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Resource Selection Probability Functions for Gopher Tortoise: Providing a Management Tool Applicable Across the Species' Range

Virginia A. Kowal · Amelie Schmolke · Rajapandian Kanagaraj · Douglas Bruggeman

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Abstract The gopher tortoise (*Gopherus polyphemus*) is protected by conservation policy throughout its range. Efforts to protect the species from further decline demand detailed understanding of its habitat requirements, which have not yet been rigorously defined. Current methods of identifying gopher tortoise habitat typically rely on coarse soil and vegetation classifications, and are prone to overprediction of suitable habitat. We used a logistic resource selection probability function in an information-theoretic framework to understand the relative importance of various environmental factors to gopher tortoise habitat selection, drawing on nationwide environmental datasets, and an existing tortoise survey of the Ft. Benning military base. We applied the normalized difference vegetation index (NDVI) as an index of vegetation density, and found that NDVI was strongly negatively associated with active burrow locations. Our results showed that the most parsimonious model included variables from all candidate model types (landscape features, topography, soil, vegetation), and the model groups describing soil or vegetation alone performed poorly. These results demonstrate with a rigorous quantitative approach that although soil and vegetation are important to the gopher tortoise, they are not sufficient to describe suitable habitat. More widely, our results highlight the feasibility of constructing highly accurate habitat suitability models from data that are widely available throughout the species' range. Our study shows that the widespread availability of national environmental datasets describing important components of gopher tortoise habitat, combined with existing tortoise surveys on public lands, can be leveraged to inform knowledge of habitat suitability and target recovery efforts range-wide.

Keywords Gopher tortoise · *Gopherus polyphemus* · Habitat selection · Habitat suitability · Resource selection probability function · NDVI

Introduction

The gopher tortoise (*Gopherus polyphemus*) is a keystone species of the longleaf pine ecosystem that dominated large parts of the southeastern U.S. before the arrival of European settlers in the region (Frost 1993; Jose et al. 2007). Since then, the species has drastically declined in numbers along with the destruction of its habitat (Diemer 1986). Estimates suggest that the overall tortoise population has been reduced to less than 20 % of its historical size (Diemer 1986; Hermann et al. 2002), and recent surveys show a decline in numbers even on protected lands (McCoy et al.

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Present Address:
V. A. Kowal · D. Bruggeman
Ecological Services and Markets, Inc., 8 Bay Street, Asheville, NC 28801, USA

A. Schmolke · D. Bruggeman (✉)
Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, USA
e-mail: dougbrugg@gmail.com

Present Address:
A. Schmolke
Ecological Modeling Services, 321 NW Harrison Street, Pullman, WA 99163, USA

R. Kanagaraj
Department of Ecological Modelling, UFZ, Helmholtz Centre for Environmental Research - UFZ, Permoser Str. 15, 04318 Leipzig, Germany

2006; Tuberville and Dorcas 2001; Waddle et al. 2006). The species is currently listed as threatened under the Endangered Species Act in the western part of its range (U.S. Fish and Wildlife Service 1990), and is a candidate for listing in the eastern portion of its range (U.S. Fish and Wildlife Service 2011). To protect the species, the U.S. Fish and Wildlife Service has called for the priority identification of high quality habitat (U.S. Fish and Wildlife Service 2012a), and this requires that such habitat be rigorously defined. Translocation of tortoises is also an important conservation tool (Ashton and Burke 2007; Tuberville et al. 2005) and requires that managers have high confidence in the suitability of translocation sites.

The natural habitat of the gopher tortoise is in the deep, sandy soils of the longleaf pine (*Pinus palustris*) ecosystem of the Southeast, characterized by frequent fires, sparse canopy, and abundant herbaceous ground cover (Auffenberg and Franz 1982; Van Lear et al. 2005). The tortoises spend more than 90 % of their time in burrows that they construct in the soil, which aid in thermoregulation and protection from predators (Eubanks et al. 2003). Sandy well-drained soils are essential for burrow construction (Auffenberg and Franz 1982). Ample sunlight is thought to be required for basking, the development of eggs, and to promote the growth of grasses and herbaceous vegetation that are the tortoises' diet (Aresco and Guyer 1999a; Garner and Landers 1981; Landers et al. 1980; MacDonald and Mushinsky 1988).

Although the importance of sandy soils and sparse overstory vegetation are widely recognized (Aresco and Guyer 1999b; Auffenberg and Franz 1982; Diemer 1986), the importance of other landscape characteristics to gopher tortoises remains unclear. Elevation, slope, distance to water, and distance to roads have been suggested to be important to gopher tortoises (Auffenberg and Franz 1982; Baskaran et al. 2006; Eubanks et al. 2003; McCoy et al. 1993), but their importance has not yet been tested in a rigorous way. A previous quantitative suitability model constructed for the species by Baskaran et al. (2006) combined some of these variables with categorical landcover classes to predict burrow occurrence. Though the model is of high accuracy for the site at which it was developed, it relies on landcover classifications that are not easily biologically interpreted and does little to clarify the relative importance of individual site characteristics to the gopher tortoise. Another quantitative study by Jones and Dorr (2004) suggested that soil texture and vegetation density are more important than elevation in determining active burrow locations, but did not consider other more detailed site requirements. Despite many thorough natural history reports from the field, a comprehensive, statistically rigorous, and biologically relevant test of important habitat characteristics has not yet been demonstrated for this species.

Because of the uncertainty regarding these additional habitat variables, current efforts to identify suitable habitat most often make use of soil series and vegetation types alone. This coarse categorical approach can lead to overprediction of suitable habitat. Hermann et al. (2002) conducted surveys for gopher tortoise burrows in areas of highly suitable soils, but found that 64 % of sampled sites did not contain burrows. Similarly, Hoctor and Beyeler (2010) used binary classifications of soil type, landcover classes, and canopy closure to predict potential primary and secondary habitat on a regional scale. The U.S. Fish and Wildlife Service (2011) assessed the results as follows: "There is a noticeable disparity between the apparently large area … of potential gopher tortoise habitat reported [by Hoctor and Beyeler (2010)] and actual numbers of individual tortoises known from populations that have been surveyed." The incongruity evidenced by these two studies may certainly have been affected by factors such as site history: for example, tortoises may be absent from suitable habitat because of past human harvest (Diemer 1986), or due to slow recolonization of newly restored habitat (Ashton et al. 2008). Even if the absence of tortoises from some suitable habitat is assumed, however, the discrepancies between the area of suitable habitat predicted by these studies and the distribution of gopher tortoises there suggests that habitat suitability cannot be captured accurately with soil and vegetation classifications alone.

Further hampering understanding of gopher tortoise habitat requirements is the lack of a comprehensive survey across the species' range. The great majority of land where the tortoise occurs is privately owned (Hoctor and Beyeler 2010), making intensive monitoring difficult (Hermann et al. 2002; Underwood et al. 2012). Many surveys for gopher tortoise burrows have been conducted, however, on public lands throughout the range (e.g., Ashton et al. 2008; Berish et al. 2012; McCoy et al. 2006; Smith et al. 2009; Stober and Smith 2010; Styrsky et al. 2010; Wigley et al. 2012). These intensive small-scale surveys combined with the widespread availability of fine scale remote sensing data describing vegetation and landscape features (Kerr and Ostrovsky 2003) can inform a more detailed understanding of gopher tortoise habitat requirements across the region where it occurs.

Recent advances in remote sensing provide the opportunity for ecologists to use satellite-based indices such as the normalized difference vegetation index (NDVI; Tucker 1979) as a proxy for vegetation productivity. Recent research has shown that NDVI is a useful proxy for linking vegetation dynamics with the distribution, abundance, and dynamics of animal populations, especially in habitat selection studies where NDVI is an effective indicator of vegetation quality (Borowik et al. 2013; Olson et al. 2011; Pettorelli et al. 2011; Ryan et al. 2012; Singleton et al. 2010; Tirpak and Giuliano 2010; Wiegand et al. 2008). NDVI has also been shown to improve the performance of species distribution models that contain climatic and topographic factors (Amaral et al. 2007). Interestingly, no attempt has yet been made to explore the usefulness of NDVI in understanding gopher tortoise habitat requirements. The widespread availability of NDVI data, together with national datasets such as the National Elevation Dataset and the Soil Survey Geographic Database, provides an untapped opportunity to greatly increase understanding of gopher tortoise habitat distribution range-wide.

In this study, we use a rigorous statistical approach to compare the relative influences of different environmental variables on habitat suitability for the gopher tortoise. In addition, we investigate whether broadly available environmental datasets such as NDVI can be used to increase our understanding of habitat selection by gopher tortoise and to identify and prioritize habitats for management initiatives. In collaboration with the U.S. Army installation Ft. Benning and The Nature Conservancy of Georgia's Chattahoochee Fall Line Project, we were able to take advantage of an existing burrow survey and combine it with environmental datasets that are largely available throughout the species' range. We apply an advanced statistical technique in an information-theoretic framework to accomplish two related objectives: (1) to compare the relative importance of various environmental factors to gopher tortoise habitat suitability; and (2) to demonstrate the feasibility of constructing accurate suitability models from data that are readily obtained for use throughout the gopher tortoise range.

Methods

Study Area

Ft. Benning (centered on 32.408°N, 84.823°W) is a 73,800 ha U.S. Army installation that spreads across portions of Muscogee and Chattahoochee counties in Georgia and Russell County in Alabama, in the northern portion of the gopher tortoise range (Fig. 1). The predominantly rolling terrain is highest in the east, with maximum elevations of 220 m above mean sea level (MSL), and lowest in the southwest along the Chattahoochee River (approximately 50 m above MSL). Dominant soils on the installation include Troup, Nankin, and Cowarts series; Norfolk, Lakeland, and Wagram soils are also common on the installation and are occupied by gopher tortoise burrows. Prior to acquisition by the federal government beginning in the 1940s, most of the land comprising Ft. Benning was clearcut and farmed. The installation was subsequently planted with loblolly pine (*Pinus taeda*) and slash pine (*P. elliottii*), which were managed for timber until the 1990s (Causey et al. 2010). Since then, an intensive program of longleaf pine restoration and prescribed burns on a 3-year return interval have gradually improved gopher tortoise habitat quality.

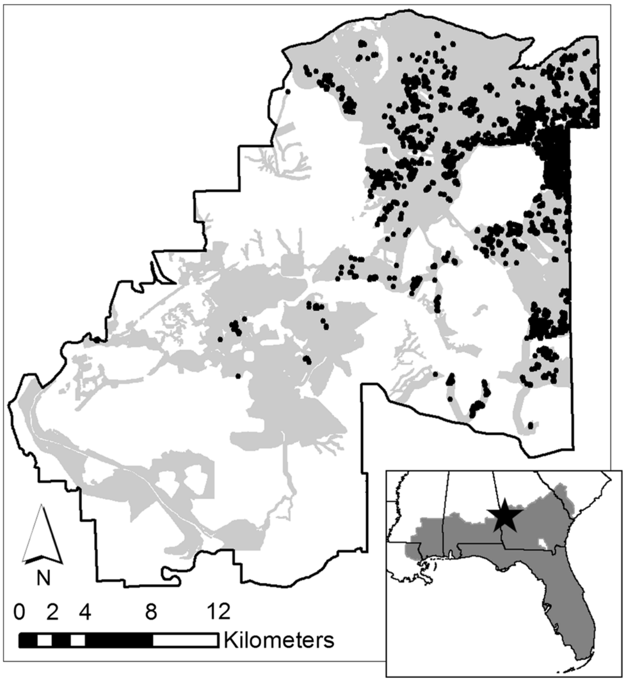

Fig. 1 Locations of active gopher tortoise burrows on Ft. Benning (Causey et al. 2010). The area covered by the burrow survey is shaded in *light gray*. *Inset* current distribution of the gopher tortoise in the southeastern U.S. (adapted from U.S. Fish and Wildlife Service 2012b). *Black star* indicates the location of the study area in Georgia

Study Species

The range of the gopher tortoise stretches across the Coastal Plain of the southeastern U.S. (Fig. 1). The species is named for its habit of creating burrows, which turn the soil and are frequently used by many other species (Alexy et al. 2003; Witz et al. 1991). The tortoises spend more than 90 % of their time inside their burrows, which may exceed 4 m in length and 1 m in depth (Eubanks et al. 2003; Jones and Dorr 2004). Gopher tortoises in Georgia are active from April through October, leaving the burrow periodically to seek mates, forage for food, and bask in the sun (Eubanks et al. 2003; McRae et al. 1981). Mate-seeking by males occurs within home ranges that encompass several burrows, and foraging trips by both sexes are usually completed within 30 m of a burrow (Boglioli et al. 2003; McRae et al. 1981; Smith et al. 1997; Yager et al. 2007).

Species Data

Gopher tortoise burrows can be easily identified by the characteristic mound of sand (the apron) at the burrow entrance and the half-moon shape of the entrance itself (McCoy and Mushinsky 1992). Burrow surveys such as that used in our study provide a quantitative measure of gopher tortoise presence, and can be used to estimate population sizes when combined with occupancy data (Nomani et al. 2008). Burrow locations were taken from a survey of Ft. Benning that was completed between 2008 and 2010 (Causey et al. 2010). The burrow survey covered the large sections of the installation (42 % of total area) that were deemed to be broadly suitable for gopher tortoise in terms of soil and vegetation community composition (Fig. 1). Parallel line transects a maximum of 10 m apart were used in all stands, and gopher tortoise burrows were flagged to prevent re-counting. Burrows were classified according to their activity into active, inactive, and abandoned burrows. Only active burrows (tracks and/or tortoise feces present at the burrow entrance) were included in analysis. Because this survey method does not account for burrow detectability and because the survey did not cover the entire installation, we were careful to ensure that our analytical method did not treat non-detection of burrows in a region as absence, but instead as available areas for gopher tortoise (Lele and Keim 2006; Nomani et al. 2008).

Environmental Variables

We drew important environmental variables from nationwide environmental datasets. We grouped the environmental covariates into variable sets describing topography, soil characteristics, landscape features, and vegetation (Table 1). Topographic variables (elevation and slope) were calculated from USGS Digital Elevation Models (http://seamless.usgs.gov, Gesch 2007). Landscape features (water bodies and paved roads) were extracted from landcover data shared with us by the Engineer Research and Development Center (ERDC) Environmental Laboratory of the Army Corps of Engineers. As part of the Ecosystem Characterization and Monitoring Initiative at Ft. Benning, these data were identified from a Landsat 5 Thematic Mapper image taken in 2007 at 30 m resolution and classified by the ERDC Environmental Laboratory as described in Bourne and Graves (2001). Soil variables, including composition in the top 1 and 3 m of soil and soil drainage index, were calculated from Soil Survey Geographic Database (SSURGO) soil maps for the three counties at 30 m resolution (Soil Survey Staff 2012). The soil drainage index is an ordinal measure of the long-term wetness of a soil, and is derived primarily from a soil's taxonomic subgroup classification (Schaetzl 2012; Schaetzl et al. 2009).

We calculated NDVI from winter and summer scenes taken by Landsat 5 Thematic Mapper in 2008 and 2009

Table 1 Environmental covariates used to build RSPF models for the gopher tortoise

Variable set	Abbreviation	Source
Topography		Calculated from digital elevation model
Elevation (m)	El	
Slope (%)	Sl	
Soil		Calculated from SSURGO soils database
Sand in top 1 m (%)	Sa	
Sand in top 3 m (%)		
Clay in top 1 m (%)		
Clay in top 3 m (%)		
Silt in top 1 m (%)		
Silt in top 3 m (%)		
Soil drainage index (ordinal variable)	DI	
Landscape Features		Landsat 5 Thematic Mapper, 2007
Distance to water (m)	DW	
Distance to paved roads (m)	DR	
Vegetation		Landsat 5 Thematic Mapper, 2008 and 2009
Winter NDVI	wNDVI	
Difference between winter and summer NDVI	dNDVI	

(30 m spatial resolution), coinciding with the dates of the burrow survey. It was necessary to mosaic two scenes together to cover the installation, and to obtain cloud-free images we were forced in some cases to utilize scenes taken several months apart (as is frequently done to cover large areas; Kramer et al. 2003). Therefore, we compiled images taken on 16 November 2009 (path 19, row 37) and 16 January 2009 (path 19, row 38) for winter, and 21 May 2008 (path 19, row 37) and 5 May 2008 (path 19, row 38) for summer. Visual inspection of the imagery confirmed no obvious differences between mosaicked scenes due to large separations in time. We obtained cloud-free, radiometrically and geometrically corrected images from the USGS Earth Explorer data repository (http://earthexplorer.usgs.gov). We corrected the images for atmospheric interference using the dark object subtraction method of Chavez (1988) implemented in the landsat package for R (Goslee 2011), with correction coefficients from Chander et al. (2009). Following atmospheric correction of each band, we calculated NDVI from bands 3 and 4 (i.e., red and near infrared reflectance bands) and combined adjacent scenes to achieve full coverage of the installation.

Because gopher tortoises are generally associated with pine forests (Auffenberg and Franz 1982), evergreen and deciduous vegetation are expected to have differing impacts on habitat suitability. Winter NDVI primarily reflects evergreen vegetation, and on Ft. Benning it is strongly positively associated with pine basal area (Online Appendix 1). We calculated the difference between winter and summer NDVI to capture the deciduous fraction of vegetation (McDonald et al. 2007), which on Ft. Benning is strongly associated with hardwood basal area and midstory vegetation (Online Appendix 1). To evaluate the ability of these data to describe forest composition on Ft. Benning, we estimated the relationship between NDVI and forest metrics, including pine and hardwood basal area, midstory and herbaceous vegetation, that were collected on the ground but only available in restricted areas (Online Appendix 1).

We resampled all environmental variables to align at a pixel size of 30 m (0.09 ha per grid cell) using the nearest neighbor method in ArcGIS 10 (ESRI 2011). This spatial resolution is biologically relevant to the gopher tortoise and corresponds to the scale of an individual tortoise foray (Diemer 1992b; Eubanks et al. 2003; Guyer et al. 2012; McRae et al. 1981).

Resource Selection Probability Function

Because it is likely that some burrows were overlooked, as is common in transect surveys (Nomani et al. 2008) and because the burrow survey at Ft. Benning did not cover the entire installation, the absence of gopher tortoises cannot be assumed in areas where no burrows were recorded. We used a logistic resource selection probability function (RSPF; Lele et al. 2012; Lele and Keim 2006) to account for the uncertainty introduced by such a design where absences cannot be confirmed. The logistic RSPF compares environmental conditions at used sites, where the animal was known to be present, with available sites that are drawn at random from the study area and that summarize the "available" resources within the study area. The technique draws from the weighted distribution to give a maximum likelihood estimation of "the probability that a particular resource, as characterized by a combination of environmental variables, will be used by an individual animal" (Lele and Keim 2006).

Because gopher tortoises abandon their burrows at a rapid pace in deteriorating habitat conditions (Aresco and Guyer 1999b), we base our analysis on the assumption that sites containing active burrows are characterized by suitable habitat. Accordingly, we used only active burrows as "used" locations in the RSPF, to more safely assume that measured habitat conditions at burrow locations were suitable for the tortoises. Raster cells (30 × 30 m) including at least one active burrow were defined as used sites, and available sites were drawn at random from the installation. With large numbers of covariates, it is recommended that the number of available sites should substantially outnumber used sites (Lele 2009); we chose to use three times as many available sites as used sites. Thus, a total of 2,197 used sites (active burrow locations that intersected covariate data coverage) and 6,591 available sites were subjected to analysis. Analysis was completed with the "ResourceSelection" package in R (Lele et al. 2012; R Core Team 2012).

Model Selection and Evaluation

We compared the performance of five candidate models that were constructed from combinations of various habitat components (Table 2). We followed an information-theoretic approach for the selection of our candidate models (Burnham and Anderson 2002; Johnson and Omland 2004), because our primary objective was to compare the support received by several *a priori* candidate models on the

Table 2 Candidate models evaluated as predictors of gopher tortoise burrow presence

Model		Variable sets
I	Soil	Soil
II	Vegetation	Vegetation
III	Soil and vegetation	Soil and vegetation
IV	Abiotic	Soil, topography, landscape features
V	Global model	Soil, topography, landscape features, vegetation

For variable set definitions see Table 1 factors that determine tortoise burrow presence at Ft. Benning. Because biological knowledge is used in the process of variable selection for developing *a priori* candidate models, this approach allows one to make biological interpretations of the resultant models. In addition, using this approach the relative levels of support for the competing models can be assessed and inferences can be drawn from the whole set of models (Burnham and Anderson 2002; Johnson and Omland 2004).

The first three of the five candidate models reflect only soil and/or vegetation, the factors most often used to define suitable habitat (Hermann et al. 2002; Hoctor and Beyeler 2010; Kramer et al. 2003), and their combined effect. Elevation, slope, and distances from water and roads have also been suggested as factors in gopher tortoise habitat selection (Auffenberg and Franz 1982; Baskaran et al. 2006; Eubanks et al. 2003). We constructed a fourth model from the combination of soil data with topography and landscape features, i.e., a model based on abiotic data only. The final model is a global model that combines topography, landscape features, soil, and vegetation variables.

We performed a variable elimination procedure by first calculating Spearman rank correlations of all environmental variables in each candidate model block and, when two or more variables were highly correlated ($\rho > 0.7$), removing the variable with weakest bivariate support. We then calculated variance inflation factors (VIF) for each candidate model and when two or more variables showed VIF greater than 3, we eliminated one variable with weakest bivariate support. We used the Akaike information criterion (AIC) to select the best model from the complete set of competing models. We addressed the model selection uncertainty by calculating Akaike weight, which can be interpreted as the probability of the particular model being the best model in the set of candidate models for the observed data (Burnham and Anderson 2002; Wagenmakers and Farrell 2004).

Accuracy of the suitability models was measured using the AUC statistic (Fielding and Bell 1997). The area under the curve (AUC) is calculated from the receiver operating characteristic (ROC) that measures the ability of the model to discriminate recorded presences from recorded absences (Fielding and Bell 1997). In our case, the ROC was used to measure the model's ability to identify the locations that were actually occupied by gopher tortoise as used locations and the remaining locations as available locations. It describes the probability that locations that were classified as used by the model are more likely to be used than the locations that were not actually used (Manlove et al. 2011). AUC values range from 0 to 1; a value of 0.5 indicates a model that classifies cases randomly, while a value of 1 indicates a model that correctly classifies all cases (Fawcett 2006). We also performed a tenfold cross-validation (e.g., Fernandez et al. 2003) to ensure that no over-fitting occurred using the "DAAG" package in R (Maindonald and Braun 2012). In this method, the dataset was divided into ten random subsets and each of the subsets was used once for testing, while the remaining nine subsets were used for model fitting.

The output of the RSPF model consists of a predicted probability of burrow presence for each grid cell of the model coverage. We used the best-performing model to create a map of habitat suitability for gopher tortoise across Ft. Benning.

Results

A total of 5,281 burrows were surveyed on the installation; of these, 2,215 were judged to be active (tracks and/or tortoise feces present at the burrow entrance; Causey et al. 2010). In all, 2,197 active burrows intersected with covariate data coverage and were included in our analysis. All soil composition variables were highly correlated ($\rho > 0.7$), and bivariate regressions showed that percent sand in the top 1 m of soil was a stronger predictor of gopher tortoise burrow presence than clay or silt. Percent sand in 1 m was also a stronger predictor than percent sand in the top 3 m of soil. Therefore, only one soil composition variable, percent sand in the top 1 m of soil, was retained.

The global model, describing soil, vegetation, topography, and landscape features, was the most strongly supported by the data (Table 3). All other models were highly inferior to the global model, with Akaike weights less than 0.001. However, the ranking of the models relative to each other lends some insight into the importance of different components of habitat for gopher tortoise. The abiotic model ranked second among the five candidate models, suggesting that at least within Ft. Benning, the combination of topography and landscape features with soil is more informative than the combination of NDVI and soils data. The latter combination ranked third, and it is not surprising that the combination of soil and vegetation variables is a better predictor of gopher tortoise presence than either soil or vegetation in isolation. The model ranking also shows that our variable set describing vegetation, composed of NDVI variables, was more predictive of burrow presence than soil alone (Table 3).

Evaluation of model performance by AUC ranked models in the same order as AIC. All models scored AUC >0.8, and the global model performed very well with AUC >0.9. Cross validation supported AIC and indicated that models did not over-fit the data, even in the case of the highly accurate global model (Table 3). Table 4 shows detailed results from the global model, including parameter estimates that indicate the strength and direction of burrow

Table 3 Summary of RSPF models for gopher tortoise habitat suitability on Ft. Benning, Georgia

Model		Variables	AIC	Δ_i AIC	Akaike w_i	AUC	CV (%)
I	Soil	DI, Sa	35,246	2,788	<0.001	0.825	78
II	Vegetation	wNDVI, dNDVI	34,806	2,348	<0.001	0.838	76
III	Soil and vegetation	DI, Sa, wNDVI, dNDVI	33,890	1,432	<0.001	0.875	82
IV	Abiotic	El, Sl, DR, DW, DI, Sa	33,354	896	<0.001	0.885	83
V	**Global model**	**El, Sl, DR, DW, DI, Sa, wNDVI, dNDVI**	**32,458**	**0**	**1**	**0.909**	**84**

The best model is in bold type

For variable set definitions, see Table 2. AIC is Akaike's information criterion; Δ_i is $(\mathrm{AIC})_i - (\mathrm{AIC})_{\mathrm{min}}$; Akaike w_i is the Akaike weight; AUC is the area under the curve; CV is the percent of cases accurately predicted in cross validation

Table 4 Parameter estimates for the global model (model V in Table 3) of gopher tortoise habitat selection

Covariate	Estimate	SE	z	P
Intercept	−7.53	0.20	−38.26	<0.001
% Sand in top 1 m	0.06	0.001	42.45	<0.001
NDVI difference	−6.99	0.28	−25.32	<0.001
Distance to roads	0.0005	0.00002	23.30	<0.001
Winter NDVI	−4.77	0.21	−22.97	<0.001
Elevation	0.02	0.001	22.17	<0.001
Soil drainage index	−0.02	0.002	−11.27	<0.001
Distance to water	0.0004	0.00004	9.72	<0.001
Slope	−0.09	0.01	−6.19	<0.001

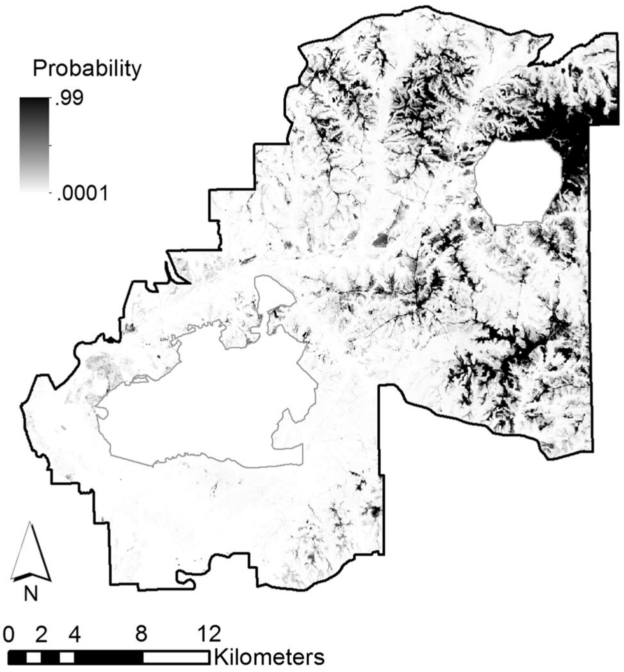

Fig. 2 Predicted probability of gopher tortoise burrow presence on Ft. Benning based on the global model. Model coverage was limited by the availability of soil series data in two large impact areas in the northeast and southwest portions of the installation, outlined in *gray*

association with each environmental covariate. As expected, gopher tortoise burrows were strongly positively associated with percent sand in the top 1 m of soil and strongly negatively associated with NDVI difference, reflecting a strong preference for deep sandy soils and a strong aversion to dense deciduous vegetation (mainly corresponding to hardwood basal area; Online Appendix 1). Tortoise burrows were also very strongly predicted by distance to roads, winter NDVI, and elevation, being more likely to occur in areas distant from paved roads, with sparse coniferous stands and higher elevation. The direction of association and strength of covariates were consistent among all candidate models. For full model results, see Online Appendix 2.

When the global model was used to estimate the predicted probability of gopher tortoise burrow presence across Ft. Benning, predicted probabilities of burrow presence ranged from near 0 to 0.99. The resulting prediction map showed that high-quality habitat is scattered in small pockets primarily in the northeast section of Ft. Benning (Fig. 2). Coverage of the prediction map was limited in two large impact areas in the northeast and southwest corners of the installation, which contain unexploded artillery and are not included in soil surveys.

Discussion

The gopher tortoise is a keystone species that is of great conservation concern throughout its range. Recovery efforts to protect the species rely on detailed understanding of its habitat requirements (U.S. Fish and Wildlife Service 2012a), which have not yet been rigorously defined (Hermann et al. 2002; Hoctor and Beyeler 2010). We applied advanced analytical techniques to a widely available dataset of NDVI and other environmental covariates at Ft. Benning, Georgia to model habitat suitability for this important species. We constructed candidate models to understand the relative importance of various components of habitat for the gopher tortoise, and demonstrated the feasibility of constructing highly accurate habitat suitability models from data that are available for use throughout the species' range. Our study also illustrated for the first time the potential for incorporating NDVI in models of gopher tortoise habitat suitability.

Our use of the logistic RSPF (Lele and Keim 2006) explicitly accounts for the possibility that gopher tortoise burrows were not detected by the survey, a reality that is common to most survey techniques (Nomani et al. 2008) but not usually acknowledged in analysis (e.g., Baskaran et al. 2006; Jones and Dorr 2004). Despite this conservative assumption, the models that we tested showed high accuracy. The AUC of over 0.9 for the global model indicates that it is a very good model (Swets 1988), and shows that the model captures most of the environmental factors that characterize active burrow sites. The strong relative importance of soil sand content and vegetation density evidenced by our models is also consistent with long-standing qualitative knowledge about the tortoises' preferences.

Sandy soils and sparse canopy cover are known to be important to gopher tortoises (Aresco and Guyer 1999b; Auffenberg and Franz 1982; Diemer 1992b), and our analysis supports their primacy. Sand content in the top 1 m of soil and the difference between summer and winter NDVI, reflecting hardwood canopy and midstory vegetation density (Online Appendix 1), are the strongest predictors for gopher tortoise burrow presence on Ft. Benning among the variables that we tested. The high relative importance of variables describing topography and landscape features in the global model, however, emphasize that soil and vegetation are not the only important attributes of habitat on Ft. Benning. Comparisons between alternative models that represent subsets of environmental variables corroborate this point. The reduced model that included soil variables only (model I in Table 3) performed poorly in comparison to the global model. We obtained similar results for the reduced model that was based purely on vegetation data (model II). Although they are obviously important, soil or vegetation variables alone are not sufficient to predict gopher tortoise habitat.

The abiotic model (model IV in Table 3) that included topography, landscape features, and soils, was supported to a much greater degree than the model that combined soil with vegetation (model III). Tortoise burrows were negatively associated with paved roads and water bodies, and significantly associated with higher elevation and lower slope. These results partially contradict earlier findings by Baskaran et al. (2006), who found that tortoise burrows were positively associated with roads but not significantly related to slope. It is not clear whether Baskaran et al. included unpaved roads in their analysis; if so, this may account for the discrepancy with the results of the current study. The sunny, elevated verges of small roads without substantial traffic may be an attractive burrow location when surrounding areas have dense canopy cover (Aresco and Guyer 1999b; Diemer 1986; Hermann et al. 2002). The choice of Baskaran et al. to include abandoned burrows as locations where tortoises were assumed to be present, and their treatment of areas without reported burrows as absences, may also partly explain these differences. Our results also suggest that while other studies have shown that tortoises tolerate some burrow flooding (Means 1982), on Ft. Benning most burrows are located at higher elevations and distant from water bodies.

The abiotic model also provides an excellent opportunity to target areas for habitat restoration. Habitat restoration for gopher tortoises typically consists of the reintroduction of fire or mechanical thinning to decrease canopy cover (Ashton et al. 2008; Breininger et al. 1994; Yager et al. 2007). Such efforts to improve vegetation conditions, in order to be maximally effective, should be carried out in areas that are otherwise of high suitability. The abiotic model presented here could be readily applied to identify such areas, and in general we expect that restoration of sparse canopy cover for gopher tortoises would be most effective when focused in areas with sandy soils, high elevation, low slope, and distance to waterbodies and paved roads.

To the best of our knowledge, this is the first time that NDVI has been applied to habitat modeling for the gopher tortoise, although it has been shown to be relevant to such diverse animals as ungulates (Borowik et al. 2013; Olson et al. 2011; Pettorelli et al. 2006; Ryan et al. 2012), brown bear (Wiegand et al. 2008), birds (Bar-Massada et al. 2012; Singleton et al. 2010; Tirpak and Giuliano 2010), and insects (Levanoni et al. 2011). We found that winter NDVI and the difference between winter and summer NDVI were most strongly associated with pine and hardwood canopy vegetation, respectively; these are known to influence habitat suitability for gopher tortoises (Aresco and Guyer 1999b; Breininger et al. 1994). Because NDVI is an index that describes the interception of solar radiation by photosynthetically active vegetation (Gamon et al. 1995), it is directly biologically relevant to gopher tortoises, who prefer sunny open areas with low canopy cover (Auffenberg and Franz 1982; Aresco and Guyer 1999b; Diemer 1986). Therefore, there is reason to expect that NDVI should be a useful tool for modeling gopher tortoise habitat suitability throughout the species' range. Though our analysis in Online Appendix 1 shows that NDVI does not fully capture ground-level vegetation that may provide forage for tortoises, other studies have suggested that herbaceous ground cover is not a significant driver of habitat suitability when compared to canopy vegetation (Aresco and Guyer 1999b; Jones and Dorr 2004).

The models presented here demonstrate a significant advance in understanding of the relative importance of environmental characteristics to gopher tortoises at Ft. Benning. They also lay the groundwork for a range-wide programmatic effort to define habitat suitability for gopher tortoise across the southeastern U.S. A major impediment to gopher tortoise conservation is the difficulty of identifying suitable habitat across the species' range (U.S. Fish and Wildlife Service 2012a). Methods currently in use rely on soils (Hermann et al. 2002), vegetation (e.g., Kramer et al. 2003), or their combination (e.g., Hoctor and Beyeler 2010; Keller 2005). However, as mentioned previously, these approaches suffer from over-prediction of suitable habitat (U.S. Fish and Wildlife Service 2011). For example, Dissanayake et al. (2012) recently applied the suitability map developed by the Georgia GAP analysis project (Kramer et al. 2003) to identify priority relocation sites for gopher tortoises on Ft. Benning. The suitability map was produced by classification of vegetation types only, and omitted topographic and soils information (Kramer et al. 2003). Consequently several of the relocation sites suggested by Dissanayake et al. (2012) fell in areas of low elevation and lower soil sand content (i.e., areas predicted to be of low suitability according to our analysis).

Gopher tortoise habitat preferences likely vary to some extent across the range. Ft. Benning encompasses a limited range of environmental variation, so we do not suggest that the fitted models that we developed for Ft. Benning should be applied to predict suitability in other areas. Instead, our results provide a framework with which to investigate those preferences explicitly by combining readily available high-quality nationwide environmental datasets with a site-specific burrow survey. Although there has been no comprehensive effort to survey gopher tortoise populations across the region where they occur, many intensive surveys have been carried out within smaller areas throughout the range (e.g., Ashton et al. 2008; Berish et al. 2012; McCoy et al. 2006; Smith et al. 2009; Stober and Smith 2010; Styrsky et al. 2010; Wigley et al. 2012). Such small-scale surveys, in combination with the approach outlined here, can be leveraged to inform knowledge of habitat suitability and target recovery efforts range-wide.

Despite what we see as evidence of great potential utility, the models presented here necessarily omit some important factors. One weakness of our model, as well as those previously derived, is its inability to include the influence of social factors. The proximity to existing burrows may represent an essential factor in tortoises' location choice, because most individuals use several burrows over the course of an active season (Diemer 1992a; Guyer et al. 2012; McRae et al. 1981). Males are known to travel long distances to visit females at their burrows (Boglioli et al. 2003; McRae et al. 1981; Smith et al. 1997), and it has been suggested that females may also play an active role in seeking encounters with males (Guyer et al. 2012; Johnson et al. 2009). Thus, interactions between behavioral aspects of tortoise home range use and environmental variables are likely crucial factors in burrow site selection.

Another component of habitat suitability that we were unable to include with our current approach is the influence of military training. Training activities such as heavy vehicle traffic can compact soil, crush vegetation, collapse burrows, and even cause direct mortality of tortoises (Berry et al. 2006). These activities have likely impacted the gopher tortoise population of Ft. Benning, but they are not reflected in the environmental variables included in our models. It is also possible, however, that some aspects of military exercises are beneficial to gopher tortoises. Areas of heavy military training on Ft. Benning are characterized by increased dominance of pines and decreased overall canopy vegetation density (Dilustro et al. 2002). Unlike the detrimental effects of training activities, we expect that these compatible aspects of military training are reflected in our estimates of vegetation density.

We have shown that powerful suitability models for the gopher tortoise can be constructed with data that are available nationwide. We confirm the importance of soil and vegetation, but our results suggest that these two aspects of habitat are not sufficient to describe suitability. Future efforts to identify priority areas for gopher tortoise conservation, translocation, and habitat restoration should consider elevation, slope, and distance to water bodies and roads in addition to soil and vegetation when possible. Additionally, the method we have demonstrated here provides a ready opportunity to develop more accurate models for gopher tortoise habitat suitability than those that are currently in use. Improved models derived from the combination of soil, topography, landscape features, and remotely sensed vegetation can be fitted with the detailed burrow surveys that have been conducted throughout the species' range. Such models could readily be implemented to inform understanding of the distribution of gopher tortoise habitat range-wide.

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