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Article in Journal of Coastal Research - June 2013
DOI: 10.2112/JCOASTRES-D-12-00201.1

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Multiscale Burrow Site Selection of Gopher Tortoises (Gopherus polyphemus) in Coastal Sand Dune Habitat

Anthony Lau†‡ and C. Kenneth Dodd Jr.‡

School of Biological Sciences
The University of Hong Kong
Pokfulam
Hong Kong, China
antlau1@gmail.com

University of Florida
Department of Wildlife Ecology & Conservation
Gainesville, FL 32611, U.S.A.

ABSTRACT

Lau, A. and Dodd, C.K., Jr., 0000. Multiscale burrow site selection of gopher tortoises (Gopherus polyphemus) in coastal sand dune habitat. Journal of Coastal Research, 00(0), 000–000. Coconut Creek (Florida), ISSN 0749-0208.

The gopher tortoise (Gopherus polyphemus) is a keystone species in upland sandhill ecosystems of the SE United States, and its habitat requirements have been well documented. Few studies have been conducted on populations that occur in coastal sand dunes. Because of close proximity to the ocean and highly fragmented linear habitat, coastal populations of gopher tortoises are affected by unique landscape factors that are not observed in upland contiguous populations. In this study, burrow site selection of gopher tortoises in a coastal sand dune site was quantitatively modeled. Significant biological, environmental, and anthropogenic factors that may influence burrow site selection at fine and coarse spatial scales were identified. Land cover type, distance to edge, soil resistance, percentage of herbaceous cover, slope angle, and number of tortoise burrows have significant influences on burrow site selection probability. Factors that influence burrow locations in coastal populations thus might differ in importance from those that influence burrow locations in more spatially contiguous upland populations. Our results indicate that coastal gopher tortoise populations require site-specific management that focuses on the limited availability of optimal burrow construction sites.

ADDITIONAL INDEX WORDS: Landscape ecology, habitat selection, model selection, keystone species, semifossorial.

INTRODUCTION

For centuries, humans have resided near and visited coastal beaches and adjacent dunes. However, conflicts among conservation of coastal natural resources, land development, and sustainability of economic activities have been increasing substantially since the mid-20th century (Faggi and Dadon, 2011). The coastal sand dunes of Georgia and Florida are home to some of the most iconic and charismatic wildlife species of the SE United States, such as eastern diamondback rattlesnakes (Crotalus adamanteus), gopher tortoises (Gopherus polyphemus), and myriad shorebirds. In some cases, coastal dunes serve as refuge for imperiled taxa, such as several endangered subspecies of beach mouse (Peromyscus polionotus). These coastal dunes and associated beaches are also some of the most heavily used areas in North America for human-oriented recreation and tourism.

Coastal beach and dune communities are hostile environments to most plants and animals because of constant exposure to high temperatures, drought conditions, low nutrient levels, unstable soil, salt spray, and saltwater (Barnett and Crewz, 1997). The plants and animals found along coastal beaches and dunes rely on special morphological and physiological adaptations to survive the harsh environment. For example, many dune plants have dense root systems, rapid growth rates, and profuse flower and seed production, which allow them to overcome innutritious soils and constant stress from sand burial and saltwater (Barnett and Crewz, 1997; Maun, 1998). In contrast, mobility allows animals to actively select suitable habitat within beach and dune communities to forage, reproduce, and thermoregulate (McLachlan, 1991).

Habitat selection is a fundamental concept in ecology and has direct applications to conservation. Disproportionate use of habitat, resources, or both presumably improves the fitness and survivorship of a species (Block and Brennan, 1993; Thomas and Taylor, 1990). Physical and biological factors have significant influences on wildlife habitat selection at multiple spatial scales. Anthropogenic factors may be influential in highly disturbed areas. However, seldom have the interactions of all three of these factors been studied simultaneously, although several studies have attempted to discriminate their relative importance (Burger and Gochfeld, 1991; Gallant et al., 2009; Mahan and Yahner, 1996; Meager, Schlacher, and Nielsen, 2012; Peters and Otis, 2007). Work on river otters (Lontra canadensis), for example, suggested that environmental factors were more influential than anthropogenic factors in describing habitat selection patterns, but anthropogenic disturbances could indirectly affect habitat selection of otters.
by causing the loss of important habitat features (e.g., beaver ponds; Gallant et al., 2009).

In addition to the indirect effects on habitat selection, anthropogenic disturbances may affect certain aspects of species behavior, such as the communication of social information, that are difficult for investigators to detect (Berry, 1986; Betts et al., 2008; Citta and Lindberg, 2007). Anthropogenic disturbances such as road construction and timber management negatively affect habitat selection among some amphibians (Baldwin, Calhoun, and de Maynadier, 2006; Blomquist and Hunter, 2009; Graeter, Rothermel, and Gibbons, 2008).

A number of studies have investigated the effects of anthropogenic disturbances on wildlife in coastal systems. Bird, Branch, and Miller (2004), for example, found that lights reduce the foraging frequency and efficiency of beach mice, suggesting that artificial lighting should be mitigated in conservation planning and management. Witherington and Martin (2000) found that artificial lighting also prevents hatching sea turtles from reaching the ocean by disorienting them. Coastal areas worldwide are subject to rapid human encroachment and coastal ecosystems are under tremendous anthropogenic pressure. In addition to light pollution, wildlife in coastal ecosystems are subjected to invasive exotic plants, feral and domestic predators, habitat degradation, loss and fragmentation, sand mining, and global climate change leading to a rising sea level. Coastal ecosystems (marshes, mangroves, reefs, and dunes) worldwide are important to humans because they provide essential ecosystem services such as storm buffering, fisheries production, and enhanced water quality (Barbier et al., 2008). The indigenous plants and animals of these fragile ecosystems thus may require special management to ensure long-term persistence and ecosystem function.

The gopher tortoise is a moderately sized, semidigging tortoise that occurs in a variety of habitats in SE North America. The species is threatened by habitat loss and fragmentation throughout its range, and the decline of this species may consequently affect many wildlife species that share its habitat. The literature on the ecology of this species is extensive, but few studies focus solely on populations that occur in coastal habitats (but see Breininger, Schmalzer, and Hinkle, 1991, 1994; Kushlan and Mazzotti, 1984; Waddle, Mazzotti, and Rice, 2006). Burrows excavated by gopher tortoises are important habitat features in many ecosystems. The burrow and its associated apron are important for a tortoise because they are used for resting, basking, courting, sheltering from predators and fire, and nest deposition; they are also the center of feeding activities. The tortoise burrow provides shelter during cold, drought, and fire, and some animals are obligate commensals that can only be found in tortoise burrows. Thus, the distribution and survivorship of these burrow commensals directly depends upon the habitat modifications made by the gopher tortoise.

Gopher tortoises occur in habitats with well-draining, sandy soils and abundant low growing herbaceous cover, but the exact habitat features and mechanisms that trigger a tortoise to excavate a burrow are poorly understood. Because tortoises spend most of their time in a burrow, previous studies on habitat selection of gopher tortoises have focused on the

**STUDY AREA**

This study was conducted in Guana Tolomato Matanzas National Estuarine Research Reserve (GTMNERR; 30°37’34” N, 81°20’53” W.) located on the NE coast of Florida, St. Johns County. The 78-ha study area (7.1 km long; 90–145 m wide) is composed of mostly high energy beach dune and coastal strand habitat (Florida Natural Areas Inventory, 2011; Figure 1). The beach dune is a herbaceous community built by a number of coastal specialist grasses, such as sea oats (Uniola paniculata) and bitter panicgrass (Panicum amaratum), whose stems trap the sand grains blown off the beach and form the foundation of the dune. Other plants commonly seen in the beach dune are railroad vine (Ipomoea pes-caprae spp. brasiliensis), seacoast marsh elder (Iva imbricata), saltmeadow cordgrass (Spartina patens), beach morning glory (I. imperati), Indian blanket (Gaillardia pulchella), bull thistle (Cirsium horridulum), and prickly pears (Opuntia spp.). Coastal strand is a woody plant community located farther inland and directly behind the beach dune. It is dominated by dense saw palmetto (Serenoa repens) and cabbage palm (Sabal palmetto) on the seaward edge and red bay (Persea borbonia), red cedar (Juniperus virginiana), yaupon holly (Ilex vomitoria), and tough bullw (Sideroxylon tenax) farther inland. Habitat heterogeneity and vegetation community succession at this site are driven by primarily waves and wind and occasionally by fire (Barnett and Crewz, 1997). Stout (1980) gave a more detailed account of typical plants found in these habitats. In the beach dune, plants on the foredune are constantly exposed to salt spray and sand burial from onshore wind blowing from the Atlantic Ocean, while plants on the upper dune are subjected to the same stresses, in addition to occasional inundation by storm tides and destruction by strong waves. The plants on the beach dune are adapted to withstand these stresses. In the coastal
strand, continual winds from the ocean function to maintain a low, even canopy of hardwoods. The natural fire frequency in this community is unknown. However, the major vegetative component (*S. palmetto*) is highly flammable, and fires typically spread rapidly in the coastal strand when started.

The study site is bordered by a high-use road (Florida state road, or SR, A1A) to the west, the Atlantic Ocean to the east, and private residences to the north and south. It includes some of the only undeveloped dunes on the eastern coast of Florida. The beach is accessible by humans through three boardwalks.

Figure 1. (A) Gopher tortoise habitat in coastal sand dunes in GTMNERR, South Ponte Vedra Beach, Florida. Foreground: beach dune land cover; background: coastal strand land cover. (B) A gopher tortoise foraging along the edge between the two land cover types.
located 0.66, 1.76, and 5.46 km north of the southernmost point of the study site. In addition to these three boardwalks, numerous foot paths dissect the beach dune at various locations. These paths were created by the frequent foot traffic of beachgoers before the public beach accesses were made in the 1990s. Public access to the beach dune is restricted to protect the vegetation community of the coastal beach dune.

Gopher tortoises are present at the site in varying densities (Figure 2). Based on burrow surveys conducted by GTMNERR staff from 2005–07 and by the authors during the present study, the overall density of tortoise burrows in dunes ranges from 0.64 to 3.05 burrows per hectare. Burrow density of the northern section (12.17 burrows per hectare) is much higher than that of the southern section (0.75 burrows per hectare), probably due to the varying width, topographic profile, and vegetative community structure between the two sections (Figure 2). Many other animals use tortoise burrows in the sand dunes as temporary shelters or permanent homes; during the course of this study, eastern coachwhips (Masticophis flagellum, n = 3), marsh rabbits (Sylvilagus palustris, n = 2), and a southern toad (Anaxyrus terrestris, n = 1) were observed using tortoise burrows. Footprints of eastern woodrats (Neotoma floridana) also have been observed in front of a tortoise burrow.

Distinctive foraging trails created by gopher tortoises during their feeding forays can be found near tortoise burrows in the study area. Gopher tortoises may be important stressors on fine-scale heterogeneity of the herbaceous plant community in the sand dune. The role of tortoises as seed-dispersing agents has been discussed by several authors (Carlson, Menges, and Marks, 2003; Cobo and Andreu, 1998; Strong and Fragoso, 2006); as one of the major herbivores in the coastal community in GTMNERR, gopher tortoises may be important seed dispersers.

METHODS

Burrow Survey and Available Burrow Sites

The study area was searched systematically from January to May 2010 to locate and categorize gopher tortoise burrows. Five 7.1-km-long, 10-m-wide belt transects parallel to the shoreline were established in the study area using geographic information system (GIS) software; the transects were at least 10 m apart. The survey was conducted by walking each transect from north to south, mimicking burrow surveys conducted by GTMNERR staff and volunteers in 2005–07. The search effort was not equal among different land cover types, because it was extremely time consuming to move through the much thicker vegetation in the coastal strand. The overall area covered by the line transect was approximately 350,000 m² (~48%) of the study area. From March through August 2010, additional burrows were found by following 20 radio-tagged tortoises in the study site.

A unique identification was given to each burrow upon discovery, and the location of each burrow was recorded (~3 m) using a handheld global positioning system unit (Garmin GPSMAP 60CSx; Garmin International Inc., Olathe, Kansas, U.S.A.) and categorized as active, inactive, or abandoned, according to criteria described by Auffenberg and Franz (1982). Of the 238 burrows located from the belt transect survey and radio-tagged tortoises, 100 active burrows were randomly selected using a random number generator to determine factors influencing burrow placement. The random numbers (i.e. burrow identifiers) were generated using the RAND function in Microsoft Excel 2003 with the interval restricted to 1 and 238.

For comparison with randomly selected burrow sites, 100 random points within the study site were generated as available habitat using the Geospatial Modelling Environment extension in ArcGIS (Spatial Ecology, 2010).

Burrow Site Selection

Three groups of explanatory variables (five physical, nine biological, and two anthropogenic; Table 1) were measured at two spatial scales to determine factors that may influence burrow site selection of gopher tortoises: microhabitat scale (1-m radius) and home-range scale (20-m radius) from the burrow opening. The 1-m radius is assumed to be an appropriate scale for microhabitat habitat selection because tortoises are thought to have good vision, which allows them to discriminate finely detailed objects (e.g. foliage; Eskildsen, Oleen, and Jones, 2004) and recognize particular spatial habitat features, such as burrows (Diemer, 1992; Harless et al., 2009) and conspecifics (Wilkerson et al., 2010). The 20-m radius is assumed to be an appropriate scale for home-range scale selection, because it is the radius of the mean annual home ranges of gopher tortoises in the sand dune, based on radiotelemetry work conducted at the study site from March 2010 to March 2011 (Lau, 2011). The home ranges were 95% kernel estimates, which are conservative estimates of the tortoises’ home-range sizes. On-the-ground measurements (i.e. microhabitat variable) were made at both burrow and random locations from May to August 2010, whereas landscape variables were measured using GIS software in September 2011.

Soil resistance was measured to the closest kilogram per square centimeter using a handheld pocket soil penetrometer (Geotest Instrument E280; Geotest Instrument Corp., Evanston, Illinois, U.S.A.) with a 2.54-cm-diameter adapter foot. Elevation was measured to the closest foot (0.3048 m) using a 1-ft contour map generated by light detection and ranging in GIS software (ArcMap 9.3, ESRI, Redland, California, U.S.A.). Slope was measured as the percentage change in elevation within 1 m using a meter stick and a level. Slope angle is the orientation of the respective slope and was measured to the closest degree using a compass. Soil type is defined as the dominant soil type of each location, following U.S. Department of Agriculture (2010) Soil Survey Geographic Database classifications. Canopy cover is defined as the presence or absence of canopy-forming plants (>2 m in height) at each location. Percentages of bare ground, herbaceous cover, grass, scrub and vines, and litter coverage were visually estimated to the closest 10% in a 1 × 1 m quadrat at each location. At burrow locations, the soil deposit (apron) excavated by the tortoise during its burrowing activity was not included in the 1 m² quadrat. Distance to edge was defined as the shortest distance in meters from each location to a different land cover type (i.e. between coastal scrub and sand dune habitat), following Williams, Nichols, and Conroy (2002). Distance to edge was
measured on aerial images of the study site using GIS software. Land cover type was defined as the dominant land cover type of each location following the Florida Natural Area Inventory (2011) classifications. Number of tortoise burrows was the count of gopher tortoise burrows (adults and subadults) located within a 20-m radius of each location. Distance to road was the perpendicular distance of each location to the closest road. Distance to beach access was the perpendicular distance of

Figure 2. Aerial photographs of the coastal sand dune study site (left: north; right: south) for gopher tortoises burrow site selection in GTMNERR. The study site is bordered by a high-use road (Florida SR A1A) to the west, the Atlantic Ocean to the east, and private residences to the north and south. Open circles represent random points, and closed circles represent active tortoise burrows.
Table 1. Potential factors influencing burrow site selection for gopher tortoises in coastal sand dunes of GTMNERR, 2010.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Spatial Scale</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Physical factors</strong></td>
<td></td>
</tr>
<tr>
<td>Soil resistance</td>
<td>Microhabitat</td>
</tr>
<tr>
<td>Elevation</td>
<td>Microhabitat</td>
</tr>
<tr>
<td>Slope</td>
<td>Microhabitat</td>
</tr>
<tr>
<td>Slope angle</td>
<td>Microhabitat</td>
</tr>
<tr>
<td>Soil type*</td>
<td>Home range</td>
</tr>
<tr>
<td><strong>Biological factors</strong></td>
<td></td>
</tr>
<tr>
<td>% Bare ground</td>
<td>Microhabitat</td>
</tr>
<tr>
<td>% Herbaceous cover</td>
<td>Microhabitat</td>
</tr>
<tr>
<td>% Grass</td>
<td>Microhabitat</td>
</tr>
<tr>
<td>% Woody scrub and vines</td>
<td>Microhabitat</td>
</tr>
<tr>
<td>% Litter</td>
<td>Microhabitat</td>
</tr>
<tr>
<td>Canopy cover*</td>
<td>Microhabitat</td>
</tr>
<tr>
<td>Distance to edge</td>
<td>Home range</td>
</tr>
<tr>
<td>Land cover type*</td>
<td>Home range</td>
</tr>
<tr>
<td>No. tortoise burrows</td>
<td>Home range</td>
</tr>
<tr>
<td><strong>Anthropogenic factors</strong></td>
<td></td>
</tr>
<tr>
<td>Distance to road</td>
<td>Home range</td>
</tr>
<tr>
<td>Distance to beach access</td>
<td>Home range</td>
</tr>
</tbody>
</table>

* Categorical variables.

each location to the closest beach access. Both distances were measured in meters on high-resolution aerial images of the study site using GIS software.

We used logistic regression models to predict the probability of burrow site selection as a function of factors measured in both spatial scales to identify factors that influence burrow site selection. The response variables were whether or not a habitat was selected (burrow locations) or available (random locations).

We used the generalized linear model with binomial link function in statistical analysis software (Statistical Applications Systems, Cary, North Carolina, U.S.A.) to estimate regression coefficients of each factor in logistic models.

Data Analysis

A Spearman’s nonparametric correlation matrix was created to identify factors that were strongly correlated (r > 0.6) to address potential multicollinearity. Factors that were strongly correlated were excluded from the final models. Distance to edge was strongly correlated with both elevation and distance to road. Distance to road and elevation were both dropped from the models because the road was parallel to the elevation gradient and these two variables provided essentially the same information as distance to edge. Percent coverage of woody scrubs and vines was strongly correlated with the percent coverage of bare ground. The latter was dropped because it is essentially the reciprocal of the former. Nine logistic models containing different combinations of factors were created: eight based on a priori hypotheses and one global model, which included all 13 factors (Table 2). The best approximating model was selected using Akaike’s Information Criterion corrected for small sample sizes (AICc; Anderson, 2008; Burnham and Anderson, 2002). Wald’s chi-square tests were used to test for factor significance. A factor was considered significant if p < 0.05. The relative importance of factors was determined by summing the Akaike weight of the models containing these factors. The factor with the highest summed Akaike weight was considered the most important explanatory factor (Burnham and Anderson, 2001).

RESULTS

Gopher tortoise burrow site selection was influenced by both physical and biological factors at microhabitat and home-range spatial scales. The physical + biological model was the most robust and parsimonious model, and the global model was within 2 AICc units and therefore considered a statistical equivalent of the best model. The two best models contained the same factors except distance to beach access (an anthropogenic factor) and have a combined model weight of 0.997 (Table 2).

Six of 12 factors were statistically significant at α = 0.05, indicating they are good predictors for burrow site selection (Table 3). Of the continuous variables, soil resistance, distance to edge, percentage of herbaceous cover, and number of tortoise burrows were statistically significant. While holding all other factors constant, burrow site selection probability decreased as soil resistance increased (β = −0.93 ± 0.35, Wald χ² = 7.05, p = 0.0079; Figure 3A). Burrow site selection probability also decreased as distance to edge increased (β = −0.07 ± 0.02, Wald χ² = 7.71, p = 0.0055; Figure 3B). In contrast, burrow site selection probability increased as the percentage of herbaceous cover increased (β = 0.04 ± 0.02, Wald χ² = 5.09, p = 0.0241), while other factors were held constant (Figure 3C).

Table 2. Burrow site selection models based on a priori hypotheses for gopher tortoises (n = 198) in the coastal sand dunes of GTMNERR.

<table>
<thead>
<tr>
<th>Model</th>
<th>Factors</th>
<th>K</th>
<th>−2LL</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>w</th>
</tr>
</thead>
<tbody>
<tr>
<td>Physical + biological*</td>
<td>SR SL SA HE GR SV LI CA SO LC TB DE</td>
<td>13</td>
<td>125.14</td>
<td>153.13</td>
<td>0.00</td>
<td>0.5378</td>
</tr>
<tr>
<td>Global*</td>
<td>SR SL SA HE GR SV LI CA SO LC TB DE DA</td>
<td>14</td>
<td>128.14</td>
<td>155.45</td>
<td>0.32</td>
<td>0.4588</td>
</tr>
<tr>
<td>Biological + anthropogenic</td>
<td>HE GR SV LI CA TB DE DA</td>
<td>10</td>
<td>142.88</td>
<td>164.06</td>
<td>10.93</td>
<td>0.0023</td>
</tr>
<tr>
<td>Biological only</td>
<td>HE GR SV LI CA LC TB DE</td>
<td>9</td>
<td>147.55</td>
<td>167.55</td>
<td>13.38</td>
<td>0.0007</td>
</tr>
<tr>
<td>Home range only</td>
<td>SO LC TB DE DA</td>
<td>6</td>
<td>155.10</td>
<td>167.55</td>
<td>14.42</td>
<td>0.0004</td>
</tr>
<tr>
<td>Physical + anthropogenic</td>
<td>SR SL SA SO DA</td>
<td>7</td>
<td>179.76</td>
<td>194.36</td>
<td>41.23</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Microhabitat only</td>
<td>SR SL SA HE GR SC LI CA</td>
<td>9</td>
<td>202.19</td>
<td>221.16</td>
<td>68.03</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Physical only</td>
<td>SR SL SA SO</td>
<td>5</td>
<td>222.84</td>
<td>233.15</td>
<td>80.02</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Anthropogenic only</td>
<td>DA</td>
<td>2</td>
<td>258.72</td>
<td>262.78</td>
<td>109.65</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

* Best models, chosen based on AICc. The AICc is based on −2 log likelihood (−2LL), which is the value of the maximized log-likelihood function of the model factors given the data set, the number of factors (K), and the ΔAICc is the AICc differences relative to the smallest AICc in the model set. SR = soil resistance, SL = soil slope, SA = slope angle, HE = % herbaceous cover, GR = % grass cover, SV = % woody shrubs and vines cover, LI = % litter cover, CA = presence or absence of canopy (>2 m) cover, SO = soil type, LC = land cover type, TB = number of tortoise burrows within a 17-m radius, DE = distance to the nearest edge, DA = distance to the nearest beach access.
Land cover type and distance to edge were the most important factors in determining burrow site selection, followed by percentages of grass, woody scrub and vine, herbaceous, and litter cover, as well as the presence or absence of canopy cover (Tables 2 and 3). Land cover type was the only significant categorical variable. Burrow site selection probability was greater for coastal sand dune habitat than for coastal strand.

**DISCUSSION**

Of the eight *a priori* models, the physical + biological model was the best fitting and the second most complex model, containing all but one of the explanatory variables. The high number of factors in the best fitting model indicated that most factors were considered to have at least some effects on burrow site selection of gopher tortoises and that the selection process is complex and involves multiple spatial scales. In effect, burrow site selection of gopher tortoises in coastal sand dunes was related to land cover type, soil resistance, percentage of herbaceous ground cover, distance to edge, number of tortoise burrows nearby, and angle of slope.

Land cover type, a home-range scale factor, was the most important and significant factor in burrow site selection, indicated by the combined model weight and Wald’s chi-square value, respectively. This was not surprising, because there are only two available land cover types (beach dune and coastal strand) and the majority of gopher tortoise burrows were located in the beach dune. The beach sand dune land cover type has an open canopy and well-draining soil, which promotes the growth of herbaceous plants and allows sunny nesting sites. Previous studies (Boglioli, Michener, and Guyer, 2000; Jones and Dorr, 2004) suggested that canopy closure is one of the main factors negatively influencing the distribution of tortoise burrows. The coastal strand, due to canopy closure, provides little forage for gopher tortoises (combined mean percent coverage for grass and herbaceous plants = 7.29%), and few burrows (4%) were found within closed canopies. Most burrows in the coastal strand were located close to the edge (mean distance to edge = 1.5 m). Gopher tortoises and their burrows were rarely observed in the coastal strand partially due to the low relative detectability of burrows in that habitat (i.e. burrows in the beach dune are more conspicuous). Therefore, it is likely that our model overestimated the relative importance of the beach dune land cover. Most of the coastal strand is

<table>
<thead>
<tr>
<th>Factors</th>
<th>Sum of model weight</th>
<th>$\beta$ (SE)</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>LC†</td>
<td>1.0000</td>
<td>-1.91 (±0.40)</td>
<td>&lt;0.0001***</td>
</tr>
<tr>
<td>DE†</td>
<td>1.0000</td>
<td>-0.07 (±0.03)</td>
<td>0.0055**</td>
</tr>
<tr>
<td>HE</td>
<td>0.9996</td>
<td>0.04 (±0.02)</td>
<td>0.0241*</td>
</tr>
<tr>
<td>GR</td>
<td>0.9996</td>
<td>0.02 (±0.01)</td>
<td>0.0539</td>
</tr>
<tr>
<td>SV</td>
<td>0.9996</td>
<td>0.03 (±0.02)</td>
<td>0.1231</td>
</tr>
<tr>
<td>LI</td>
<td>0.9996</td>
<td>-0.32 (±0.34)</td>
<td>0.3403</td>
</tr>
<tr>
<td>CA</td>
<td>0.9996</td>
<td>0.54 (±0.14)</td>
<td>0.0001***</td>
</tr>
<tr>
<td>TB</td>
<td>0.9993</td>
<td>0.93 (±0.35)</td>
<td>0.0079***</td>
</tr>
<tr>
<td>SR</td>
<td>0.9971</td>
<td>0.71 (±0.38)</td>
<td>0.0659</td>
</tr>
<tr>
<td>SO</td>
<td>0.9967</td>
<td>0.97 (±1.14)</td>
<td>0.3966</td>
</tr>
<tr>
<td>SA</td>
<td>0.9967</td>
<td>-0.01 (±0.01)</td>
<td>0.0121*</td>
</tr>
<tr>
<td>DA</td>
<td>0.4615</td>
<td>—</td>
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</tbody>
</table>

† Most important factor, which has the highest sum of the model weight. ‡ $P$ values are derived from the physical + biological model. * $p = 0.05$, **$p = 0.005$, ***$p = 0.0005$.

SE = standard error, LC = land cover type, DE = distance to the nearest edge, HE = % herbaceous cover, GR = % grass cover, SV = % woody scrubs and vines cover, LI = % litter cover, CA = presence or absence of canopy (>2 m) cover, TB = number of tortoise burrows within a 17-m radius, SR = soil resistance, SO = soil type, SL = soil slope, SA = slope angle, DA = distance to the nearest beach access.
physically inaccessible to humans because of the dense vegetation, and some tortoises use it as shelter from potential predators (i.e., humana). When approached, radio-tagged tortoises would escape toward the coastal strand when a nearby burrow was absent.

Distance to edge was another significant home-range scale factor that influenced burrow site selection. Gopher tortoises were more likely to dig burrows near the edge between beach dune and coastal strand. The edge typically occurred near the climax of the upper dune and was parallel to the elevation gradient. Because elevation and distance to edge were strongly correlated, only one factor was included in the original a priori hypotheses and the corresponding predictive models. Elevation also may be an important factor influencing burrow site selection. The lowest elevation for a burrow site found in the study site was 3.1 m above sea level, whereas the lowest for a random site was 0 m above sea level. Mean depth of gopher tortoise burrows reported in the literature varied from 2 to 4.19 m (Hansen, 1963; Kinlaw and Grasmueck, 2012). Therefore, elevation may be a limiting factor on burrow construction in coastal sand dunes because of the potential for saltwater intrusion into the burrow.

Burrow site selection probability increased as the percentage of herbaceous vegetation cover, which could serve as an indicator of food abundance, measured in the microhabitat scale increased. Gopher tortoises mostly forage within 50 m of their burrow (Auffenberg and Franz, 1982), and most foraging activities are concentrated on areas with high herbaceous ground vegetation. Comparably, earlier work on a tortoise population in coastal scrub habitat suggested a positive correlation between tortoise burrow densities and percentage of herbaceous cover (Breininger, Schmalzer, and Hinkle, 1994). The results of this study suggested that the amount of herbaceous vegetation cover could be a visual cue that gopher tortoises use to select suitable burrow sites.

Gopher tortoises appear to select burrow sites with softer soil, but the exact mechanism they use to determine soil resistance is unknown. At the coastal sand dune site, the soil in the foredune mostly consists of coarse mollusk-shell fragments, whereas the soil in the upper dune consists of finer, smaller-grained sandy soils. Gopher tortoises are prolific burrowers with morphological adaptations that improve burrowing efficiency (Auffenberg, 1966), and it is possible that tortoises are able to differentiate soil textures, soil compaction, and moisture content by the effort it takes to dig a burrow.

The number of tortoise burrows within a 20-m radius of each location correlates positively with the probability of burrow site selection, which is likely an autocorrelation. However, based on radiotelemetry work conducted on 20 adult tortoises at the GTM-NERR study site, gopher tortoises may use multiple burrows concurrently, and the burrow used most frequently was usually located at the center of their respective home range (Lau, 2011). It is unlikely that a tortoise uses only burrows dug by itself inasmuch as multiple gopher tortoises may occupy a single burrow on occasion. An alternative approach (e.g., via experimental manipulation) is needed to determine whether the probability of gopher tortoise site selection is positively correlated with the number of tortoise burrows.

The results of this study are largely consistent with literature reports at upland sites. Jones and Dorr (2004) found that gopher tortoise occurrence in an intensively managed pine plantation was influenced by soil types, total and midstory canopy coverage, and edaphic and vegetative conditions. Active burrow occurrence was related positively to increasing midstory canopy closure and certain soil types. Baskaran, Dale, and Efroymson (2006) modeled gopher tortoise habitat in a five-county region in Georgia. The model they developed predicted gopher tortoise habitat based on burrow associations with land cover type, soil type, topography, and hydrology. Land cover types, soil types, and distances to streams and roads were the most significant predictors in their model (Baskaran, Dale, and Efroymson, 2006).

Anthropogenic disturbances in the form of motorized vehicles, human activities, or introduced predators should not be disregarded, because our knowledge of impacts associated with human disturbance to gopher tortoises is limited. Although our best model did not include anthropogenic factors, the significance of distance to beach access in the global model, which is a statistical equivalent of the best model, approached significance (Wald’s $\chi^2 = 3.71$, $p = 0.054$) and had a positive coefficient estimate ($\beta = 0.00121 \pm 0.00063$), indicating that burrow site selection probability increased farther from the beach access. Based on our observations, burrow density tends to be higher in areas farther from the beach accesses, and most human activities occur within 200 m of the beach accesses. The only other anthropogenic factor measured in this study was distance to road, a factor that was dropped because of high correlations with distance to edge. However, distance to road was found to be a useful predictor of the occurrence of gopher tortoise burrows in another study (Baskaran, Dale, and Efroymson, 2006).

In studies of birds, the presence of symbolic fencing (i.e., an area fenced off by ropes and a sign stating the reasons for restricting access) may correlate positively with the probability of nest site selection, whereas the frequency of human activities may negatively affect habitat selection (Meager, Schlacher, and Nielsen, 2012; Pruner, 2010). Because the quantity and quality of human activities at our study site was comparable to those observed in Meager, Schlacher, and Nielsen’s study, we hypothesized that habitat selection by tortoises in sand dunes would be similarly negatively affected by human activity. The density of tortoise burrows was considerably higher in the northernmost part of our study site (Figure 2), and based on our observations, the extent of human activities and associated disturbance was least in the same area. In the future, the distribution and frequency of human activities must be taken into the consideration of habitat quality when establishing protected areas or relocation sites for gopher tortoises in coastal areas. In addition, the limited availability of burrow sites in coastal dune habitats suggests that sea level rise could adversely affect tortoise populations by forcing them to abandon dunes and move inland, where habitats are already affected by roads and extensive human occupation. Furthermore, with the tortoises clustering in a narrow strip of habitat in the sand dune, the population may be at a higher risk to local extinction if an outbreak of infectious disease (e.g., upper respiratory tract disease) were to occur.
CONCLUSIONS

The results of this study confirm that burrow site selection of gopher tortoises in coastal habitats is a complex process involving multiple factors. Fine-scale factors that relate directly to the life history of gopher tortoises, such as percentage of herbaceous cover and soil resistance, have significant influences on habitat selection. Gopher tortoises may use visual and physical cues to select burrow sites. Future research should focus on addressing whether coastal vegetative species richness affects burrow site selection, whether tortoises are able to recognize specific vegetative species and choose their burrow sites accordingly, and whether tortoises can determine soil moisture content during burrow site selection, much as sea turtles and diamondback terrapins do when nesting in similar habitats (Burger and Montevecchi, 1975; Garmestani et al., 2000; Wood and Bjorndal, 2000). Our results suggest that coastal gopher tortoise populations require site-specific management because of the linear nature of their available habitat, which restricts locations for burrow construction.

ACKNOWLEDGMENTS

We thank the Gopher Tortoise Council for funding this project. We also thank the staff at GTMNERR, particularly J. Burgess, E. Montgomery, R. Altman, and S. Eastman, for providing logistical support. J. Berish (Florida Fish and Wildlife Conservation Commission, or FWC) and G. Johnston (Santa Fe College) generously donated equipment. In addition, we thank a number of volunteers who provided assistance in the field, particularly A. Arai, S. Harris, R. Lara, I. Skinner, C. Teal, and T. Thomas. University of Florida Department of Wildlife Ecology and Conservation provided graduate assistantship to A. Lau. This research was conducted under FWC permit LSSC-10-0005 and University of Florida Animal Research Committee permit 015-09WEC.

LITERATURE CITED


