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SPECIES AND HABITAT INTERACTIONS OF THE GOPHER TORTOISE:
A KEYSTONE SPECIES?

by

CHRISTOPHER PAUL CATANO
B.S. University of South Florida, 2007

A thesis submitted in partial fulfillment of the requirements
For the degree of Master of Science
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At the University of Central Florida
Orlando, Florida

Summer Term
2012

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ABSTRACT

Species-species and species-habitat interactions have been demonstrated to be important in influencing diversity across a variety of ecosystems. Despite generalities in the importance of these interactions, appropriate mechanisms to explain them are absent in many systems. In sandhill systems of the southeast U.S., gopher tortoises have been hypothesized to be a crucial species in the maintenance of diversity and function. However, the mechanisms and magnitude in which they influence their communities and habitats have rarely been empirically quantified. I examined how habitat structure influences tortoise abandonment of burrows and how tortoise densities influence non-volant vertebrate community diversity. Tortoise burrow abandonment is directly influenced by canopy closure, with each percent increase in canopy cover relating to a ~2% increase in the probability of burrow abandonment. In addition, tortoise burrow density was positively correlated with diversity and evenness, but not species richness. This influence was directly proportional to burrow density, supporting a dominance role for this species and rejecting the commonly asserted keystone species mechanism. I also quantified the influence of tortoises in influencing diversity relative to other environmental and habitat variables. Through this research, I have demonstrated that disturbance and habitat structure are important, but diversity responds most to density of burrows in the habitat. These findings demonstrate the intricate relationships interacting to maintaining diversity in sandhill systems. In particular, habitat change leading to declines of gopher tortoises may have drastic negative impacts on vertebrate species diversity.

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CHAPTER ONE: INTRODUCTION

Habitat loss, fragmentation, climate change, and biological invasions pose serious risks to ecosystems and can result in loss of ecological function and/or biological diversity (Vitousek et al. 1997; Chapin et al. 2000; Hooper et al. 2005). This loss of diversity can occur at all levels of biological organization from habitat diversity through populations, species, and genetic diversity among populations (Noss 1990). These changes can ultimately lead to less productive, species depauperate systems and contribute to species extinction. Despite difficulties in determining global extinction rates, recent calculations bring the consensus to 100 and 1000 times background rates (MEA 2005). Also, species extinction appears to be non-random with certain taxa at greater risk of extinction than others (Purvis et al. 2000). Often it is found that rather than extinction, community processes are altered in a way that can decrease biological complexity (i.e., diversity) or alter species interactions (Chapin et al. 2000; Hillebrand et al. 2008). These interactions may directly or indirectly influence ecosystems by altering abiotic characteristics (e.g., nutrient cycling or energy flow) or biotic characteristics (e.g., species abundance or richness). The nature and magnitude of these interactions ultimately has profound effects on how an ecosystem functions and the services it renders (Balvanera et al. 2006; Cardinale et al. 2006; Reiss et al. 2009).

Much attention is paid to studying both natural and anthropogenic stressors in addition to designing reserves to protect inhabitant species. However, many reserves are plagued by a lack of knowledge regarding species interactions, associations, and basic life history details, which mandates how management actions may respond to habitat needs. As a result, documented cases of species decline are not uncommon in the very land set aside for their survival (e.g., James et al. 1997; Perkins and Vickery 2005; McCoy et al. 2006). As the system stress from anthropogenic perturbations

intensifies, the ability to accurately describe and predict species and habitat responses becomes imperative (Clark et al. 2001). Despite general appreciation for the influence of species and habitat interactions in structuring biotic diversity, the mechanisms governing such structure are often not well understood (Messmer et al. 2011). Effective management needs to be linked to accurate scientific information. Thus it is necessary that we understand species-species and species-habitat interactions to predict how these interactions can be altered and ultimately how such changes can influence biodiversity.

The gopher tortoise (*Gopherus polyphemus*) is an iconic species present throughout upland habitats in the southeastern U.S. (Auffenberg and Franz 1982). Despite decades of research documenting the interactions between this species and its habitat and community, a mechanistic understanding of these relationships is often lacking. For example, researchers have demonstrated that tortoises are sensitive to changes in vegetation structure, but the relationship and magnitude of this response is currently unknown (Diemer 1986, Aresco and Guyer 1999; Boglioli et al. 2000). Also, gopher tortoises construct extensive burrows in the habitat, which appear to be obligatory for the survival of various other species. As a result, gopher tortoises have been alleged to act as keystone species by increasing diversity in a way that is disproportionate to their abundance (Eisenberg 1983; Guyer and Bailey 1993). However, the keystone role has never been empirically tested or quantified. Currently, the habitats and populations of this species are at risk from anthropogenic change. As a result of development, land-use change, and altered disturbance regimes (e.g., fire suppression), longleaf pine habitats have been reduced by approximately 98% of their previous extent (Noss et al. 1995). This loss and modification of habitat have largely contributed to reductions in gopher tortoise populations by as much as 80% (McCoy et al. 2006; USFWS 2011). Improved models of species-species and species-habitat

interactions for the gopher tortoise are needed to predict how this imperiled species and the systems in which they reside will respond to such changes. The goal of this thesis research was twofold: to improve models of tortoise-habitat relationships and to advance ecological understanding towards a mechanistic explanation for how gopher tortoises influence co-occurring non-volant vertebrate assemblages.

CHAPTER TWO: THE INFLUENCE OF THE GOPHER TORTOISE ON VERTEBRATE DIVERSITY

Introduction

In systems of varying complexity, a single species can be important for influencing diversity and ecological functions (e.g., foundation species, ecosystem engineers, keystone species, etc.) (Jones et al. 1994; Power et al. 2006). This influence can be exerted by way of dominance, but even rare species have been shown to significantly structure diversity (Hooper et al. 2005; Lyons et al. 2005). It has been hypothesized that some species have a disproportionately greater effect, relative to their abundance, on ecosystem function and overall species diversity than others (Paine 1969; Power et al. 1996). Because ecological communities are influenced by interactions among species, loss or decline of these keystone species can result in severe, negative effects on community structure including loss of function or diversity (Ebenman and Jonsson 2005). It is particularly important in conservation science to identify keystone species, if one exists in a particular environment, and predict how population changes of this species will impact ecological communities. Conservation and management of keystone species can thus be a crucial step to maintaining biodiversity and ecosystem function (Simberloff 1998).

However, it is not necessarily easy to identify which species are keystones or even how alleged keystone species influence their communities. The keystone species concept has historically been accompanied by many fundamental difficulties including various vague definitions, inconsistent usage of the term in scientific publications, and a focus on an unnatural duality of what is and what isn't a keystone (Hurlbert 1997; Kotliar 2000). In addition, it has been shown that 'keystoneness' of a species is not necessarily a species-specific trait, but rather a function of ecological context (i.e., disturbance,

scale, and abundance) (Menge et al. 1994; Power et al. 1996; Kotliar 2000). Thus, researchers should prioritize identifying the ecological domain in which a species acts as a keystone instead of assuming this trait is constant. Past research investigating keystone species has focused primarily on predatory effects. Yet, a keystone species may exert its influence on a community through other mechanisms including (but not limited to) mutualism, disease, pollination, competitive interactions, and habitat modification (Mills et al. 1993; Power et al. 1996; Kotliar 2000; Tews et al. 2004).

One species often claimed to be a keystone because of its influence on diversity is *Gopherus polyphemus*, the gopher tortoise (Eisenberg 1983; Guyer and Bailey 1993). The gopher tortoise is alleged to act as a keystone species through modification of the habitat. According to the 'habitat heterogeneity hypothesis', diversity should increase in habitats with more structural complexity as the potential for more niches increases (MacArthur and Wilson 1967; Tews et al. 2004). The patchy nature of tortoise burrow construction and grazing in the ground-level vegetation increases heterogeneity in both abiotic and biotic characteristics of the habitat (Diemer 1986; Kaczor and Hartnett 1990). The burrow and excavated sand mound are considered important for various other species by creating a stable microclimate and providing shelter from adverse environmental extremes such as heat, cold, fire, and aridity. In addition, the burrow is used as a site for feeding, reproduction, or nesting for many commensal species (Landers and Speake 1980; Eisenberg 1983, Lips 1991). Jackson and Milstrey (1989) compiled a list of 60 vertebrate and 302 invertebrate species that have been found in the extensive burrows constructed by gopher tortoises. However, this burrow use by vertebrate commensal species may be either obligate or facultative and may vary as frequent, occasional, or accidental (Cox et al. 1987). In addition, the importance of burrows to populations of commensal species has been demonstrated for only a few of these species (e.g., Florida mouse (*Podomys floridanus*) (Eisenberg 1983;

Layne and Jackson 1994), eastern indigo snake (*Drymarchon corais couperi*) (Landers and Speake 1980), and the gopher frog (*Rana capito*) (Eisenberg 1983; Roznik and Johnson 2009). The influence of burrows as refugia and the creation of local scale habitat heterogeneity as a result of foraging, movement, and excavation have resulted in the unquestioned acceptance of the gopher tortoise as a keystone species (Eisenberg 1983; Guyer and Bailey 1993). Despite this logical hypothesis, the relationship between gopher tortoises and diversity has not yet been empirically tested, nor has it been demonstrated how their importance varies with their abundance or the ecological context.

The goal of this research was to quantify the importance of the gopher tortoise in structuring biodiversity. Specifically, this research addressed the following questions:

- (1) What is the significance of the gopher tortoise in influencing non-volant vertebrate diversity and how does this relationship change with their abundance?
- (2) How does the relationship between gopher tortoises and non-volant vertebrate diversity vary in different ecological contexts (e.g., fire disturbance regimes)?
- (3) What is the relative importance of the gopher tortoise in structuring non-volant vertebrate diversity compared to other diversity structuring mechanisms?

Methods

Study area:

This study was conducted in sandhill habitat at Wekiwa Springs State Park (WSSP), Fl. (Figure 1). WSSP is a 31.25 km² (3125 ha) site located primarily in northwest Orange County with a small portion in western Seminole County; township 20S, range 28E, sections 15, 22, 26, 35. The topography varies from high sandhills with elevations of approximately 33 m above National Geodetic Vertical Datum (NGVD) to flooded low-lands along the Wekiva River at approximately 5 m above NGVD. The management plan for the park includes a balance between preserving natural systems and providing recreational opportunities (FDEP 2005).

The WSSP sandhills, which were modified by karst processes and seaward deposits of the Mt. Dora Ridge, are located in the Apopka Hills subdistrict (Brooks 1981). WSSP is within the mid-peninsular geomorphic zone (White 1970) described by highlands forming subparallel ridges which parallel the current Florida coastline (Soil Conservation Service 1989, 1990). The soils of sandhills in WSSP are dominated by Candler fine sand (0-5 percent slopes) and to a lesser extent Tavaris-Millhopper fine sand (0-5 percent slopes).

Sandhill is a pyric (fire-controlled) system characterized by a sparse overstory of longleaf pine (*Pinus palustris* Mill.) and understory of evergreen and deciduous oaks (*Quercus spp.*) with an herbaceous groundcover composed primarily of wiregrass (*Aristida stricta* Michx.). It is a xeric system with well drained, sandy soils (Meyers 1990; Stout and Marion 1993). WSSP employs a 1 to 3 year burn regime to mimic historical fire return intervals in sandhill habitat (FDEP 2005).



Figure 1. Sandhill habitat within Wekiwa Springs State Park (WSSP)

Burrow distribution survey:

In June 2011, I conducted total area surveys via systematic transects (10 m spacing) over approximately 350 ha of sandhill habitat. Tortoise burrows were located and recorded using Global Positioning System (GPS) (Garmin GPSMAP® 60Cx). Burrow activity status was determined as 1 of 2 categories based on external burrow characteristics (Figure 2). (1) “Active” if the burrow entrance was maintained, open, consisted of loose sand, and/or there were obvious tortoise presence indicators (i.e., plastral slides, tracks, or scat). (2) “Abandoned” if the burrow opening was occluded with debris, severely eroded, or collapsed. These burrow features are necessary to determine burrow use and tortoise occupancy of habitat because tortoises spend approximately 90% of their time underground (McCoy et al. 2006). Careful interpretation of burrow status provides unique opportunities to assess population dynamics that otherwise are unobtainable. Altogether I located and categorized 1,634 gopher tortoise burrows.



Figure 2 (A) Active: sand compacted at burrow opening from tortoise plastron. (B) Abandoned: burrow opening severely weathered and occluded with debris

Sample unit selection:

Because I was investigating the influence of gopher tortoise's on vertebrate assemblages, it was essential to have sample units that spanned the full range of variation in tortoise burrow densities. With this variation accounted for, I could then quantify the correlation between vertebrate diversity and tortoise activity (measured by burrow density and percentage of active burrows). Grids comprised of 1 ha cells were overlaid on the survey areas using ArcGIS software version 10.0 and burrow density for each cell was calculated.

In sandhill communities, fire is a crucial process structuring the habitat and can influence species diversity, composition, and vegetation structure (Abrahamson et al. 1984; Russell et al. 1999; Reinhart and Menges 2004; Driscoll et al. 2010). Sixteen sample units were chosen via stratified random sampling based on relative burrow density categories within 3 time-since-fire (TSF) classes (0-1 year, 1-3 years, 3-7 years) to account for any bias introduced by burn history. Within each of these TSF classes, sample unit selection was randomized to select units encompassing the full range of burrow densities. Because the burn data supplied by the park was not current, all but one sample unit were actually represented by a single TSF class (1-3 years). However, the full range of variation in burrow density was represented, although not *uniformly*. By chance, half (8) of the sample units were in burn zones that had been burned on average between 1 and 3 years (the natural burn frequency and target of WSSP management) (FDEP 2005) while the other half (8) were in burn zones that had longer TSF intervals than background rates or management recommendations.

Vertebrate census:

I determined non-volant vertebrate relative abundances within each sample unit using a trap array consisting of drift fences with pitfall traps and double-ended funnel traps. Drift fences are an effective method to survey herpetofaunal species present in a community (Campbell and Christman 1982; McCoy and Mushinsky 1994, 1999). The drift fence design consisted of three 8 meter arms radiating out from a centerpoint at 120° angles (to reduce directional bias). Each trap array consisted of four 19 liter pitfall traps (1 located at the terminus of each arm and 1 placed at the centerpoint of the array) and double-opening funnel traps attached to both sides of each arm midway between the centerpoint and terminus (6 total) (Figure 3). Drift fence arrays were placed at the center of each sample unit. Sherman traps were used to sample small mammals. Five traps were placed randomly within 20 m of each sample unit center.

Because sampling effort can influence estimates of diversity (Gaston 1996; Gotelli and Colwell 2001, 2009), sampling intensity was standardized among sample units. Sampling occurred from June 2011-January 2012. The trap arrays were opened and checked concurrently to avoid weather and other environment related biases among sample units. Drift fences were opened for 5 days at a time and checked every day during the summer. When temperatures cooled and animal activity decreased, each array was checked every other day. With this sampling intensity, each array was checked 30 times.

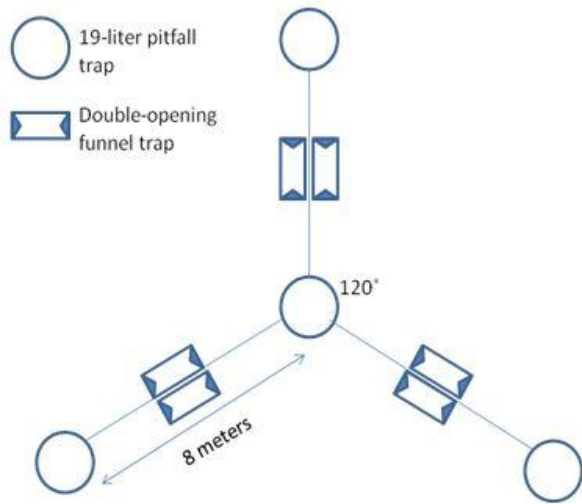


Figure 3. Three-arm drift fence (not drawn to scale)

Vegetation quantification:

Lidar was used to acquire vegetation structure data in three dimensions (Lefsky et al. 2002; Vierling et al. 2008). The National Center for Airborne Laser Mapping (NCALM; <http://www.ncalm.org>) acquired lidar data over an area of approximately 1000 ha of WSSP in June of 2011. The data were collected using an Optec Gemini Airborne Laser Terrain Mapper (with 5-35 cm elevation accuracy, laser pulse repetition frequency (PRF) of 70 kHz, and a point density of 5.07 p/m²). TerraScan software was used to filter ground and non-ground lidar point returns.

I created a 1 m resolution digital elevation model (DEM) from the lidar points classified as ground returns using FUSION version 2.90 (McGaughey 2010). I then used FUSION to calculate the number of non-ground lidar returns occurring within 1 m height intervals in each 5,000 m² sample unit (Figure 4). Due to the lack of anthropogenic structures in the study area, I assumed that all of the non-ground lidar returns were reflected off of vegetation. Finally, I calculated two metrics of vegetation

structure: relative canopy cover $[(\text{number of returns} > 3 \text{ m in height} / \text{total number of returns}) \times 100\%]$ and relative lower midstory cover $[(\text{number of returns} > 1 \text{ m and} < 3 \text{ in height} / \text{total number of returns}) \times 100\%]$. I used a relative measure of canopy cover to compensate for the spatial variability in the density of lidar returns over the study area resulting from the airborne acquisition process.

In addition to the 3D structure of the habitat, it is important to quantify the variety of functional types of ground cover. These have been shown to influence particular species distributions of herpetofauna in southeastern pine forests (Litt et al. 2001; Vitt et al. 2007; Baxley and Qualls 2009, Perry et al. 2009). The percent cover of grasses, shrubs, herbs, bare ground, litter, and woody debris was quantified using the line transect method. Three 15 meter transects were chosen using a stratified random design. The starting point of each transect was randomly selected at distances between 10-15 meters from the center of the sample unit. The direction of each transect was also randomized. A random degree orientation from north was selected within each 120 degree wedge. This stratification by 120 degrees was chosen to increase independence of transects and increase opportunity to assess variation in ground cover types across the sample unit. Line intercept coverage of each functional type was measured to the nearest centimeter. Mean percent cover and the coefficient of variation (CV) was determined for each ground cover type. In addition, diversity of ground cover types was calculated using the exponential of the Shannon Index.

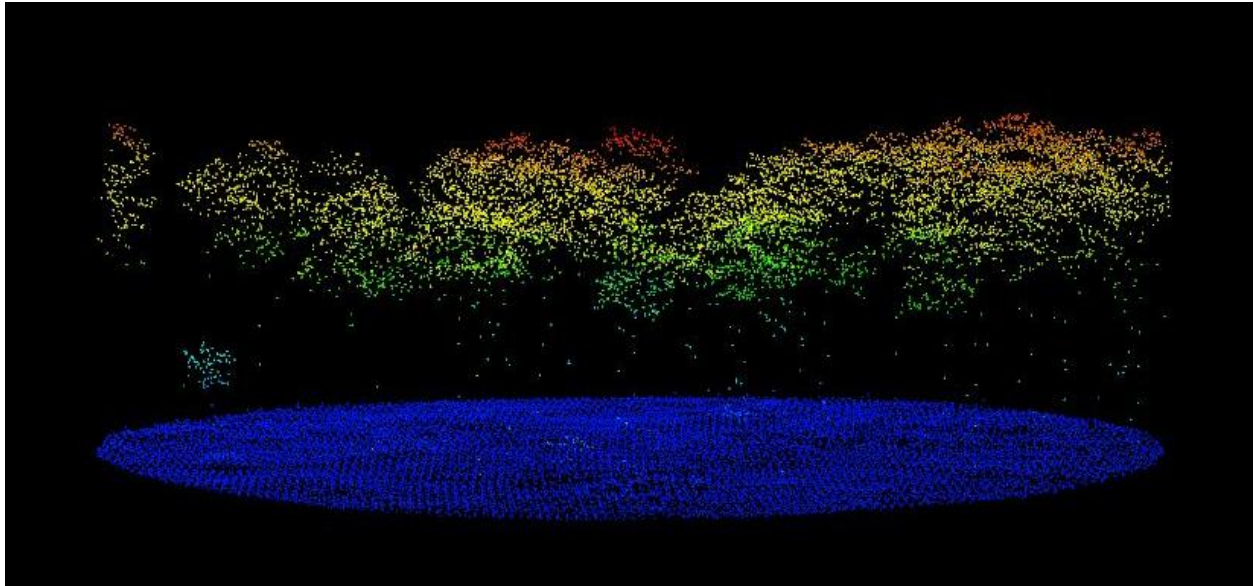


Figure 4. Point cloud data of vegetation for one sample unit. Point color is related to elevation with blue being lowest and red highest.

Vertebrate diversity estimation:

For each sample unit, diversity, evenness and richness were determined. Diversity was calculated using the Shannon exponential diversity measure (D). See equation 1:

$$D = \exp\left(-\sum_{i=1}^S p_i \ln p_i\right) \quad (1)$$

This diversity measure results from converting the Shannon entropy value into a true diversity measure by calculating the exponential of Shannon entropy (Jost 2006; Jost 2007). This change is significant because weighing species by their frequency allows a biologically interpretable value of diversity.

Diversity is comprised of two components: richness (total number of species) and evenness (relative proportions of species or dominance hierarchy) (Maurer & McGill 2011). Because a loss in richness is synonymous with loss (i.e., extinction) of species, this metric of diversity is central to many, if not most, studies investigating diversity (Cardinale et al. 2009; Duffy 2009; Gotelli & Colwell 2001, 2009; Reiss et al. 2009). The usage of richness alone yields a simple and easily interpretable metric of diversity; however, this simplicity often masks the complexity of diversity in a system. Changes in evenness and species interactions are often detected in an assemblage prior to loss of species (Chapin et al. 2001) and a less even assemblage can set a community on a trajectory to experience species loss (decreased richness) and decreased diversity. Therefore, one or both of these components of diversity (richness or evenness) can be altered in different ways, both having drastic implications for community structure and function. Thus, studies investigating the mechanisms that structure diversity should encompass the contributions of both richness and evenness. Evenness was calculated using the Shannon evenness index (J) (Maurer and McGill 2011). See equation 2:

$$J = D/S \quad (2)$$

Where D is diversity calculated from the exponential of the Shannon entropy and S is observed species richness. Richness was calculated using the Chao2 estimator, an incidence-based, non-parametric estimate of richness (Colwell and Coddington 1994; Chao *et al.* 2009). See equations 3 and 4:

$$S_{Chao2} = S_{obs} + \left(\frac{m-1}{1} \right) \frac{q_1(q_1-1)}{2(q_2+1)} \quad (3)$$

$$\text{var}(S_{Chao2}) = q_2 \left[\frac{1}{2} \left(\frac{q_1}{q_2} \right)^2 + \left(\frac{q_1}{q_2} \right)^3 + \frac{1}{4} \left(\frac{q_1}{q_2} \right)^4 \right] \quad (4)$$

Where S_{obs} is the number of species observed, m is the sample size, q_1 is the number of uniques, and q_2 is the number of duplicates. Chao2 is a conservative extrapolation of minimum richness calculated based on the number of uniques (species found in one sample) and duplicates (species found in 2 samples). With this formula I calculated the richness of the entire assemblage, including species that were not trapped or observed (Colwell et al. 2004). Because samples were taken in a systematic, uniform way and restricted to areas of relatively homogenous habitat this extrapolation was logical (Colwell and Coddington 1994; Magurran 2004). Of the various parametric and non-parametric richness estimators, Chao2 is regarded as the most precise, most accurate, and least biased based on comparative studies (Colwell and Coddington 1994; Coddington et al. 1996; Brose et al. 2003; Walther and Moore 2005; Chao et al. 2009; Gotelli and Colwell 2011). Chao2 also provides better estimates of richness in the case of small sample sizes (Silva and Coddington 1996; Chazdon et al. 1998) and can be used to obtain a minimum richness estimate in cases when sampling is finished but richness has not yet reached an asymptote (Longino et al. 2002). EstimateS software version 8.2.0 (<http://viceroy.eeb.uconn.edu/estimates>) developed by Colwell (2000) was used to derive sample-based species accumulation curves and to calculate Chao2 richness, Shannon evenness, and Shannon exponential diversity. Each diversity measure was bootstrapped (sampled with replacement) with 1000 iterations to increase precision and calculate comparable measures of variance.

Hypotheses/predictions & Results

Hypothesis (1): Gopher tortoises will have a positive influence on diversity, with faunal diversity being highest when burrow density is greatest. Specifically, I predicted that increasing burrow density will positively correlate with species richness and evenness (J) ultimately increasing species diversity (H).

Statistical Analysis:

To determine how gopher tortoises influence biodiversity, richness, evenness (J), and diversity (H) were regressed against burrow density. Multiple regression analysis was performed with diversity (H) as the response variable and burrow density and % active burrows as the predictors. The resulting model was significant ($F_{2,13}=13.5610$, $P=0.0007$, adj. $R^2=0.626141$). Burrow density was a significant predictor of diversity ($P=0.0002$) but % active burrows was not ($P=0.9243$). Thus, this predictor was dropped from the model and a simple regression was performed with only burrow density ($F_{1,14}=29.1772$, $P<0.0001$, $R^2=.675755$) (Figure 5). This improved the model and increased the amount of variation explained. Simple regressions were also performed with burrow density against richness and evenness (J). Burrow density was not a significant predictor of richness ($F_{1,14}=2.2094$, $P=0.1593$, $R^2=0.136304$) (Figure 6), but was a significant predictor of evenness ($F_{1,14}=10.3934$, $P=0.0061$, $R^2=0.426073$) (Figure 7). Both regressions of evenness and diversity satisfied assumptions of normality (Shapiro-Wilk test $p \gg .05$) and constant variance (Brown-Forsythe test $p \gg .05$). The error terms for the richness regression were not constant. Because the variance of each richness estimate was analytically calculated, I used Weighted Least Squares (WLS) regression analysis with each point weighted by the inverse of the variance. This gives more weight to points with higher precision and satisfies the constant variance assumption of regression analysis (Kutner et al. 2005). Also, to ensure independence of the

observations, I performed a spatial autocorrelation analysis using SAM version 4.0 (Rangel et al. 2010). The resulting Moran's I values were less than ± 0.05 at all distance classes under 4 km and these values oscillated randomly around zero, indicating the absence of autocorrelation in the spatial distribution of sample units in regards to diversity, richness, and evenness (Fortin and Dale 2005).

Replicate observations at multiple X (predictor) values were present for the regressions and a lack of fit test was performed for each regression to ensure a linear model was appropriate. All three regressions passed lack of fit tests ($P \gg 0.05$) suggesting linear functions were appropriate (Kutner et al. 2005).

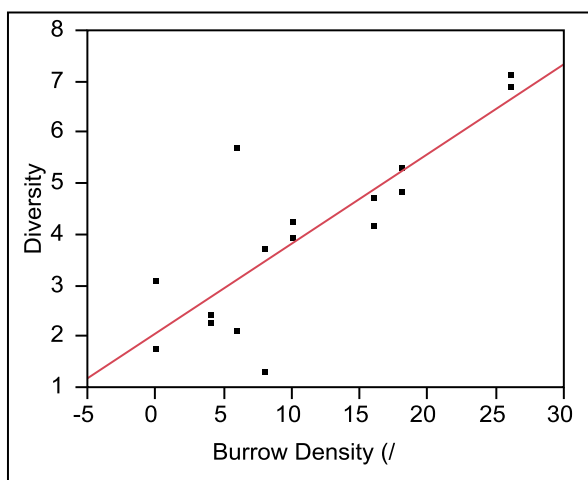


Figure 5. Regression of diversity versus burrow density ($F_{1,14}=29.1772$, $P<0.0001$, $R^2=.675755$). Regression equation: $Diversity = 2.0529167 + 0.1760417 * Burrow\ Density$

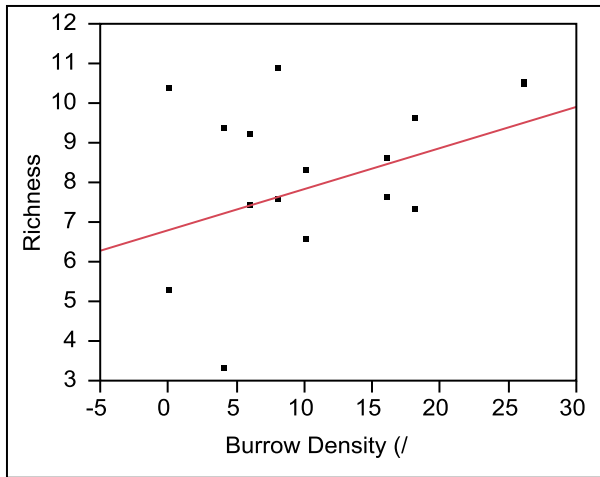


Figure 6. Regression of Richness (Chao2) versus burrow density ($F_{1,14}=2.2094$, $P=0.1593$, $R^2=0.136304$).
 Regression equation: $\text{Richness} = 6.7942326 + 0.1036543 \cdot \text{Burrow Density}$

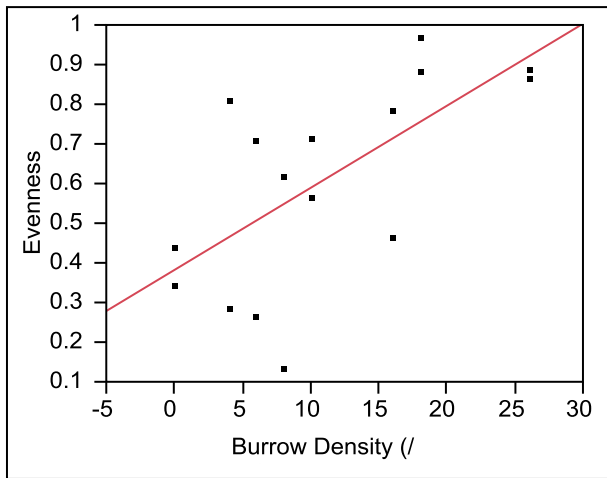


Figure 7. Regression of Evenness versus burrow density ($F_{1,14}=10.3934$, $P=0.0061$, $R^2=0.426073$). Regression equation: $\text{Evenness} = 0.3819866 + 0.020701 \cdot \text{Burrow Density}$

Hypothesis (2): The relationship between burrow density and diversity will be more important in higher disturbance (fire frequency) regimes. Because fire is the dominant disturbance regime in sandhill habitat, I predicted the relationship between burrow density and diversity will be influenced by fire frequency.

Statistical analysis:

An ANCOVA was performed to test whether there was a difference in the response of diversity (H) to burrow density in two different fire frequency classes (a frequently burned, 1-3 year return interval and a less frequently burned, > 3 year return interval). First, I tested whether the slopes of the two regressions were parallel (one of the assumptions in ANCOVA) (Kutner et al. 2005). The continuous covariate (burrow density) was significant ($P=0.0002$) and the categorical factor (fire frequency class) was marginally significant ($P=0.0923$). The interaction term was not significant ($P=0.8102$) indicating that the slopes are parallel and ANCOVA analysis is appropriate. Because the slopes are parallel, the relationship between burrow density and diversity (H) was not different in different fire frequency classes, thus rejecting my hypothesis. I refit the model without the interaction term and tested to see whether the intercept was significantly different for the response in the two fire frequency classes (Table 1; Figure 8). The resulting ANCOVA model was significant ($F_{2,13}=19.0939$, $P<.0001$, Adj. $R^2=0.706961$). After accounting for the covariate of burrow density ($P<.0001$) the factor fire frequency class was marginally significant ($P=.0803$). The line in the >3 year fire frequency class has a marginally higher intercept indicating diversity (H) was marginally higher in less frequently burned areas (Figure 9). However, a power analysis at 0.05 significance reveals low power in the ANCOVA (Power=0.4195) likely a result of small sample size ($n=16$) (Table 2).

Table 1. ANCOVA of relationship between burrow density and diversity in 2 different fire frequency classes

<i>Parameter</i>	<i>Estimate</i>	<i>SE</i>	<i>P-value</i>
BD (covariate)	0.1706532	0.030067	<.0001
FF (Factor)	0.4526351	0.238647	.0803

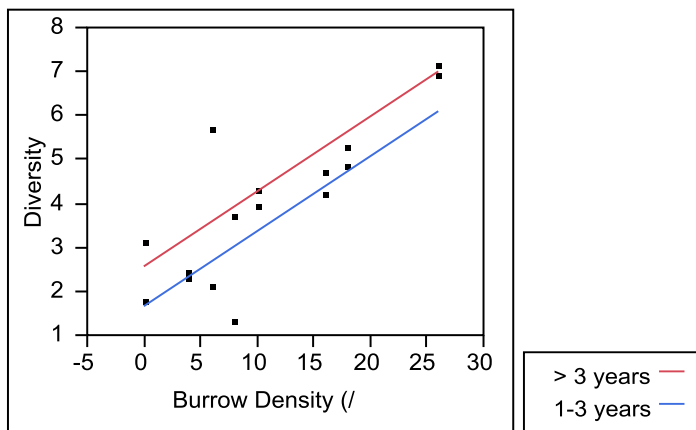


Figure 8. ANCOVA comparing regression slopes of diversity (H) versus burrow density (BD) in two fire frequency (FF) classes.

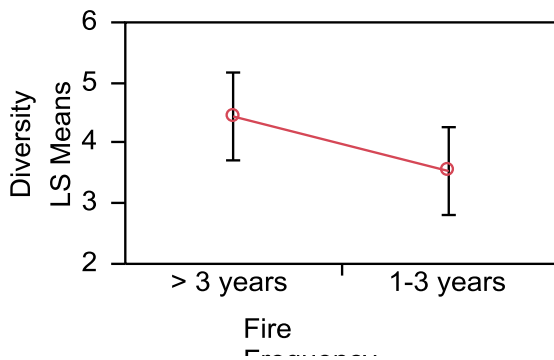


Figure 9. Least Squares means plot of diversity (H) and 95% CI's in both fire frequency classes. LS Mean for >3 year fire frequency=4.4420101, SE=0.336743. LS Mean for 1-3 year fire frequency=3.5367399, SE=0.336743.

Table 2. Power analysis with significance level (α), standard deviation of the error (σ), effect size (δ), sample size (n), and least significant number (LSN).

<i>Power</i>	α	σ	δ	n	<i>LSN</i>
0.4195	0.05	0.950316	0.45061	16	19.8

Hypothesis (3): The positive influence of burrow density on diversity will not be the most important mechanism in structuring diversity. I predicted that fire frequency will have a greater impact on diversity than burrow density.

Statistical analysis:

Multiple regression analysis was used to assess how changes in tortoise burrow density, vegetation/habitat structure, and abiotic variables influenced non-volant vertebrate diversity. Diversity (H) was plotted as the response variable with burrow density, habitat related variables (ground cover diversity, % canopy cover, % midstory cover, volume of coarse woody debris), and environmental variables (fire frequency, distance from permanent water) plotted as predictor variables.

AICc model selection was performed to test *a priori* hypotheses regarding which multiple regression models were most important for explaining variation in diversity (Table 3). AICc model ranking is useful because one can weigh the strengths of different competing hypotheses while quantifying the support for each (Burnham and Anderson 2002; Quinn and Keough 2002; Johnson and Omland 2004). Environmental models and interactive models performed worse than models including burrow densities in almost all cases. The relatively small data set may preclude detection of other possible interactions and lead to simpler additive models performing best (Anderson 2010).

Table 3. Multiple regression models of diversity (H) versus habitat and environmental variables: burrow density (BD), fire frequency (FF), coarse woody debris (CWD), % midstory cover (%MC), % canopy cover (%CC), ground cover diversity (GCD), distance from permanent water (H2O).

<i>Model</i>	<i>Adj. R²</i>	<i>AICc score</i>	Δ_i	<i>(ω_i)</i>	<i>K</i>
BD+CWD+FF	0.7934	49.57935	0	0.718184	4
BD	0.6526	52.36179	2.78244	0.178664	2
BD+CWD+%MC	0.7336	53.64720	4.06785	0.093954	4
BD+GCD+CWD+%MC+%CC	0.7789	59.74820	10.1689	0.004447	6
BD+H2O+BD*H2O	0.6032	60.02076	10.4414	0.003881	4
FF	0.2030	65.64716	16.0678	0.000233	2
FF+GCD	0.3109	66.77057	16.1912	0.000205	3
FF+%CC	0.2758	66.56555	16.9862	0.000142	3
Null	0.0000	67.30496	17.7256	0.000129	1
%MC+GCD	0.2327	67.48982	17.9105	0.000306	3
FF+H2O	0.1422	69.27523	19.6959	0.000053	3
GCD	-0.0142	69.50316	19.9238	0.000034	2
CWD+%MC+%CC	0.0909	73.28594	23.7066	0.000007	4

The best model in the analysis was an additive model that included three variables: burrow density (BD), fire frequency (FF), and coarse woody debris (CWD). This model explained over 79% (adj. $R^2 = 0.7934$, $P < 0.0001$) of the variation in diversity and was approximately four times as likely as the next best model. The model weight was approximately 72% while only one other model had a weight over 10% (model 2: ~18%). The model weight is the probability that this model is the best model in the set (Burnham and Anderson 2002, Anderson 2010). Because this model was far superior to any other model in the set, and the second best model was simply a subset of this model, I performed multiple regression analysis on this model to estimate the parameters. Because the parameters were measured in different

units, I standardized them to make them directly comparable in order to determine the relative contribution of each to structuring diversity (Table 4).

Table 4. Multiple regression ANOVA table of model 1: Diversity (H) versus burrow density (BD), fire frequency (FF), and coarse woody debris (CWD)

<i>Parameter</i>	<i>Estimate</i>	<i>Standard Error</i>	<i>P-value</i>
BD	0.79246	0.123652	<.0001
FF	-0.26591	0.123628	0.0526
CWD	0.262613	0.120824	0.0505

Based on these estimates, all three parameters were significant in explaining diversity. The parameter estimate for burrow density (BD) (0.79246, $P < .0001$) was much greater and more significant than either fire frequency (FF) (-0.226591, $P = 0.0526$) or coarse woody debris (CWD) (0.262613, $P = 0.0505$). All three variables were important for predicting diversity; burrow density was by far the most significant and influential while fire frequency had a significant negative impact on diversity (i.e., shorter fire return interval negatively affected non-volant diversity).

Discussion

Through this observational study, my results demonstrate for the first time, a correlation between gopher tortoises and the diversity of non-volant vertebrate species in sandhill habitat. This link had been hypothesized by many but had never been empirically tested or confirmed. Specifically, tortoise burrow density was associated with the evenness component of diversity, but not species richness. Although this research does not identify a causal relationship between tortoises and diversity it does improve our understanding of how gopher tortoise activity could be influencing the local community assemblage of non-volant vertebrates. Because there was no association between richness and burrow density, it is unlikely that gopher tortoises influence the number of species present in a local community. However, a significant positive relationship between burrow density and evenness leads to the hypothesis that habitat structure created by tortoises in the form of burrows may reduce competition or dominance imparted on other species in the sandhill community. Studies have demonstrated the use of burrows by commensal species for nesting and reproduction sites, food resources, and refugia (Landers and Speake 1980; Eisenberg 1983; Lips 1991). It has also been demonstrated that tortoise burrow creation and grazing modifies habitat composition and increases heterogeneity (Kaczor and Hartnett 1990). Based on the habitat heterogeneity hypothesis, it is likely that tortoise burrows added more structure and heterogeneity to the local environment. This can result in reducing the influence of dominant species and competition, leading to increased coexistence and evenness (Hillebrand *et al.* 2008).

The importance of a species to its community can vary with abundance and ecological context (Menge *et al.* 1994; Kotliar 2000). I assessed how abundance influences the role of the tortoise in structuring diversity by determining the functional form of the relationship between burrow density and

diversity. As suggested by the results, diversity increased linearly with burrow density. I was careful to incorporate sample units that spanned the total range of burrow densities present to ensure this relationship is accurate. This demonstrates that there is no particular abundance level in which the tortoise is most important to diversity, rather the linear relationship shows that diversity is directly proportional to burrow density. This is the relationship one would expect for a dominant species. A keystone species, on the other hand, would have an influence disproportionate to its abundance and would be represented by a slope much greater than 1 that increases with increasing abundance (Power et al. 1996; Kotliar 2000) (Figure 10). Thus, a more appropriate term for the gopher tortoise would be an ecosystem engineer, which modifies the structure and composition of the habitat but not necessarily in a way disproportionate to its abundance.

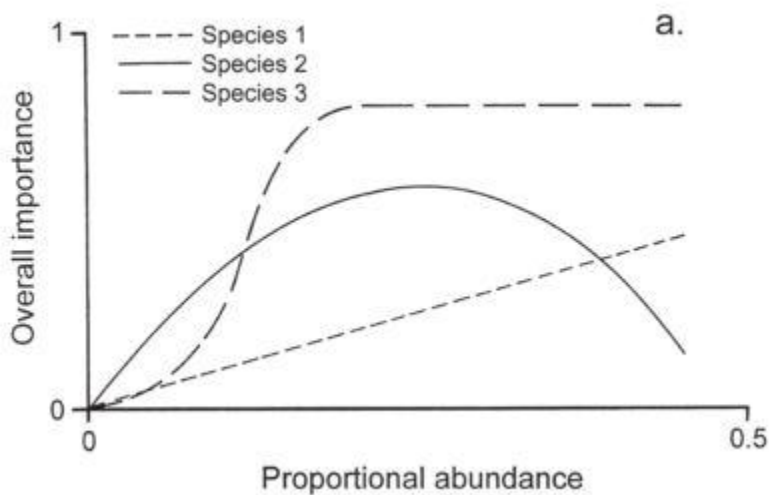


Figure 10. Three theoretical species influence curves. Species 1 represents the influence of a dominant species while Species 2 and 3 represent two theoretical keystone species (Kotliar 2000).

It is also necessary to understand this influence in a variety of ecological contexts in order to determine the domain in which the tortoise exerts this positive impact on diversity. Because sandhill

habitat is a system subject to repeated disturbance in the form of low severity fires, I assessed whether the relationship between burrow density and diversity changed under different disturbance regimes. This relationship was the same in both frequent fire return intervals (1-3 years) and infrequent intervals (> 3 years); responses were positive and parallel. Therefore, ecological context (specifically fire disturbance) does not appear to affect the influence of the gopher tortoise on diversity. At high burn frequencies, this outcome could result from burrows providing a site to escape fire mortality and recolonize habitat. This could lead to higher diversity than would be expected based on prediction from the intermediate disturbance hypothesis (IDH), which predicts lower diversity at frequent and infrequent disturbances than at intermediate disturbance (Connell 1978). At longer burn frequencies, IDH also predicts lower diversity resulting from competitive exclusion of individuals by dominant species. Burrows, shown to increase heterogeneity and potential niches, would permit commensal species to escape competition from competitively dominant species and lead to an increase in evenness and diversity. Essentially, the influence of tortoise burrow density could buffer the response of the community to that predicted by the IDH by dampening its effect on diversity. The significance of the relationship between diversity and burrow density within different burn regimes highlights the general (and consistent) importance of the gopher tortoise to maintaining diversity. Keystone species' community importance often is altered in different disturbance regimes or ecological contexts (Menge et al. 1994; Kotliar 2000); and this does not appear to be the case for the gopher tortoise in sandhill habitat. However, lack of an altered influence with ecological context doesn't exclude a species from being a keystone.

The gopher tortoise's role as an ecosystem engineer in modifying habitat structure is a likely mechanism altering niche opportunities, increasing species coexistence, and structuring diversity. Other

studies have also confirmed the influence of species which alter their habitat as a strong mechanism influencing diversity (Jones et al. 1994, 1997; Wright et al. 2002; Badano et al. 2006). However, it is generally inappropriate to assume a single cause for any ecological pattern (Scheiner et al. 2011). To better understand processes and mechanisms underlying ecology we must move beyond simple, reductionist approaches seeking single causes to explain patterns. Realistically, complex interactions among multiple factors often lead to variation in observed ecological patterns (Brose et al. 2005). The key to understanding the processes regulating species diversity relationships may be captured within this variation. In addition to the influence of ecosystem engineers and dominant species structuring diversity, other habitat and environmental variables have also been shown to influence diversity. For example, environmental variables such as precipitation, temperature, soil type, and disturbance are often important predictors of diversity. Also, vegetation structure and composition has been shown to influence diversity patterns (MacArthur and MacArthur 1961; Brokaw and Lent 1999). Although each of these different mechanisms has been shown to influence diversity, their relative contributions are rarely simultaneously assessed. To disentangle these possible different contributions to diversity I performed a multiple regression model ranking procedure.

Soil type, precipitation, and temperature were consistent throughout the study units and therefore are not likely a significant influence on diversity within relatively homogeneous environments. Instead, these environmental variables tend to largely influence diversity at larger spatial scales. In all cases, models representing purely environmental variables were not able to outperform models representing other hypotheses. The only environmental model to outperform the null model was the one that only included fire frequency. The influence of fire as an agent of disturbance and its role in influencing diversity has been demonstrated in the literature (Noss et al. 2006; Pastro et al. 2011).

Regression analysis of this model shows a significant negative linear relationship between diversity and fire frequency. This was also supported by the ANCOVA analysis that showed mean diversity was marginally higher in the treatment with longer fire frequency. The historical natural variation in fire frequency for this system has generally been shown to be 1-3 years (Meyers and White 1987; Stambaugh et al. 2011). Based on such studies, this is the burn frequency WSSP uses to manage sandhill habitat (FDEP 2005). Therefore it was surprising, at first, to see this negative effect. However, natural burns are much different than human induced burns. Natural burns are primarily ignited by lightning strikes and burn in a way that leaves a habitat mosaic within the landscape (Pastro et al. 2011). This mosaic provides areas of unburned habitat that can serve as refugia for organisms to escape fire mortality. WSSP also employs a burn mosaic management approach. However, these patches may occur at a much larger scale that doesn't represent the scale in which this mosaic was important historically. In this case, burning relatively large units extensively doesn't permit many individuals to move relatively long distances in a short amount of time to find refugia. The scale at which the mosaic effect occurs could explain why there is a negative relationship with burn frequency.

Models incorporating purely vegetation structural variables were also not among the best models describing diversity. These vegetation structural models only explained a significant amount of variation in diversity when they incorporated burrow density. In fact, over 99% of the model probability is contained in the top 3 models which all include burrow density as a parameter. The 8 models *without* burrow density combine to account for less than 1% of model probability. The high effect size of burrow density in these analyses provide strong confirmatory evidence that burrow density is among the most important influences structuring non-volant vertebrate diversity in these assemblages. In addition to burrow density and fire frequency, the best model also included coarse woody debris (CWD) as a

predictor of diversity. CWD (represented by logs and fallen trees) has been demonstrated to increase diversity by serving as cover, shelter, and a source of food and water for many species (Harmon et al. 1986; Freedman et al. 1996). This model substantiates other research demonstrating the importance of fire frequency and coarse woody material in structuring diversity. More importantly, this model substantiates claims of the gopher tortoise's importance to vertebrate diversity in sandhills and demonstrates that tortoise burrow density is the most significant predictor of diversity (relative to the other variables) in this sandhill system.

I hypothesize that not only does the tortoise influence diversity; it does so by altering the competitive interactions of species. I allege that this can be explained by the habitat heterogeneity hypothesis because the gopher tortoise creates extensive burrows and adds more structure to the habitat, thus offering more space to be exploited and relaxes competitive dominance. In turn, this may impact relative abundances of species (i.e., evenness) and lead to higher diversity. Changes in competitive interactions both among and within species have been shown to influence diversity, often a result of shifting dominance regimes (Chapin et al. 2000; Hillebrand et al. 2008). When an ecological community has lower evenness (analogous to high dominance) the species composition is simplified and the system is primarily affected by dominant species. This research has demonstrated empirical support for claims that the gopher tortoise is an important driver of non-volant vertebrate species diversity. However, caution should be used in applying the keystone designation to this species at this time; these results do not conform to the keystone role suggested by past researchers (Eisenberg 1983, Guyer and Bailey 1993). Instead, the gopher tortoise exhibits an influence characteristic of a dominant species, with their influence on diversity directly proportional to their abundance. By modifying the habitat through burrow construction and grazing, the gopher tortoise alters resource availability and demonstrates an

ecosystem engineering role. These effects are largest when tortoises achieve high densities. Jones et al. (1994) stated that the impacts from ecosystem engineers would be highest when living in high densities, over large areas, and long periods of time. The gopher tortoise satisfies all these requirements and as supported by this research, is a dominant, ecosystem engineer that is a main driver of diversity in sandhill systems. Future research should test this hypothesis in other systems that gopher tortoises are present in (e.g., scrub, flatwoods, etc.) because each habitat type has unique attributes which could modify the relationship between gopher tortoises and diversity. Also, future research should quantify this relationship over multiple spatial and temporal scales because patterns can exhibit a range of variability over different scales (Levin 1992).

CHAPTER THREE: USING LIDAR TO DEVELOP MULTI-SCALE MODELS OF BURROW ABANDONMENT

Introduction

Knowledge of species-habitat relationships is crucial to progress in developing successful conservation strategies. Currently, an important theme of ecological research is to determine the usefulness of habitat structural metrics to improve descriptive and predictive models of species-habitat relationships for biodiversity management (Elith and Leathwick 2009). Past efforts using traditional field methods to determine three-dimensional (3D) habitat structure have resulted in models which varied in their effectiveness to identify (or predict) suitable habitat for long-term survival of species (Mason et al. 2003). Due to their time/resource-intensive nature, these field methods restrict measurement to relatively small spatial scales, thus handicapping inferences regarding species-habitat relationships. Efficient methods to assess habitat structure over broader spatial scales are needed to derive ecologically relevant information on species-habitat relationships and to guide appropriate management strategies.

Light detection and ranging (lidar) remote sensing has been identified as a powerful technology for mapping the 3D structure of a variety of ecosystems with fine-grain resolution over broad spatial extents (Lefsky et al. 2002; Vierling et al. 2008). To date, however, the vast majority of habitat-related applications of lidar have been limited to avian species. Despite the potential advantages of lidar based models of vegetation structure and their uses in ecological research, natural resource managers have been slow to adopt the use of this powerful technology in conjunction with field survey methods. To demonstrate that lidar is an effective tool for natural resource managers, studies are needed that

document ecologically meaningful relationships between lidar-derived metrics of habitat structure and functional responses of species. I present a novel use of lidar technology to better understand the relationship of a threatened terrestrial species to changes in vegetation structure.

Model species: Gopher tortoise

The gopher tortoise (*Gopherus polyphemus*), once widespread throughout the southeastern United States, has suffered population declines of approximately 80%, primarily from habitat loss and degradation (McCoy et al. 2006). It is listed as “Threatened” by the U.S. Fish and Wildlife Service in the western portion of its range and is state listed as “Threatened” in Florida. A recent review by the U.S. Fish and Wildlife Service (USFWS 2011) concluded that the best-available scientific evidence demonstrates the tortoise’s need for range-wide federal protection and it is now a candidate species eligible for protection under the Endangered Species Act. In addition, the burrows created by this semi-fossorial species are important to the persistence of various other species, many of which are protected by state regulations (McCoy et al. 1996).

Gopher tortoises are specialists of longleaf pine habitats, which have been reduced by as much as 98% of their previous extent (Noss et al. 1995). Remaining longleaf pine habitat is often degraded (due to fire suppression or improper management) leading to structural changes in the vegetation. Diemer (1986) demonstrated that gopher tortoises respond to physical vegetation structure, not plant species composition. Sparse canopy cover is important for tortoise persistence because light penetration to ground level is necessary for egg incubation, thermoregulation, and feeding (Landers and Speake 1980). Burrow abandonment occurs when a tortoise leaves the immediate area, most often as a result of declining habitat suitability, and settles elsewhere. Previous studies have documented the

importance of an open canopy to maintain suitable habitat for the gopher tortoise (Aresco and Guyer 1999; Boglioli et al. 2000). However, traditional field methods used to measure vegetation structure limit the ability to implement multi-scale approaches and derive a functional response of gopher tortoise abandonment to changes in vegetation structure. A simple statement of difference or an arbitrary cutoff for suitable/unsuitable habitat doesn't provide natural resource managers with appropriate ecological information to make efficient management decisions.

In this study, I derived estimates of relative canopy cover and 3D vegetation structure from discrete-return lidar acquired over 350 ha of managed gopher tortoise habitat in central Florida. I used these structural metrics to develop logistic regression models to predict the probability of burrow abandonment as a function of relative canopy cover at multiple spatial scales.

Methods

Study area:

I conducted the survey in Wekiwa Springs State Park (WSSP) in central Florida (28° 44' 50" N, 91° 29' 44" W) because it contains a large and contiguous area of highly suitable gopher tortoise habitat. I limited the survey to sandhill habitat, the primary habitat of the gopher tortoise across its range (Diemer 1986; McCoy et al. 2006). Because gopher tortoises often achieve highest densities in this habitat, it serves as an ideal model system. Frequent prescribed fire maintains sandhill as a savannah-like habitat dominated by a wiregrass ground cover and a sparse canopy of longleaf pine and occasional turkey oaks. Lightning season prescribed burn management has been a priority at WSSP and the park often serves as a model for simulating natural conditions in sandhill (e.g., 1-3 year burn interval). I was thus able to relate tortoise response to 3D vegetation structure over a broad spatial extent where burrow

abandonment was unlikely to be influenced by small patch size, isolation, or other problems related to poor habitat quality.

Field methods: Burrow location and classification:

Assessment of tortoise burrow features is necessary to determine burrow use and tortoise occupancy of habitat because gopher tortoises spend approximately 90% of their time underground (McCoy et al. 2006). Careful interpretation of burrow status provides unique opportunities to assess population dynamics that otherwise are unobtainable. Total area surveys were conducted via systematic transects (10 meter spacing) over approximately 350 ha of sandhill habitat. Tortoise burrows were located and recorded using GPS (Garmin GPSMAP® 60Cx). Burrow activity status was determined as 1 of 2 categories based on external burrow characteristics: (1) “active” if the burrow entrance was maintained, open, consisted of loose sand, and/or there were obvious tortoise presence indicators (plastral slides, tracks, or scat), (2) “abandoned” if the burrow opening was occluded with debris, severely eroded, or collapsed (Figure 2). Altogether, I located and categorized over 1500 burrows.

Remote sensing methods: Lidar data acquisition and processing:

The National Center for Airborne Laser Mapping (NCALM; <http://www.ncalm.org>) acquired the lidar data over an area of approximately 1000 ha of WSSP in June of 2011. The data were collected using an Optec Gemini Airborne Laser Terrain Mapper (with 5-35cm elevation accuracy, laser pulse repetition frequency (PRF) of 70 kHz, and an average point density of 5.07 p/m²). TerraScan software was then used to filter ground and non-ground lidar point returns.

I created a 1 m resolution digital elevation model (DEM) from the lidar points classified as ground returns using FUSION version 2.90 (McGaughey 2010). I then used FUSION to calculate the number of non-ground lidar returns occurring both above and below 1 m in height in each 1 m by 1 m cell of the study area. Due to the lack of anthropogenic structures in the study area, I assumed that all of the non-ground lidar returns were reflected off of vegetation. Finally, I calculated the relative percent canopy cover in each cell as $(\text{number of returns} > 1 \text{ m in height} / \text{total number of returns}) \times 100\%$ (Figure 11). I used a relative measure of canopy cover to compensate for the spatial variability in the density of lidar returns over the study area intrinsic to the airborne acquisition process.

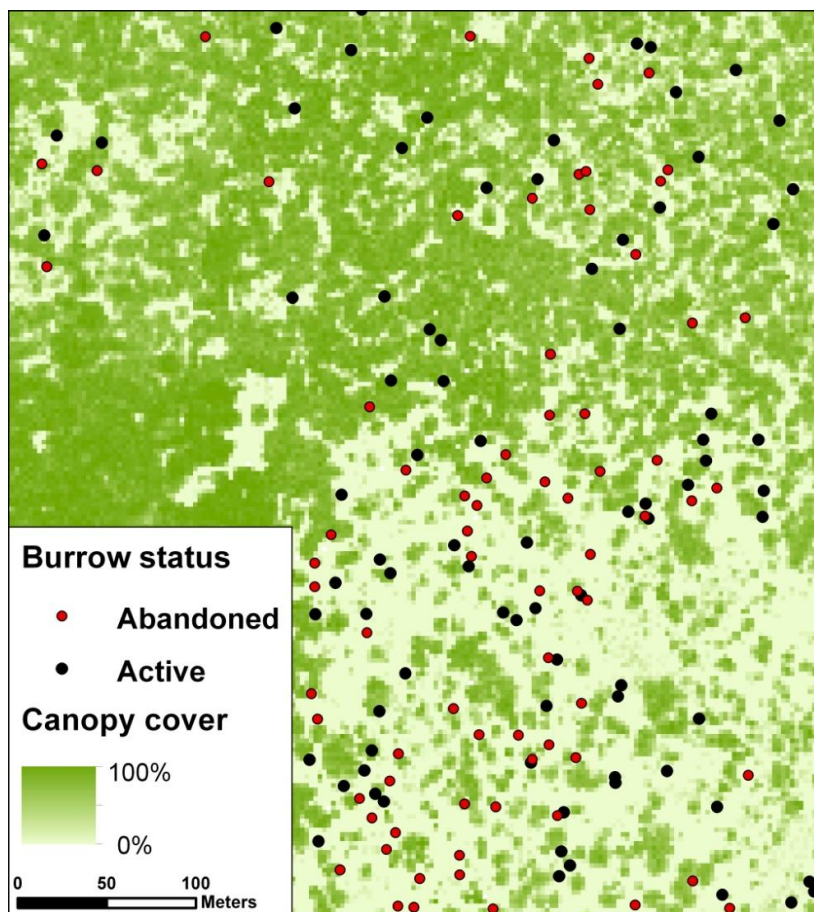


Figure 11. Map of a portion of the WSSP study area showing burrow distributions and activity status with relative percent canopy cover.

Statistical analyses

I classified the status of each burrow as a binary response variable (1 = “abandoned”, 0 = “active”) and fit a series of logistic regression models of burrow status versus relative canopy cover with the *glm* function of R version 2.11.1 (R Development Core Team 2010). Because *glm* uses maximum likelihood (ML) estimation and the sample size was large ($n > 1500$), the parameter estimates possessed the large-sample properties of ML estimators, including asymptotic normality and optimality (i.e., minimum variance) (Hosmer and Lemeshow 2000). Also, to ensure that the burrows represented independent observations, I performed a spatial autocorrelation analysis using SAM version 4.0 (Rangel et al. 2010). The resulting Moran’s I values were less than ± 0.05 at all distance classes under 4 km and these values oscillated randomly around zero, indicating the absence of autocorrelation in the spatial distribution of burrow statuses (Fortin and Dale 2005).

To estimate the relative canopy cover in the area surrounding a burrow, I used ESRI ArcGIS version 10.0 (Redlands, CA) to calculate the mean canopy cover from lidar analyses, in circles of varying radii (0 m, 5 m, 10 m, and 15 m) centered at each burrow entrance (Figure 12). I then used Akaike’s Information Criterion (AIC) to select the logistic regression model with the best fit to the observed data. I also fitted models with time since fire (TSF) as a covariate because several studies have documented the relationship between fire and its effects on the vegetation structure and probability of burrow abandonment by gopher tortoises (Aresco and Guyer 1999, Ashton et al. 2008). Finally, I performed a Hosmer-Lemeshow goodness-of-fit test to assess the overall fit of the final logistic regression model (Hosmer and Lemeshow 2000).

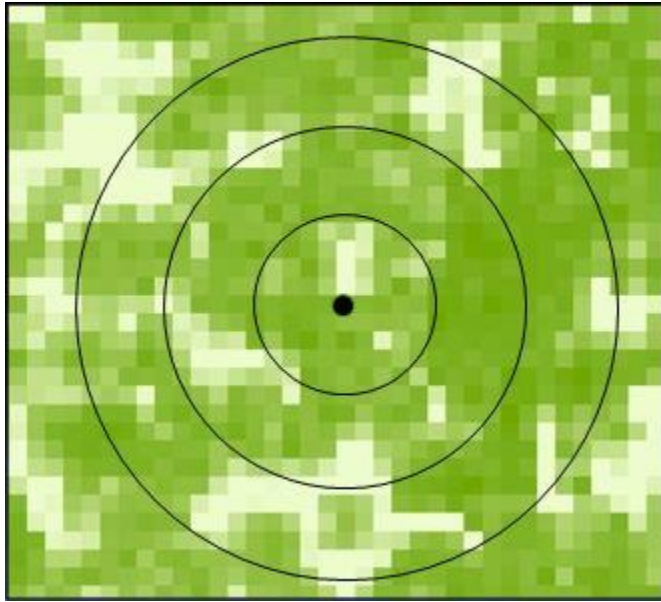


Figure 12. Canopy cover within circles of increasing radii (0, 5, 10, 15 m) of a burrow. Each cell is 1 x 1 meter and color coded based on relative canopy cover as derived from lidar data. Darker green corresponds to more canopy cover.

Results

Average relative canopy cover within a 10 m radius surrounding the burrow entrance most effectively predicted whether a burrow was abandoned (Table 5). The AIC score decreased from 2180.0 for the model with no radius to 2152.4 for the model with a 10 m radius, and then increased to 2159.3 for the model with a 15 m radius. Including TSF as a covariate resulted in less efficient models (i.e., higher AIC scores than those without this predictor) in all cases. For example, the AIC for the TSF model with a 10 m radius was 2157.7 (compared to 2152.4 for the same model that excluded the TSF covariate).

Table 5. Logistic regression models of burrow abandonment status versus % relative canopy cover.

<i>Circular radius around burrow entrance</i>	<i>Relative canopy cover parameter estimate</i>	<i>Relative canopy cover parameter Std. Error</i>	<i>Relative canopy cover parameter P-value</i>	<i>Model AIC score</i>
0 m	0.001355	0.001365	0.321	2180.0
5 m	0.009567	0.002502	0.000132	2166.1
10 m	0.016926	0.003204	< 0.0001	2152.4
15 m	0.016118	0.003498	< 0.0001	2159.3

Based on these results, I used mean relative percent canopy cover in a 10 m radius, with no TSF predictor, to predict the mean probability of a gopher tortoise burrow being classified as “abandoned” (Figure 13). The logistic probability of abandonment increases in a positive, nearly linear manner from a mean of 0.389 (95% confidence interval: 0.336 – 0.441) with 0% relative canopy cover to a mean of 0.775 (95% confidence interval: 0.698 – 0.853) with 100% relative canopy cover. The Hosmer-Lemeshow goodness-of-fit test with 20 equiprobable intervals failed to reject the null hypothesis that this final logistic regression model was a good fit to the observed data ($\chi^2 = 20.117$, $df = 18$, $P = 0.3263$).

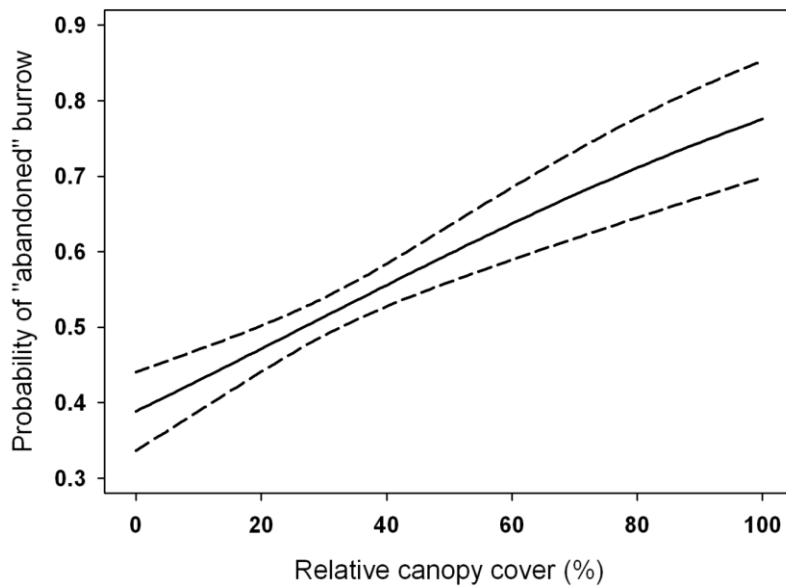


Figure 13. Probability of gopher tortoise burrow with “abandoned” status (solid line is mean probability, dashed lines represent 95% confidence interval) as a function of relative canopy cover within a 10 m radius of the burrow entrance.

Discussion

These results indicate that the probability of a burrow being classified as abandoned is about twice as often under full canopy cover as without canopy cover, with a nearly linear transition between those extremes. I base this estimate on a multi-scale assessment of canopy cover using lidar over >1500 burrows, demonstrating that a combination of field-based and remote sensing data yields a robust predictive habitat structure model for a threatened species. Ecologists and natural resource managers have long sought to link habitat structure to species viability. This is particularly important for many terrestrial species such as the gopher tortoise. This is the first study to quantify this effect at multiple spatial scales for the gopher tortoise; a necessity to truly understand species-habitat relationships.

Based on the best model, each percent increase in vegetation structure within a 10 m radius of the burrow increases the probability of abandonment by 1.7%. This functional relationship will help parameterize descriptive or predictive models aimed at identifying gopher tortoise response to various ecological threats. This model may vary at other sites, and should be tested, but an important point is that natural resource managers are no longer confined to limited inference based on a simple statement of difference or limited sampling protocols. Previous studies have linked burrow abandonment to canopy closure but have done so at single spatial scales and over limited spatial extents (e.g., Arresco and Guyer 1999, Boglioli et al. 2000).

Significantly, the use of lidar technology has allowed me to derive a more accurate and realistic understanding of the functional response of gopher tortoises to changes in vegetation structure for at least three reasons. First, lidar data allowed me to assess the relationship between tortoise burrow abandonment and vegetation structure at multiple spatial scales. The results of this research have demonstrated that vegetation structure within a 10 meter radius of the burrow is most important to predicting burrow abandonment; beyond this distance, the strength of this relationship decreases. This makes intuitive sense because vegetation at a short distance from the burrow can impede light penetration when the sun is at shallower angles. Second, with the use of lidar, I was able to obtain fine-grain resolution of vegetation structure over a broad spatial extent. This in turn has allowed me to assess the relationship between burrow abandonment and vegetation structure over a relatively homogeneous landscape. An understanding of species responses to changes in structural vegetation within a homogeneous landscape is currently lacking and needs to be further explored (Goetz et al. 2010). Finally, because lidar provides the means to measure 3D vegetation structure over a broad spatial

extent, at multiple spatial scales, and within a homogenous landscape I was able to quantify how burrow abandonment changes as a function of structural vegetation change.

While lidar collection involves an initial investment, it saves a significant amount of money long term (Asner et al. 2011) and allows researchers and managers to derive ecological information regarding the relationship between biodiversity and habitat structure not otherwise attainable. Access to lidar data for a substantial portion of the U.S. has already been made publically available by the U.S. Geological Survey (USGS; <http://lidar.cr.usgs.gov>) and the establishment of the National Ecological Observatory Network (NEON; <http://www.neoninc.org>) will increase the areas with lidar coverage. The ability to collect relevant multi-dimensional data will allow researchers to produce models that more accurately detect and quantify drivers of ecological change. Lidar data can also be used to monitor various important habitat/species metrics such as prescribed burning impact (Streutker and Glenn 2006), carbon mapping (Asner et al. 2011), and species response to vegetation change (Vierling et al. 2008). In an increasingly unsuitable landscape for species persistence, many populations are subjected to threats at a variety of spatial scales. Unfortunately, traditional field methods alone do not permit one to accurately assess species' responses to changes in vegetation structure at multiple spatial scales. This demonstration of a novel use of lidar remote sensing to augment field methods and address ecological problems should encourage use of such a powerful technology in ecological research and habitat/species management.

CHAPTER FOUR: CONCLUSION

Effective management should be driven by the principles developed by rigorous scientific studies of processes and the patterns they produce (Levin 1992). This science-based management is necessary to effectively conserve native biota and ecosystems. The immediate challenge is to identify mechanisms that structure diversity and to develop realistic descriptive and predictive models of species-species and species-habitat relationships. Studies likely to inform this critical need must investigate the multiple factors which interact to influence diversity at various scales in time and space. Simple approaches investigating a single mechanism to explain a pattern are often unrealistic and do not generate accurate models of diversity relationships. Biological diversity can be broken down into three categories: functional diversity, structural diversity, and compositional diversity (Noss 1990). Interactions among these aspects of diversity have been shown to influence community interactions among species and ecosystem function (Chapin et al. 2000). Therefore, studies seeking to understand mechanisms structuring diversity should incorporate aspects of all three of these components.

The objective of this thesis was to investigate the mechanisms likely responsible for explaining the structure of non-volant vertebrate diversity within sandhill systems of the southeast U.S. Specifically, the aim was to quantify the role of the gopher tortoise in maintaining diversity in this system. Because the gopher tortoise is susceptible to changes in habitat structure and are hypothesized to be an integral agent in maintaining diversity, they are an ideal model to investigate these mechanisms. Also, there is a pressing need to identify tortoise-habitat and tortoise-species interactions to better understand how changes in their habitat and populations may impact these systems. A recent study by McCoy et al. (2006), which showed continued tortoise population declines on protected lands, underscores the need for more accurate information regarding gopher tortoise ecology.

This thesis has increased our understanding of this imperiled species in two ways. First, gopher tortoise and sandhill ecology was advanced by critically evaluating the role of the gopher tortoise as a keystone species. Despite claims since the early 1980's, compelling evidence does not exist to support this hypothesis. I demonstrated that the tortoise exhibits an influence that is proportional to its abundance, and thus does not meet the requirements of a keystone species. Instead, this ecosystem engineer appears to influence the community via way of dominance. I also demonstrated that the influence on diversity is through altering relative abundances of species in the community, not richness. This influence is positive and appears to be one of the primary mechanisms structuring diversity in sandhill systems.

Secondly, I empirically demonstrated a methodology to improve species-habitat models for the gopher tortoise. I showed how using lidar technology to measure vegetation structure can enhance these models by incorporating high resolution data over broad spatial extents to develop multi-scale models of species-habitat interactions. The use of this method to quantify the influence of vegetation change on tortoise burrow abandonment led to a deeper understanding of this relationship. Past recommendations regarding appropriate vegetation structure to promote gopher tortoise persistence was variable. Instead of an arbitrary designation, I was able to show a functional response of the relationship between canopy closure and abandonment. The model I developed showed that there is a linear relationship and that with each percent increase in canopy cover, the probability of burrow abandonment increased by ~2%. Thus, there is no arbitrary cut off for suitable versus unsuitable vegetation structure; the response is on a continuum.

Ultimately this thesis highlights the importance of the gopher tortoise and its burrow system in explaining the structure of the non-volant vertebrate assemblage in sandhills and the assemblage's

response to habitat change. The former vagueness of habitat change is brought into focus as the process of canopy closure. Failure of land managers to use prescribed fire at proper fire return intervals results in canopy closure. Changes in the vertical structure of the forest result in local shifts in gopher tortoise populations from areas with increasing canopy development to habitat with reduced canopies. A better understanding of the role of this endemic, semi-fossorial tortoise in these rapidly deteriorating habitats will have important implications for conservation and management of these rare ecosystems. Specifically, conservation of gopher tortoises may offer protection to many species, increasing biodiversity, and thus contribute to the goal of maintaining ecosystem functions. By quantifying the interaction of ecological functions such as fire and vegetation structure with gopher tortoise activity, this study provides opportunities for managers to better combine the advantages of single-species conservation for the gopher tortoise with the benefits of ecosystem management to promote biodiversity (Simberloff 1998).

APPENDIX A: SPECIES PRESENCE IN EACH SAMPLE UNIT

Species Observed	Sample Unit															
	11-19	11-16	9-6	14-12	15-2	18-1	30A-25	30B-15	30B-8	30B-1	30C-20	30C-8	30C-24	30C-29	38-5	40-1
<i>S. h. holbrooki</i>	X		X	X	X	X	X	X			X	X	X			X
<i>A. terrestris</i>	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X
<i>H. gratiosa</i>																X
<i>H. cinerea</i>	X	X	X	X	X										X	X
<i>E. planirostris</i>								X	X						X	
<i>G. carolinensis</i>	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X
<i>A. carolinensis</i>		X	X						X		X			X	X	X
<i>S. undulatus</i>	X	X	X		X	X	X	X	X	X	X	X	X		X	X
<i>A. s.sexlineatus</i>	X	X	X	X		X		X	X	X	X	X	X	X		X
<i>P. inexpectatus</i>		X		X		X	X		X			X	X		X	X
<i>P. e. onocrepis</i>	X							X								
<i>T. s. sirtalis</i>			X			X										
<i>C. c. priapus</i>	X		X		X					X	X					X
<i>H. platyrhinos</i>				X	X											
<i>S. m. barbouri</i>				X		X	X			X						
<i>G. pinetis</i>	X	X	X	X	X	X										
<i>S. aquaticus</i>					X											
<i>B. carolinensis</i>						X						X	X			
<i>P. gossypinus</i>					X		X		X	X	X				X	
<i>P. floridanus</i>											X					
<i>S. hispidus</i>	X	X	X					X			X	X	X	X		X
<i>C. f. flagellum</i>											X					

APPENDIX B: SCIENTIFIC & COMMON NAMES OF SPECIES

	Scientific Name	Common Name	Source
Frogs	<i>Anaxyrus terrestris</i>	Southern Toad	Crother 2008
	<i>Eleutherodactylus planirostris</i>	Greenhouse Frog	
	<i>Gastrophryne carolinensis</i>	Eastern Narrow-mouthed Toad	
	<i>Hyla cinerea</i>	Green Treefrog	
	<i>Hyla gratiosa</i>	Barking Treefrog	
	<i>Scaphiopus holbrooki holbrooki</i>	Eastern Spadefoot	
Lizards	<i>Anolis carolinensis carolinensis</i>	Green Anole	
	<i>Aspidoscelis sexlineatus sexlineatus</i>	Six-lined Racerunner	
	<i>Plestiodon egregius onocrepis</i>	Peninsula Mole Skink	
	<i>Plestiodon inexpectatus</i>	Southeastern Five-lined Skink	
	<i>Sceloporus undulatus</i>	Eastern Fence Lizard	
Snakes	<i>Coluber constrictor priapus</i>	Southern Black Racer	
	<i>Coluber flagellum flagellum</i>	Eastern Coachwhip	
	<i>Heterodon. platyrhinos</i>	Eastern Hog-nosed Snake	
	<i>Sistrurus miliarius barbouri</i>	Dusky Pigmy Rattlesnake	
	<i>Thamnophis sirtalis sirtalis</i>	Eastern Garter Snake	
Turtles	<i>Gopherus polyphemus</i>	Gopher Tortoise	Wilson and Reeder (2005)
Mammals	<i>Scalopus aquaticus</i>	Eastern Mole	
	<i>Blarina carolinensis</i>	Southern Short-tailed Shrew	
	<i>Peromyscus gossypinus</i>	Cotton Mouse	
	<i>Podomys floridanus</i>	Florida Mouse	
	<i>Sigmodon hispidus</i>	Hispid Cotton Rat	
	<i>Geomys pinetis</i>	Southeastern Pocket Gopher	

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