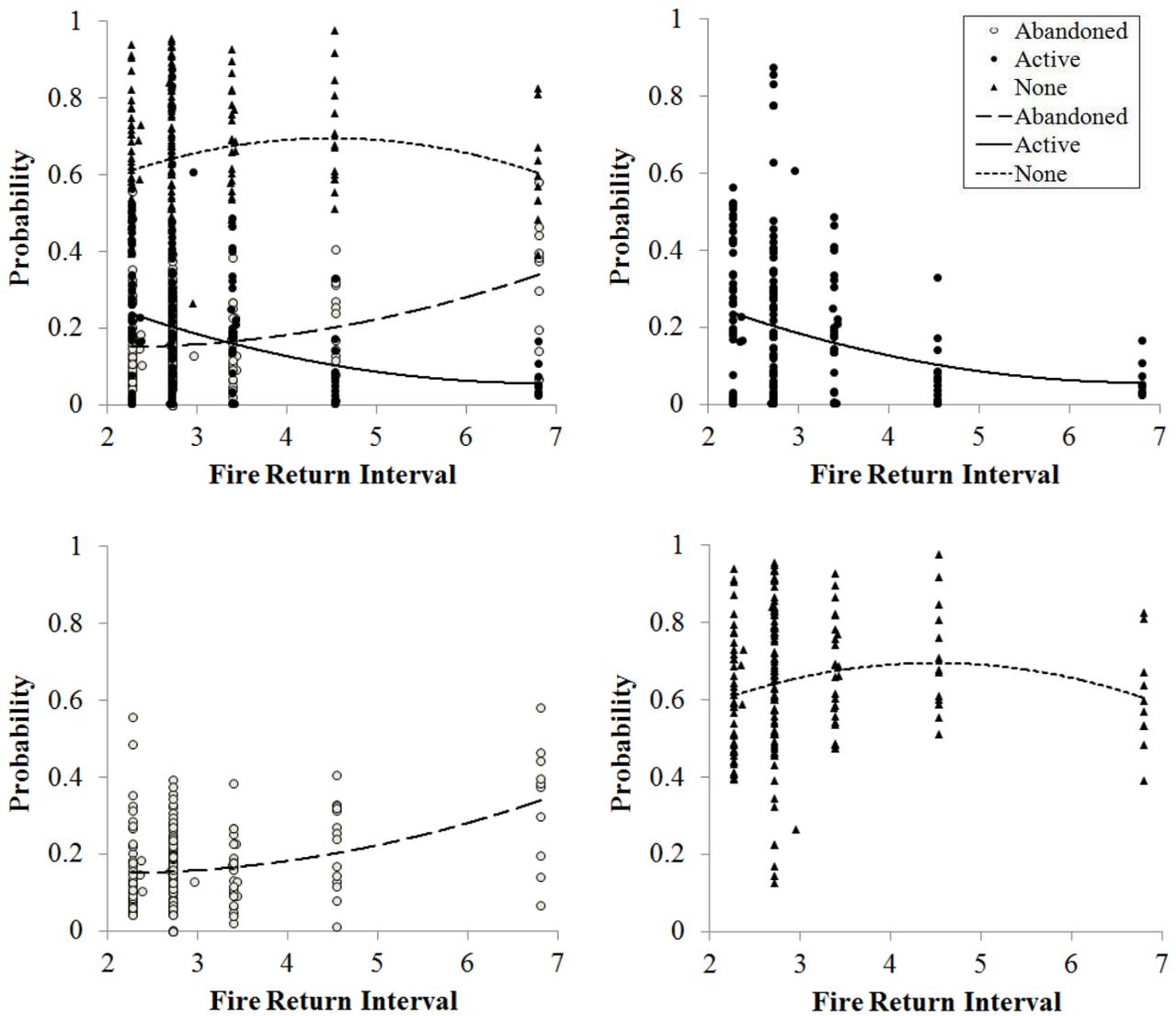


Figure 2.9 Scatter plots of burrow probabilities and associations with fitted polynomial regression lines against fire return interval in years.

Biological Assessment

Total basal area, basal area of longleaf pines, percent woody plant ground cover, and percent palmetto ground cover were not included in PCs with associations to burrow probabilities, but observation of the polynomial regression lines and scatter plots suggest they have influence. Total basal area ranged from 0 to 46 m²/acre and the polynomial regression lines

and scatter plots (Fig. 2.10) showed that as total basal area increased, active burrow probabilities decreased while abandoned burrow probabilities increased. When total basal area was greater than 21 m²/acre, abandoned burrow probabilities became greater than active burrow probabilities. Basal area of longleaf pine also ranged from 0 to 46 m²/acre. The polynomial regression lines and scatter plots (Fig. 2.11) showed that active burrow probabilities decreased as basal area of longleaf pines increased, but abandoned burrow probabilities did not exhibit any relationship with the basal area of longleaf pines. However, when the basal area of longleaf pines was greater than 23 m²/acre, active burrow probabilities were less than abandoned burrow probabilities.

Percent woody plant ground cover ranged from 0 to 85%. The polynomial regression line (Fig. 2.12) showed that as % woody plant ground cover increased, both active and abandoned probabilities decreased and no burrow probabilities increased but according to the scatter plot the relationship is unclear. Percent palmetto ground cover ranged from 0 to 38%. The polynomial regression lines and scatter plots (Fig. 2.13) showed no relationship with the probabilities of no burrows and abandoned burrows, but active burrow probabilities clearly decreased with increasing palmetto cover.

DISCUSSION

I identified three variable assemblages, Lakeland vs. Scranton PC, Grassland vs. Longleaf PC, and Xeric vs. Longleaf PC, that were associated to burrow probability rates, but inspection of the plots for linear predictors of burrow probability rates and polynomial regression lines revealed that not all of the PC assembled variables exhibited biological significance. Soil type, habitat type, and dominant canopy were included in the model as categorical variables thereby

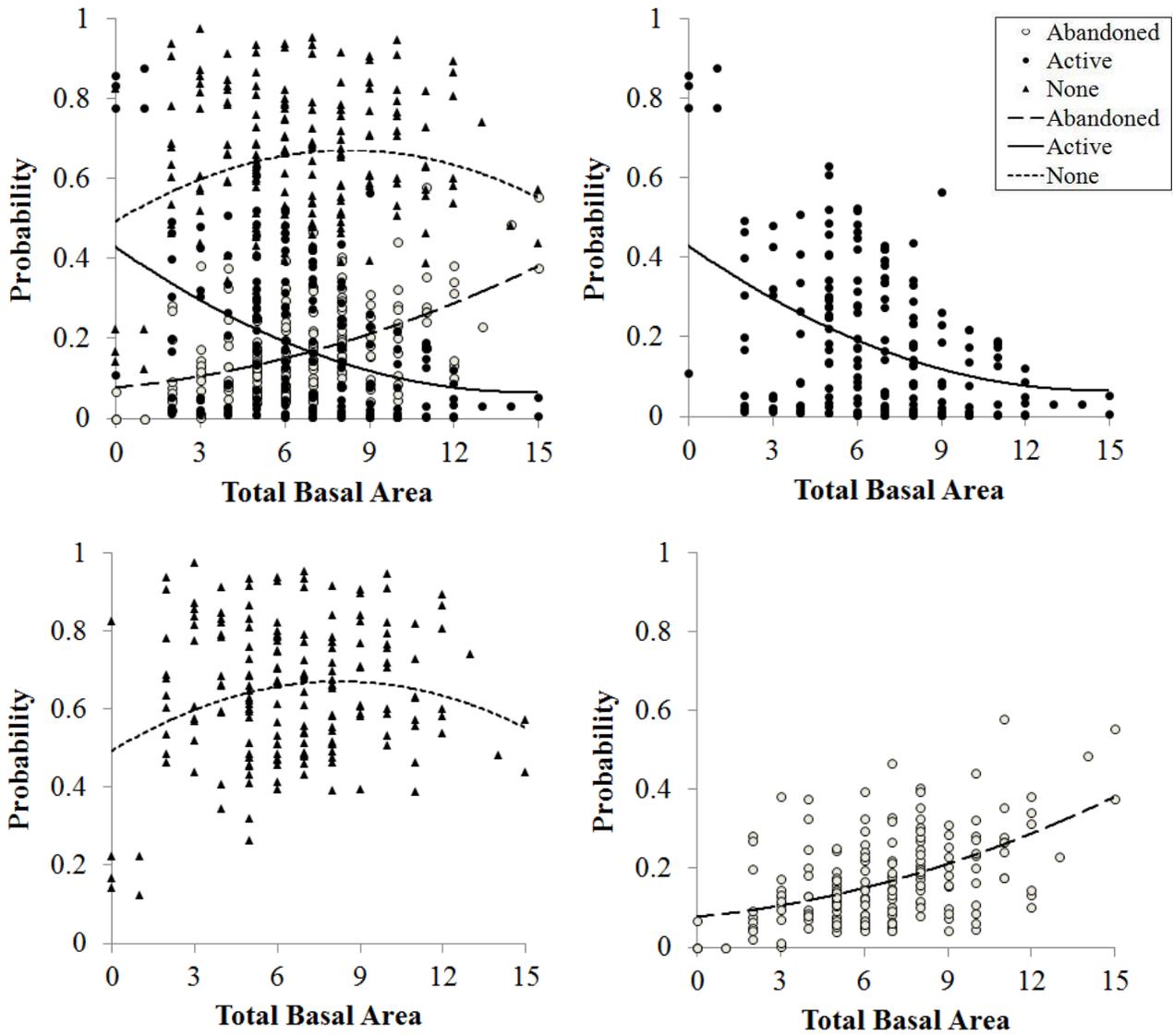


Figure 2.10 Scatter plots of burrow probabilities and associations with fitted polynomial regression lines against total basal area.

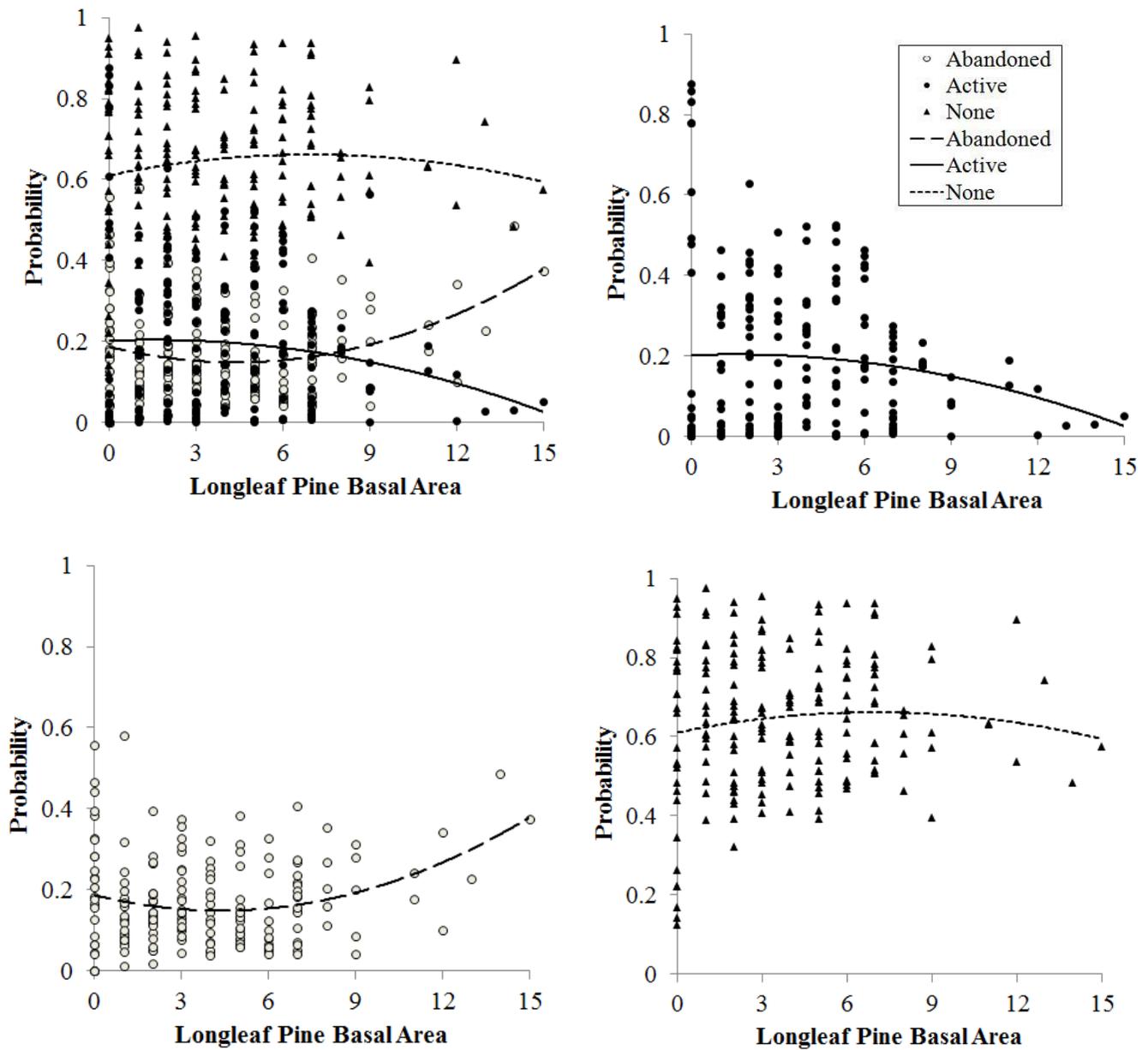


Figure 2.11 Scatter plots of burrow probabilities and associations with fitted polynomial regression lines against longleaf pine (*Pinus palustris*) basal area.

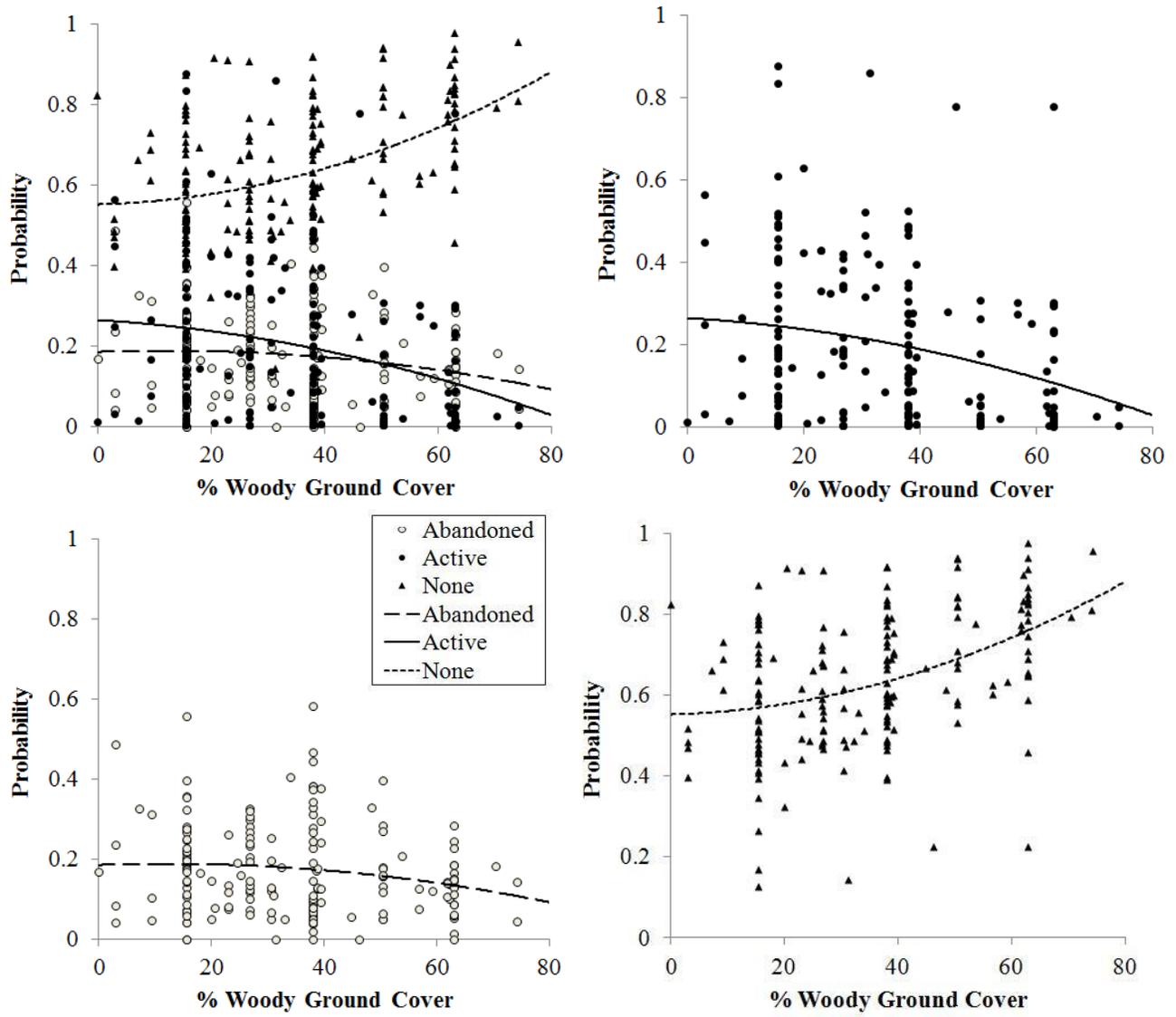


Figure 2.12 Scatter plots of burrow probabilities and associations with fitted polynomial regression lines against percent woody ground cover.

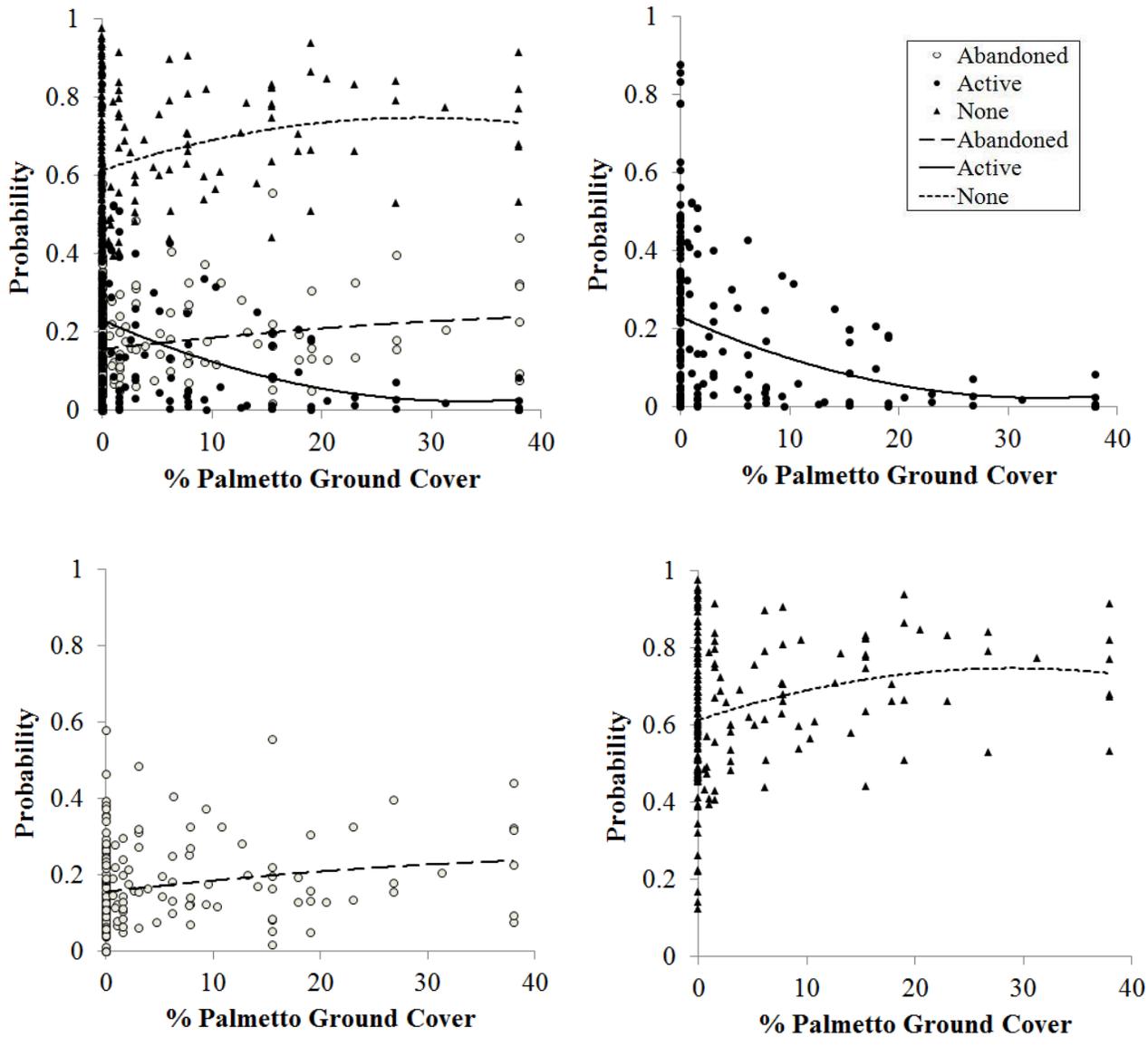


Figure 2.13 Scatter plots of burrow probabilities and associations with fitted polynomial regression lines against percent palmetto ground cover.

making these variables impossible to plot, but their inclusion in PCs and relevance to burrow probability rates are discussed in the following. .

Lakeland vs. Scranton PC

Active burrow probabilities were higher in areas with the following characteristics; Lakeland soils, Sandhill habitats, canopy dominated by longleaf pines, dominant arboreal midstory of turkey and/or bluejack oaks, wiregrass presence, and high elevations. Lakeland soils in Wakulla County are sandy, excessively drained, have a depth to water table greater than 1.8 m range from 0-2 m deep, and have a clay content that ranges from 1-8% (Allan, 1991). These characteristics agree with previous reports that gopher tortoises prefer well-drained sandy soils that are greater than 1 meter deep, with low clay content and high depth to water tables (Landers, 1980; Landers and Speake, 1980; Auffenberg and Franz, 1982; Campbell and Christman, 1982; Jones and Dorr, 2004; Baskaran *et. al.*, 2006). Gopher tortoises have also long been affiliated with longleaf pine-oak uplands (Auffenberg, 1979; Landers and Speake, 1980; Auffenberg and Franz, 1982; Campbell and Christman, 1982; Diemer, 1986), which are characteristic of Sandhill habitats (FNAI, 2010) and the high probability of burrow activity in these areas thus was not surprising. The presence or absence of bluejack and/or turkey oak along transects did not seem to be an influencing factor on burrow activity, but rather tied by correlation to Lakeland assembled variables. However, areas that have not been maintained by frequent fires exhibit increased oaks densities, and thus increased canopy closure which leads to successional changes such as considerable reduction in herbaceous vegetation, increased recruitment of deciduous plant species, reduced fuels, and reduced sunlight areas necessary for thermoregulation and egg incubation, all leading to reduced population densities and reduced nesting efforts (Landers, 1980; Auffenberg and Franz, 1982; Campbell and Christman, 1982; Peet and Allard, 1993;

Aresco and Guyer, 1999; Kush and Mendahl, 2000; Ashton *et al.*, 2008). This model coupled with previous reports suggests the presence of these xeric oak species are tolerated by gopher tortoises if confined to the understory and maintained at low densities associated with each successional habitat (Landers and Speake, 1980).

Wiregrass has been reported as an important seasonal food source, particularly for adult gopher tortoises, but is avoided in favor of broad-leaved grasses and forbs, especially by juveniles (Landers, 1980; Garner and Landers, 1981; Auffenberg and Franz, 1982; MacDonald and Mushinsky, 1988; Mushinsky *et al.*, 2003; Birkhead *et al.*, 2004). The proportion of plots with wiregrass present on transects was correlated to Lakeland assembled variable, but further inspection showed that it did not influence active burrow probabilities. In Florida, wiregrass is affiliated with sandy soils and longleaf pine ecosystems as both a fire indicator and facilitator (Wells and Shunk, 1931; Myers, 1990) and is likely related to burrow activity more because of this habitat correlation than as a dominant food source when other more nutritious herbaceous vegetation is available.

Active burrow probabilities did not show a clear positive relationship with increased elevations which reflects the reliance of elevation occurring on Lakeland soils and Sandhill habitats (among the other variables correlated with this PC). This supports the findings of Jones and Dorr (2004) that elevation can be used to predict the presence of active burrows, but only in combination with other variables. Low probabilities for active burrows at higher elevations likely reflect areas that fell outside the bounds of favorable features for gopher tortoises.

Active burrow probabilities were negatively associated with the following characteristics: Scranton soils, Mesic Flatwoods habitats, canopy dominated by mixed longleaf and slash pines, high basal area of other pine species and trees with a DBH greater than 25 cm, other hardwoods

as the dominant midstory species, and high % tree canopy. Scranton soils are poorly drained and are common of flatwoods habitats (Allan, 1991); therefore the negative association to this soil also agrees with reports that gopher tortoises prefer well drained soils (Landers and Speake, 1980; Auffenberg and Franz, 1982; Campbell and Christman, 1982; Diemer, 1986; Cox *et al.*, 1987; Jones and Dorr, 2004; Baskaran *et. al.*, 2006).

Historic Mesic Flatwoods were characterized by an open canopy of longleaf pine but over the last century, were invaded by slash pine in areas where longleaf pines had been logged and fire was inhibited (FNAI, 2010). Aresco and Guyer (1999) reported high rates of burrow abandonment in mature slash pine plantations as a result of canopy closure; however the results of this study show a negative association of active burrow probabilities in similar areas suggesting unsuitable underlying habitat conditions. Lohofener and Lohmeier (1981) found that conversion of longleaf pine forests to slash pine forests was associated with deciduous shrub invasion and reduced foraging areas, forcing gopher tortoises to migrate to more open areas. The results of this study revealed that active burrows were negatively associated to Mesic Flatwoods in which slash pines were integrated with longleaf, and is further validated by the trend line showing decreased probability of burrow activity with increasing basal area of other pines (notably slash pine on this study area). The presence or absence of other hardwoods along transects did not seem to be an influencing factor on burrow abandonment, but was rather tied by correlation to Scranton correlated variables. Active burrow probabilities exhibited some decreased with increasing trees having a DBH greater than 25 cm"; which could reflect that larger trees create larger areas of total canopy cover than an equal number of smaller trees. Furthermore, the trend line for % tree canopy demonstrated that active burrow probabilities declining dramatically with increased % tree canopy, providing further evidence that canopy

cover is highly influential on burrows probability rates (Landers, 1980; Landers and Speake, 1980; Auffenberg and Franz, 1982; Cox *et al.*, 1987; Aresco and Guyer, 1999; Jones and Dorr, 2004; Ashton *et al.*, 2008). Mesic Flatwoods habitats that better represent historic conditions (*i.e.* dominated by longleaf pines rather than slash pines) could be suitable for gopher tortoises if located on well drained soils in which an open canopy and abundant herbaceous forage plants are maintained.

Grassland vs. Longleaf PC

Active burrow probabilities were positively associated to variables correlated to Grassland habitats. Even though there was a low proportion of transects in Grassland habitats (exemplified by an open canopy and high percentages of herbaceous plants in the ground cover), conditions represented high levels of burrow activity. The Grassland habitats on St. Marks NWR are not natural grasslands, but rather are represented by three agricultural fields that have not been undergone succession. Auffenberg and Franz (1982) describe these habitats as ‘ruderal communities’ and having high gopher tortoise densities if herbaceous vegetation is abundant, which is evident in these results. Although these areas have not been managed as separate compartments from juxtaposed habitats, the open canopy has been maintained by repeated prescribed fires which in turn allows for early successional species to persist. This study only covered one of the three blocks of Grassland habitats at St. Marks NWR but gopher tortoise burrows are densely distributed over all three (personal observation) and it is assumed that additional transects in these areas would have only strengthened these results.

Percent herbaceous plants in the ground cover were correlated to grassland habitats and the polynomial regression line showed that active burrow probabilities increased with increasing herbaceous plants, but the scatter plot of linear predictors was less convincing. This study

covered a large assortment of habitat and environmental conditions and low active burrow probabilities in areas with high % herbaceous ground cover likely reflect areas with unsuitable underlying conditions such as mesic flatwoods habitats and unfavorable soil conditions among others, while areas with high active burrow probabilities are related to areas with more favorable conditions and reiterates the importance of underlying environmental conditions. However, there was a clear decrease in abandoned burrow probabilities with percent herbaceous plants. Gopher tortoises are primarily herbivorous and there have been numerous reports that the density of herbaceous plants is a primary driver of gopher tortoise distributions (Auffenberg and Iverson, 1979; Landers, 1980; Landers and Speake, 1980; Lohofener and Lohmeier, 1981; Garner and Landers, 1981; Auffenberg and Franz, 1982; Diemer, 1986; MacDonald and Mushinsky, 1988; Breininger *et al.*, 1994; Mushinsky *et al.*, 2003; McCoy *et al.*, 2006). Even though the scatter plot did not show a clear relationship between active burrow probabilities and herbaceous plant cover, the relationship has been well documented and in the absence of unsuitable underlying conditions such as soils with high clay content, mesic habitats, and low elevation among others, the relationship likely exists. Assuming this, the polynomial regression lines showed that when percent herbaceous ground cover was greater than 19%, active burrow probabilities were higher than abandoned burrow probabilities, and when greater than 78%, active burrow probabilities were higher than no burrow probabilities which in nearly all other instances were exceptionally higher.

There is little or no canopy cover in these Grassland habitats which evidently influenced the previous finding regarding % tree canopy. Moreover, all variables associated to canopy cover (*i.e.* four basal area variables and two canopy cover variables) demonstrated that active burrow probabilities were highest when basal area and canopy cover values were lowest; further

reiterating the findings from the previous PC (Lakeland vs. Scranton PC) and previous studies that report active burrow densities are reduced by canopy (Landers, 1980; Landers and Speake, 1980; Auffenberg and Franz, 1982; Cox *et al.*, 1987; Aresco and Guyer, 1999; Jones and Dorr, 2004; Ashton *et al.*, 2008). Areas with low basal area and low canopy cover allow abundant sunlight to penetrate the forest floor, facilitating growth of herbaceous plants and creating abundant sun lit areas necessary for thermoregulation and egg incubation (Landers, 1980; Diemer, 1986; Cox *et al.*, 1987; Jones and Dorr, 2004;).

Xeric vs. Longleaf PC

Abandoned burrow probabilities increased within the following categories: Xeric Hammock habitats, with xeric hardwoods as the dominant canopy species and sand live oak or other hardwoods as the dominant arboreal midstory species. Abandoned burrow probabilities also increased linearly with the other variables correlated to this PC: % canopy cover (densiometer), % litter ground cover, and mean years between burns. These habitat correlations follow the description of Xeric Hammocks by the FNAI Guide to the Natural Communities of Florida (2010) who reported that Xeric Hammocks develop when Sandhills experience insufficient mean years between burns or prolonged periods of fire exclusion. As a result oak species (such as clonal sand live oaks) encroach and grow into the canopy, shade out herbaceous food plants and create intermixed areas of moist leaf litter with areas of bare ground that further inhibit the spread of fires, impeding longleaf pine regeneration and eventually cause xeric communities to develop mesic conditions that are unfavorable for gopher tortoises (Landers, 1980; Auffenberg and Franz, 1982; Myers, 1985; Myers, 1990; Guerin, 1993; Aresco and Guyer, 1999; Gilliam and Platt, 1999; Kane *et al.* 2008; Loudermilk *et al.*, 2011;). The correlation of mean years between burns in this PC provides evidence to suggest that Xeric Hammock

development (more commonly described as longleaf habitat degradation) explained by the FNAI (2010) has occurred, and the significant association of abandoned burrows to these areas indicates previous suitability. Furthermore, the scatter plot of linear predictors for active burrow probabilities against mean years between burns suggested a negative relationship. Even though this study did not address cause and effect, it is apparent that increased hardwood encroachment from insufficient mean years between burns can cause gopher tortoises avoid or abandon these areas (Landers, 1980; Landers and Speake, 1980; Auffenberg and Franz, 1982; Campbell and Christman, 1982; Diemer, 1986; Aresco and Guyer, 1999). Figure 2.14 depicts areas in which abandoned burrows were documented (that are not juxtaposed to active burrows) and should be considered as potential areas for restoration initiatives.

Abandoned burrow probabilities were lower in areas with longleaf pine as the dominant canopy species, having an arboreal midstory dominated by pine saplings, and having high % herbaceous ground cover. Because areas with high burrow activity should have lower abandonment, the reduced probabilities of abandonment in these areas support the findings from Lakeland vs. Scranton PC of high burrow activity in areas with longleaf pine dominated as the dominant canopy species. In addition, abandoned burrow probabilities decreased with increasing % herbaceous ground cover, supporting the findings that active burrow probabilities increased with increasing % herbaceous ground cover. Alternatively, the presence or absence of pine saplings in the arboreal midstory did not seem to be an influencing factor on burrow probabilities, but rather was tied by correlation to Longleaf assemblages. This is similar to how bluejack and/or turkey was tied by correlation to Lakeland assembled variables, and how sand live oak and other hardwoods were tied by correlation to Xeric Hammocks. The overall lack of influence of dominant arboreal midstory species on burrow probability rates supports the idea

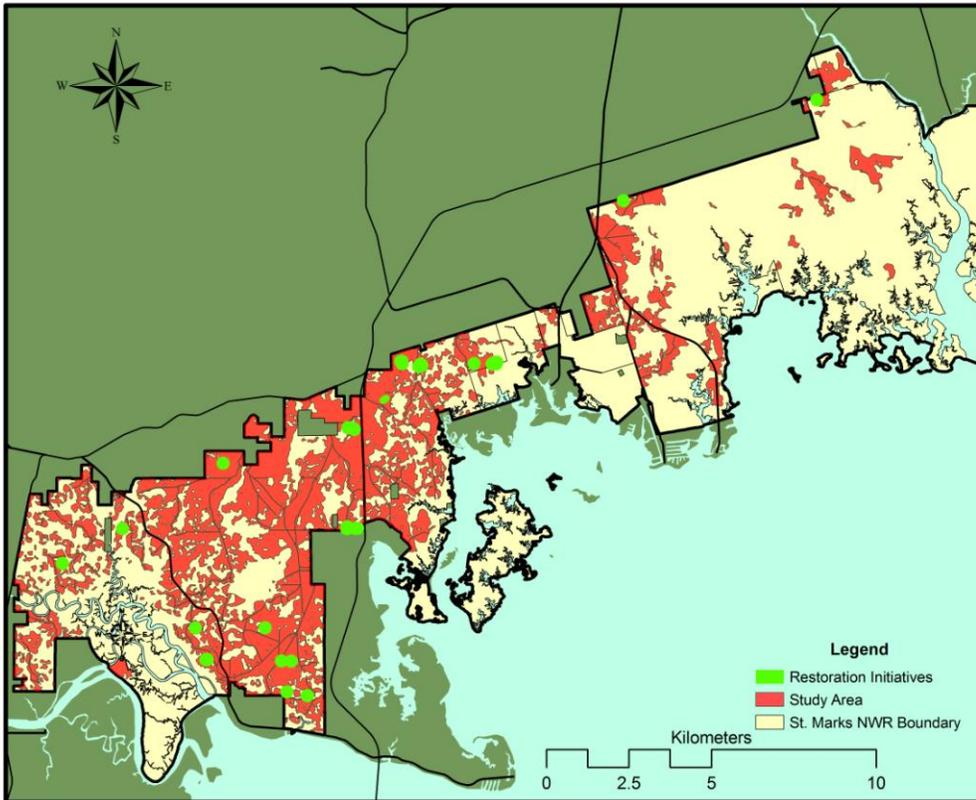


Figure 2.14 Areas with documented abandoned burrows that are not juxtaposed to active burrows that should be considered as potential areas for restoration initiatives.

that gopher tortoises respond to physical habitat characteristics rather than specific plant associations (Campbell and Christman, 1982). Even though pine saplings did not seem to directly influence burrow probability rates, the presence of these pine saplings does indicate the areas have sufficient years between burns to facilitate longleaf pine regeneration.

Other Variables of Interest

The basal area of trees with a DBH greater than 25 cm and the basal area of other pine trees were both included in statistically significant PC correlations, but are included here for a more thorough view of how burrow probabilities are influenced by tree density and forest species

composition. The probabilities of active burrows declined with all four basal area variables but most dramatically with basal area of other pine trees slash pine, which exhibited the lowest active burrow probabilities of any basal area variable. The relationship of abandoned burrow probabilities with basal area variables was less apparent. There seemed to be a slight positive relationship with total basal area, and although the polynomial regression lines showed that abandoned burrow probabilities increased at higher basal areas of longleaf pine and other pine species, the scatter plots were not conclusive. The polynomial regression lines for abandoned burrow probabilities do however provide a line of reference for the basal area values that should maintain higher probabilities of active burrows than abandoned burrows.

Ground cover dynamics and their effect on gopher tortoise burrow densities has been the subject of numerous studies, most notably herbaceous ground cover. Of the six ground cover variables included in this analysis, only two were correlated to statistically significant PCs; % herbaceous ground cover and % litter ground cover (see Grassland vs. Longleaf and Xeric vs. Longleaf). Percent fern and bare ground cover did not exhibit evidence to suggest any influence on burrow probabilities. However, both percent palmetto and woody plants appear to have some influence on burrow probabilities. Breininger et al. (1994) found that habitats with saw palmetto and habitats with both oak and saw palmetto exhibited lower tortoise densities. In this study, palmetto ground cover did not influence abandoned burrows, but was negatively associated with active burrows. Lastly, active and abandoned burrow probabilities decreased as percent woody plant ground cover increased. Areas with dense layers of woody plants in the ground and shrub layer may act as a barrier gopher tortoise movement (Lohoefer and Lohmeier, 1981) and would explain the decline of both.

CONCLUSIONS AND RECOMMENDATIONS

This study showed that predictive habitat models can be created from encounter rates taken during a LTDS pilot study, allowing biologists and managers to evaluate and modify current habitat management plans to benefit local populations. The model depended upon a combination of GIS-based landscape level variables and a suite of category-based habitat plots relevant to forest species composition and spatial dynamics. In addition to supporting previous reports regarding gopher tortoise habitat requirements; this model was able to predict changes in three categories of burrow probability rates with changes in habitat characteristics combining a suite of habitat variables collected along transects with accessible GIS landscape into PCs that three were statistically significantly associated to burrow probability rates.

The results of this study showed that on St. Marks NWR there are 1) areas that are not suitable and will never be able to support gopher tortoise population because of life history requirements regardless of habitat management, 2) areas in which current management practices are beneficial and seem to support active gopher tortoise populations, though repeated surveys should be implemented to evaluate population sustainability and ensure ecosystem integrity, and 3) areas in which gopher tortoise population and other longleaf associated species would benefit from initiatives to reduce tree canopy, reduce hardwood densities, and increase mean years between burns.

It is important to note that even though mean years between burns was only correlated to one of the PCs associated to burrow probabilities, natural and prescribed fires drive forest dynamics in these systems (Rebertus *et al.*, 1989; Frost, 1993; Streng *et al.*, 1993; Glitzenstein *et al.*, 1995; Peterson and Reich, 2001; Glitzenstein *et al.*, 2003; Ford *et al.*, 2010) and the lack of correlations can be explained by the inconsistencies of this mean years between burns GIS

layers. Inconsistent historic burn records only allowed for burns that occurred between 1998 and 2011 to be included in analysis because burn records were not uniform in previous years (M. Keys, St. Marks NWR, pers. comm.), and possible sources of error include 1) over-representing burn frequencies that did not spread entirely over burn compartments, and 2) missing unrecorded burn events. Furthermore, burn season and intensity were not evaluated which can have further impact on vegetative response than the number of burns alone (Rebertus *et al.*, 1989; Streng *et al.*, 1993; Glitzenstein *et al.*, 1995; Peterson and Reich, 2001; Glitzenstein *et al.*, 2003). If the burn data had been more complete and consistent, it is probable that more correlations with mean years between burns would have been observed. Even though this data obviously lacked quality, mean years between burns was correlated within a PC with a statistically significance association to abandoned burrow probabilities providing strong evidence of the importance that fire plays in both the dynamics of the habitat and its influence of burrow presence.

Even though Lakeland was the only soil type to be correlated within a PC with a positive association to active burrows; tortoise encounter rates were frequent enough on Ortega and Ridgewood soils (as well as Lakeland soils) to allow their inclusion in the final LTDS survey. When situated in appropriately high elevation, these three soil types should be targeted as potential gopher tortoise habitat, and managed as such. Furthermore, both Sandhill and Grassland habitats that exhibit features like those described for the PC in which they are correlated (Table 2.3) seem to have habitat management practices that benefit local gopher tortoise populations.

Specific recommendations for these soil and habitat types include continued monitoring to ensure that longleaf pines remain the dominant canopy species. In mature pine forests, basal area of older large trees should be maintained at less than 13 m²/acre, but can be as high as 21

m²/acre in younger longleaf pine forests. However, in all instances, slash pines should be eliminated or at least maintained with a basal area of no more than 6 m²/acre. Even though there was no obvious impact from species composition in the arboreal midstory, fire tolerant and clonal oak species should be maintained at moderate to low densities and mechanically removed as they grown into the canopy to avoid successional habitat changes, mesic hardwoods should be completely eliminated. Total canopy coverage (including coverage from midstory hardwood species) should be no more than 42%, but less is better; and herbaceous ground cover should be maintained at a minimum of 19% to avoid abandonment, however higher levels of herbaceous ground cover (greater than 78%) are highly recommended. To facilitate these recommendations, mean years between burnss should not exceed 3.3 years but less is better, and emphasis should be placed on implementing prescribed fires during the growing season if conditions allow.

The evidence from this model suggests that burrow abandonment was tied to successional changes resulting from hardwood encroachment and mean years between burns that exceed 3 years. To benefit gopher tortoises, efforts should be taken to restore Xeric Hammocks where abandoned burrows have been documented by means of mechanical hardwood thinning or removal followed by frequent growing season burns. Lastly, Mesic Flatwoods located on suitable soils should be managed to reduced canopy closure by thinning or removal of slash pines in efforts to convert to more favorable historic Mesic Flatwoods conditions. However, Mesic Flatwoods situated over soils with high clay contents that are poorly drained and occur at low elevations should not be managed as potential gopher tortoise habitat.

CHAPTER 3. SUMMARY

Increasing concerns over declining populations coupled with economical and financial constraints bring about a need for survey techniques capable of obtaining reliable population estimates that can simultaneously assess suitable occupied habitat as well as identify habitats in which restoration initiatives would prove beneficial to species of concern. Line transect distance sampling (LTDS) is the preferred method of obtaining gopher tortoise population estimates because of its efficiency and accuracy (Carthy *et al.*, 2005; Meyer *et al.*, 2008; Nomani *et al.*, 2008)), however prior to this study, no efforts had been made to couple these survey techniques with habitat modeling techniques. This study used burrow encounter rates obtained from a LTDS pilot study executed by a single observer during the summer of 2010 to test two different habitat modeling approaches. The first modeling approach tested the correlation of active and inactive burrow encounter rates to values of a Habitat Suitability Index (HSI) model created from three Geographic Information System (GIS) landscape layers (habitat type, soil type, and elevation). This model did not show a positive correlation to burrow encounter rates; however it did demonstrate an ability to eliminate unsuitable habitat, thereby confirming the defined sampling frame. Possible reasons for the lack of correlation include inappropriate suitability rankings and model simplicity. The inclusion of additional GIS layer such as percent tree canopy and mean years between burns as well as the re-evaluation of suitability ranking could improve this model's ability to predict the presence of gopher tortoise burrows.

The second approach incorporated five GIS variables and a suite of microhabitat variables to create a more sophisticated statistical model. Principal component analysis (PCA) was used to reduce the large number of input variables into correlated groups (principal components; PCs), and a generalized linear mixed model (GLMM) was used to test for

significant association of PCs to three categories of burrow encounter rates (active, abandoned, and none). This model successfully identified three PCs associated to burrow activity, abandonment, and absence and further predicted changes in burrow probability rates with changes in habitat characteristics. Furthermore, this model detected a positive relationship between mean years between burns and burrow abandonment which reflects the importance of fire in maintaining suitable gopher tortoise habitat, and even though this relationship is widely accepted, it is poorly documented.

The following is based on personal communications and unpublished data from St. Marks NWR. Tortoise encounter rates from the pilot study suggested that 137 km of transects within 2200 ha of suitable habitat needed to be surveyed to obtain a population estimate within a 15% confidence interval. During the summer of 2011, a three person survey team covered 123.9 km of transects during which, 803 burrows were recorded; 311 were active, 195 were inactive, and 9 were undetermined. Of the 506 active and inactive burrows, 114 were occupied (23%) which is comparable to the 22% occupancy rate of the pilot study. The final population was estimated at 661 tortoises (standard error = 108, coefficient of variation = 16.29), with a 95% confidence interval between 481 and 908 tortoises.

The combined results from the pilot study, the full LTDS survey, and the two habitat models have provided St. Marks NWR with valuable baseline information that with repeated surveys will allow biologists to detect population trends over time that can further be used to measure the success of management practices. Even though the second sophisticated model identified areas associated to both active and abandoned burrows, because these data were compared over space and not over time, one can only assume that gopher tortoise populations are stable in areas associated to activity and have declined in areas associated to abandonment, and

although seemingly intuitive, this may not be the case at all. Therefore, if identical habitat data are collected during future LTDS pilot studies, then biologists can evaluate how changes in habitat variables reflect changes in population levels and thus determine if areas associated to burrow activity are in fact capable of maintaining stable gopher tortoise populations.

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VITA

Christina Legleu was born October, 1981 in Hobbs, New Mexico, but was raised amidst a large and tight knit family in Baton Rouge, Louisiana. Even though she grew up in suburban surrounding, she has had a lifelong affinity for animals, wildlife and nature. Christina got her first of taste working with wild animals as a primate and carnivore keeper at BRECs Greater Baton Rouge Zoo but soon after realized her future belonged in conserving and restoring wildlife in their natural habitats. Thus she found her way into Louisiana State University's Renewable Natural Resources Department where she received a Bachelor of Science in Renewable Natural Resource Ecology and Management with an area of concentration in conservation biology. During her undergraduate career, she landed a student job with the U. S. Fish and Wildlife Service, where she has worked ever since on refuges in both Louisiana and Florida. Upon completion of her graduate degree requirements, Christina will eagerly receive a position as a wildlife biologist with the U.S. Fish and Wildlife Service where she anticipates leaving a positive footprint in the ongoing battle to restore and conserve America's endangered wildlife and habitats. When not enjoying nature and its splendors, Christina spends most of her time with her husband, family and friends. She also loves music, attending concerts and festivals, playing both the guitar and the piano, cooking, watching movies, and has a long, nearly criminal record of rescuing and finding homes for stray animals of all kind, some of which can be found in her private mini zoo.