Am. Midl. Nat. 155:335–351

# Habitat Modeling Within a Regional Context: An Example Using Gopher Tortoise

LATHA M. BASKARAN[1], VIRGINIA H. DALE AND REBECCA A. EFROYMSON
*Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee 37831*

AND

WILLIAM BIRKHEAD
*Department of Biology, Columbus State University, Columbus, Georgia 31907*

ABSTRACT.—Changes in habitat are often a major influence on species distribution and even survival. Yet predicting habitat often requires detailed field data that are difficult to acquire, especially on private lands. Therefore, we have developed a model that builds on extensive data that are available from public lands and extends them to surrounding private lands. This model is applied for a five-county region in Georgia to predict habitats for the gopher tortoise (*Gopherus polyphemus*), based on analysis of documented locations of gopher tortoise burrows at the Fort Benning military installation in west central Georgia. Burrow associations with land cover, soil, topography and water observed within the military installation were analyzed with binary logistic regression. This analysis helped generate a probability map for the occurrence of gopher tortoise burrows in the five-county region surrounding Fort Benning. Ground visits were made to test the accuracy of the model in predicting gopher tortoise habitat. The results showed that information on land cover, soils, and distances to streams and roads can be used to predict gopher tortoise burrows. This approach can be used to better understand and effectively carry out gopher tortoise habitat restoration and preservation activities.

## INTRODUCTION

Land-use practices and land cover affect environmental conditions within a local area and the ability of an area to support particular species can be influenced by conditions of the surrounding region (*e.g.,* Steffan-Dewenter, 2003; Winton and Leslie, 2004). Habitat for a species of concern and the resources required by its population can be improved or compromised by the environmental conditions of a landscape (*e.g.,* Hanowski *et al.*, 1997; Collinge *et al.*, 2003; Cederbaum *et al.*, 2004; Donnelly and Marzluff, 2004; Moffatt *et al.*, 2004). Understanding and predicting how the pattern of land use and land cover affects habitat at multiple scales is a key concern of conservation biology (Saunders *et al.*, 1991).

Predicting the presence of suitable habitat across diverse land ownerships can be a challenge. Such predictions often rely on detailed field data, but collection of such data can be expensive and time consuming, and so habitat information may not be readily available. The Gap Analysis Program of the U.S. Geological Survey provides an assessment of the degree to which native animal species and natural communities are, or are not, represented on existing conservation lands (*e.g., see* Pearlstine *et al.*, 2002), but private lands also offer hospitable habitat (Scott *et al.*, 2001). However dealing with different ownerships can raise a variety of management issues (*e.g.,* Thompson *et al.*, 2004). Often data collected on

[1] Corresponding author: Environmental Sciences Division, Oak Ridge National Laboratory, P.O. Box 2008, 1 Bethel Valley Road, Oak Ridge, Tennessee, 37831. Telephone: (865) 576-1397; FAX: (865) 574-4665; e-mail: baskaranl@ornl.gov

public land may be detailed, but little may be known about conditions on private lands. Therefore, we developed a procedure that uses the detailed information about species and their habitat on public land (in this case a military base) and show how it can be extended to private land and thus incorporate the diversity of ownerships across a region.

Military installations and their environs offer a special case for examining how activities on the land can affect habitat, because these lands can have ecological importance and the military adopts a proactive management approach. Military installations support a number of endangered and threatened plant and animal species (Leslie *et al.*, 1996). In many cases, the military installations support more native species, and especially more rare species, than the surrounding lands (Groves *et al.*, 2000; NatureServe, 2004). Some reasons for this relative abundance of native and rare species on military lands as compared to the surrounding region likely lie in differences in land cover and land-use practices. Department of Defense lands provide oases for numerous species, through protection from the widespread urban, exurban, and rural development. This phenomenon is also observed on many Department of Energy lands (Mann *et al.*, 1996; Dale and Parr, 1998) and park lands (*e.g.*, Rivard *et al.*, 2000).

Typically, the military collects considerable information about rare species within their installations; yet protection of species requires understanding the distribution of habitat for rare species inside and outside the installation boundaries (Efroymson *et al.*, 2005). Therefore, we have developed a procedure for using the detailed information on species within an installation to predict habitat in the surrounding region. The procedure is illustrated using data on gopher tortoise (*Gopherus polyphemus*) from the Fort Benning military installation in west central Georgia, United States. Fort Benning maintains several rare or threatened plant and animal species, including the gopher tortoise. The procedure described here could be adapted for use in any situation where there are local habitat data, yet the natural resources management questions are regional.

Gopher tortoises are found in the southeastern United States, from southern South Carolina to southeastern Louisiana (Auffenberg and Franz, 1982). Their typical habitat includes longleaf pine (*Pinus palustris*) forests, sandhills, scrub oak woodlands, xeric hammocks, pine flatwoods, dry prairies, coastal grasslands and dunes and mixed hardwood-pine communities where the soils have a high sand content (Auffenberg and Franz, 1982; Kushlan and Mazzotti, 1984; Diemer, 1986). They prefer open-canopied and sparse understory regions. The name *gopher tortoise* derives from their tendency to dig deep burrows. The gopher tortoise is considered to be a keystone species, and up to 300 other species have been recorded in their burrows (Hubbard, 1893; Lago, 1991; Frank and Layne, 1992; Wilson *et al.*, 1997; Alexy *et al.*, 2003).

The gopher tortoise is federally listed as threatened in its western populations in Louisiana, Mississippi and western Alabama, and is listed as threatened by the state of Georgia. Over 80% of the population has been lost in past decades due to activities such as farming, fire suppression and habitat degradation (Hermann *et al.*, 2002). However, gopher tortoises are locally abundant on suitable soils at Fort Benning, where more than 8000 burrows were identified between 1996 and 1999 (USFWS, 1999).

Land use and land-management practices are important determinants of gopher tortoise burrows (Russell *et al.*, 1999; Hermann *et al.*, 2002; Jones and Dorr, 2004) and their abandonment (Aresco and Guyer, 1999). Farming and urban development, habitat changes, such as forest conversions, habitat loss and human exploitation, have a negative impact on the survival of this species (Wilson *et al.*, 1997; Aresco and Guyer, 1999). The impact of the proximity of gopher tortoise burrows to roads and streams is not clear. The presence of roads with heavy traffic can be detrimental to a sustainable gopher tortoise population because of road kills (Auffenberg and Franz, 1982). In a number of cases, however, gopher tortoises are found close to roads (Hal Balbach, U.S. Army Engineer Research and Development Center, pers. comm., 22 March 2004). Studies by Kushlan and Mazzotti (1984) show that gopher tortoises avoid burrowing in areas subject to flooding or overwash. However, other findings imply that the tortoises use moist burrows near riverbeds during winter months (McRae *et al.*, 1981; Means, 1982).

Understanding gopher tortoise habitat is important for the conservation and preservation of the species. Gopher tortoises can benefit from management that is focused on ecosystem processes and habitat structure (Hermann *et al.*, 2002). Management efforts may include restoration of the longleaf pine ecosystem, habitat maintenance through controlled burning and establishment of reserves (Landers *et al.*, 1995; Wilson *et al.*, 1997; Eubanks *et al.*, 2003). Several populations of gopher tortoises have also been relocated from their current declining habitat to potentially sustainable habitats. During relocation, repatriation, and translocation of species, it is important to characterize biological, habitat, biophysical and demographic constraints (Dodd and Seigel, 1991; Witz *et al.*, 1991). Hence, a good understanding of the potential habitat is vital.

Within the study area, burrows are predominantly located in areas supporting longleaf pine stands and a relatively sparse canopy cover and understory. However, vegetation structure is not sufficient to predict potential gopher tortoise habitat, since land cover, which mostly indicates current vegetation, does not indicate the long-term sustainability of a species (Mann *et al.*, 1999). Other factors such as soil and terrain type also contribute to the occurrence and persistence of a population. Gopher tortoises are known to inhabit well-drained sandy soils (Auffenberg and Franz, 1982) and to avoid clay soils, probably due to the difficulty of burrowing (Jones and Dorr, 2004). At a large geographical scale, topographic relief has also been found to be an important factor affecting the burrow distribution, with burrows oriented in the primary direction of relief (McCoy *et al.*, 1993).

The purpose of our study was to develop a means of predicting gopher tortoise habitat in a five-county region surrounding Fort Benning. Animal habitat is a better factor to model than animal location, since it is more consistent over time than demographics (Aebischer *et al.*, 1993). Furthermore, the number and density of gopher tortoise burrows can be used to estimate numbers of tortoises, provided that a reliable conversion factor can be determined (McCoy and Mushinsky, 1992). Our model of habitat for gopher tortoises was based on the presence of burrows within Fort Benning and then field-tested for the five-county region surrounding the installation.

## METHODS

### STUDY AREA AND DATA

Our study was conducted on a five-county region (Harris, Muscogee, Chattahoochee, Marion and Talbot) containing Fort Benning (Fig. 1). Much of this land is forested or used for agriculture. This region also includes the city of Columbus and several other smaller communities. Human activity in this region has been intense and of long duration (Kane and Keeton, 1998; Dale *et al.*, 2005). For example, longleaf pine forests have been declining for decades, and only 4% of the original pine forest remains in the southeastern United States (Noss, 1989).

At Fort Benning, the military has put much effort into identifying locations of burrows to avoid destruction of gopher tortoise habitat. Locations of gopher tortoise burrows from 1996 to 1999 were collected in a survey undertaken for the U.S. Fish and Wildlife Service (USFWS, 1999). This survey identified about 8100 active, inactive and abandoned

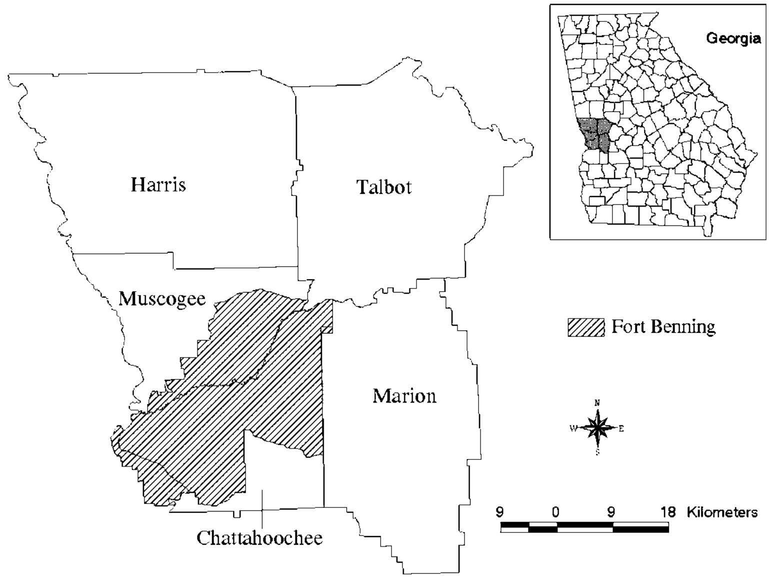


FIG. 1.—Map of the five-county study region in Georgia

burrows. Active burrows were defined as those currently maintained by a gopher tortoise. Inactive burrows were those that have been unoccupied for some time but still had a clear burrow entrance. Abandoned burrows were defined as unoccupied burrows where the entrance was covered by plants and nearly closed (Auffenberg and Franz, 1982). All three types of burrows were considered in our analysis, because it was important to identify potential habitats.

To identify resources and other factors vital for the gopher tortoise burrow, the probability of a resource unit (habitat variable) being used had to be determined. Resource selection functions provided a theoretical framework to identify such probabilities of use (Alldredge *et al.*, 1998; Boyce *et al.*, 2002; Manly *et al.*, 2002). In our study, the data on presence and absence of burrows in Fort Benning were used as the basis to model the resource selection function. One thousand locations of burrow presence and 1000 locations of burrow absence were selected. Since all the locations with burrows had been identified in Fort Benning from extensive surveys by the U. S. Fish and Wildlife Service, the remaining areas were assumed to be non burrow locations. The non burrow locations were randomly selected such that they were at least 90 m from the burrow locations to avoid any overlap with gopher tortoise habitats. Hence a random selection of locations with burrows and locations without burrows helped to obtain unbiased estimates of coefficients and, in turn, probabilities of use (Keating and Cherry, 2004).

The variables considered for our gopher tortoise burrow model were distance to roads, distance to streams, slope, soil texture, percentage of clay in the upper soil layer (0 to 5 cm) and 12 land-cover categories (including transportation corridors, utility corridors, low- and high-intensity urban areas, clear-cut areas, deciduous forests, evergreen forests, mixed forests, pasture land, areas planted in row crops, golf courses and forested wetlands) (Table 1). These factors were identified through a review of existing literature that examined attributes associated with gopher tortoise behavior and life-history characteristics, such as

TABLE 1.—Variables entered into the model

| Type | Variable | Habitat characteristics |
|---|---|---|
| Terrain variable | Slope | Terrain orientation and slope can influence gopher tortoise burrows. |
| Distance variables | Distance to streams | Gopher tortoises are known to burrow in moist soils; they also avoid wetlands and regions close to streams. |
| | Distance to roads | Roads can be detrimental to gopher tortoises because of the increased chances of road kills by vehicles (Auffenberg and Franz, 1982). However, land cover adjacent to roads may also be favorable for digging and hence for gopher tortoise habitation. |
| Soil variable | Percentage of clay in the first soil layer | Gopher tortoises avoid clayey regions to make burrows because of the difficulty in digging in these regions. |
| Land–cover variables | Transportation land-cover class | In addition to the distance-to-roads variable, the transportation land cover variable is included, since gopher tortoises may be present very close to the roads and within the 30-m land cover pixel extent. |
| | Utility swaths | Clearings for transmission lines may be suitable gopher tortoise habitats because of the absence of dense vegetation that prohibits sunlight. |
| | Clear-cut regions | Clear-cut regions and regions with sparse vegetation could support gopher tortoises because of their open-canopy landscape. |
| | Deciduous, evergreen, and mixed forests | Forests without closed canopies and thick understories may be suitable gopher tortoise habitat. But dense forests may decrease the amount of sunlight reaching the ground and may limit the herbaceous understory required for gopher tortoise foraging (Hermann *et al.*, 2002). |
| | Pastures and non tilled grasses; row-crop fields | Cultivated areas, grazed lands, mowed lands, and pastures can accommodate gopher tortoises (Hermann *et al.*, 2002). |
| | Low-intensity urban | Some low-intensity urban areas such as farms or house yards could support gopher tortoise burrows. |
| | High-intensity urban | Gopher tortoise burrows are not expected in dense urban areas. |
| | Golf courses | Golf courses may not be good gopher tortoise habitats because of the frequent maintenance and disturbance in such locations. |
| | Forested wetlands | Gopher tortoises usually avoid wetlands (Kushlan and Mazzotti, 1984) |

the need for open areas for basking and movement, appropriate forage and suitable soil and topography for digging burrows (Diemer, 1986; Wilson *et al.*, 1997; Boglioli *et al.*, 2000; Hermann *et al.*, 2002). Distance-based measures have been found to be useful in quantifying habitat use for animals (Conner *et al.*, 2003). However, the association between gopher tortoise burrows and distances from roads and streams is not clear (McRae *et al.*, 1981; Auffenberg and Franz, 1982; Means, 1982; Kushlan and Mazzotti, 1984). Thus, the effects of distances to roads and streams were evaluated in our analysis. Burrows can occur very close to roads, such as on road edges. Hence, a land-cover category indicating transportation features was included to accommodate the probability of gopher tortoises on road, railroad, trail and runway land-cover pixels.

Data sets describing land cover, soils and distance to roads and streams were analyzed in conjunction with data on burrow locations. Soil characteristics, such as percentage of clay, were obtained from the State Soil Geographic (STATSGO) database (Miller and White, 1998). The land-cover categories were derived from classification of a 1998 Landsat TM image (Natural Resources Spatial Analysis Laboratory, University of Georgia). The spatial resolution of the remotely sensed land cover was 30 m. Hence, all the analyses were carried out at that resolution. The habitat model was developed with a geographic information system (GIS) to examine the regional distribution of gopher tortoise habitat.

## ANALYSIS

The prediction of the locations of gopher tortoise burrows (active, inactive and abandoned) based on physical conditions and land cover was done using binomial logistic regression in SPSS®. Logistic regression describes the relationship between a set of continuous and discrete independent variables and a binary or dichotomous outcome (Hosmer and Lemeshow, 1989; Trexler and Travis, 1993). With a random sampling design in a use—non use scenario, logistic regression can be used to establish the resource selection functions and variable relationships (Keating and Cherry, 2004).

Since the land-cover maps were available in 30-m resolution, all the variables were converted to the same spatial resolution. The land-cover classes were each considered separately as binary variables to be able to leave out classes, such as water, that were not useful in the analysis. The land-cover pixels were unique and did not overlap. The percentage of clay was used as an explanatory variable. The percentage of sand was not used because it is related to the percentage of clay. The distance variables were generated by calculating the nearest distance to a road or stream for every pixel. This approach was essentially a gridded contour of the distance to the roads or streams at 30-m intervals.

For each gopher tortoise burrow location used to build the model, corresponding explanatory variable features were extracted using GIS functionalities such as *spatial analyst*, that aid in obtaining the pixel value at a point. The variables observed at the model building points, *i.e.,* the burrow locations, were entered into the logistic regression analysis. During iterations of the model, some variables that did not significantly contribute to the variance explained were removed using stepwise backward logistic regression, which drops variables based on the order of their significance using the likelihood-ratio test (Hosmer and Lemeshow, 1989). Backward logistic regression was used instead of forward logistic regression, since the latter may fail to include important variables (Leung and Tran, 2000). The variables removed were slope, low- and high-intensity urban areas, golf courses and forested wetlands. For the slope variable, non linear relationships (square and cubed values of slope) were tested for their impact in the model. However they were found to be insignificant in effectively modeling the habitat of the tortoise.

### ACCURACY ASSESSMENT WITHIN FORT BENNING

The model was tested by examining predictions of gopher tortoise burrow sites within Fort Benning against 1000 burrow locations that had been randomly selected for the analysis and then removed from the data set that was used to develop the model. A cut-off or threshold, which is the critical amount of evidence favoring the presence of the burrow (Swets, 1988), was used for assigning a modeled location to a burrow or non–burrow category. Accuracy assessment techniques are often used for validating maps produced from remote sensing as compared with in situ data (*e.g.*, Foody, 2002; Ramsey *et al.*, 2002). Based on the observed and predicted data, the sensitivity, specificity and overall accuracy of the model were determined. Sensitivity, or the true positive fraction, and specificity, or the true negative fraction, measure the proportion of sites at which the observations and predictions are in agreement (Pearce and Ferrier, 2000). In addition to these indices that evaluate the discrimination performance of wildlife habitat models, an accuracy measure that is unbiased to the cut-off used to classify the outcome was required. The receiver operating characteristic (ROC) curve, which is a plot between the false positive fraction (1 minus the specificity) and the sensitivity at various cut–offs, provided such an accuracy measure (Swets, 1988). The area under the ROC curve (AUC) is an indication of the accuracy of the model. AUC values of 0.5 to 0.7 indicate poor models, 0.7 to 0.9 are reasonably good models and greater than 0.9 indicates high accuracy models (Swets, 1988).

### VALIDATION OF THE MODEL IN THE REGION AROUND FORT BENNING

Following the accuracy analysis within Fort Benning, the regression model was used to predict gopher tortoise habitat for the five-county study region around Fort Benning. This application was done in ArcView 3.1® using *spatial analyst* and *grid modeling* functionalities.

The ability of the model to correctly predict the presence of burrows outside Fort Benning was tested by field visits to a sample of sites that the model predicted to be gopher tortoise habitat at different levels of probability. Five categories of probabilities were divided equally based on their numeric range, from of 0 to 1 (Fig. 2). Site selection for testing was done by stratifying the study region outside Fort Benning into blocks that represented the major soil types of the area. Random points were located within each of these blocks. The points selected also occurred in all the probability categories of the predicted model. The sites were located using a global position system (GPS) and visited in May 2004. At each location the surrounding $30 \times 30$ m area was visually scanned for burrows or evidence of tortoises such as tortoise track marks. Land cover and land use in the local area were also recorded. Using the data obtained from the ground survey, the validity of the model to predict burrows was tested. The observed and predicted data were compared using accuracy statistics.

## RESULTS

Several iterations of the logistic regression model were considered using different methods for selecting input variables. The backward stepwise logistic regression model which had the smallest (–2)log likelihood value and maximum percentage of regions correctly classified, was selected for the final model (Table 2). The Wald statistic provided the statistical significance of each coefficient (B) in the model. The percentage of clay was the most significant variable present, followed by the land-cover category of pastures and the

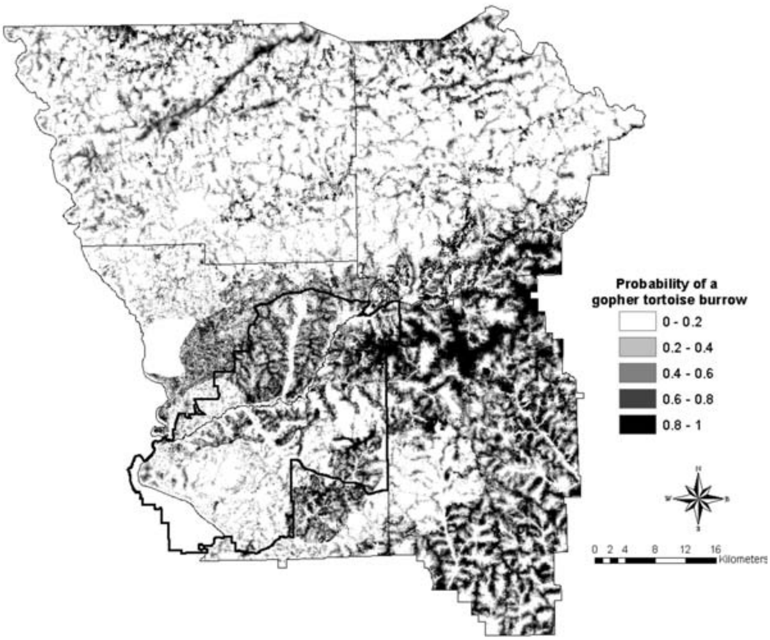


FIG. 2.—Predicted gopher tortoise habitat distribution map for the five-county study region

land-cover category of clear-cut or sparse regions. The equation of the model was summarized as

$$\text{Probability of a gopher tortoise burrow} = \frac{Exp(A)}{1 + Exp(A)}, \tag{1}$$

where

$$A = \begin{pmatrix} (Dist2strms * 0.004) - (Dist2rds * 0.003) - (\%\ clay * 0.152) \\ + (Transportation * 1.751) + (Utilityswaths * 2.327) \\ + (Clearcut * 2.684) + (Decid * 1.913) + (Evergreen * 1.004) \\ + (Mixed * 1.8) + (Pasture * 3.987) + (Rowcrop * 2.435) - 0.757 \end{pmatrix}. \tag{2}$$

Parameters are defined in Table 2.

### ACCURACY ASSESSMENT OF THE MODEL WITHIN FORT BENNING

The sensitivity and specificity of the model were 77.4% and 78.9%, respectively (Table 3). Overall accuracy of the model was 78.15%. To identify the threshold independent accuracy, the ROC curve was plotted (Fig. 3). The area under the curve was 0.858. Since this value is within the reasonable model range (0.7 to 0.9), and very close to the very good model threshold (greater than 0.9), the model is considered to be good for prediction within Fort Benning.

TABLE 2.—Variables in the backward stepwise regression model for gopher tortoise burrow locations

| Variable | Explanation | B* | SE* | Wald* | Exp (B)* |
|---|---|---|---|---|---|
| Dist2strms | Distance to streams | 0.004 | 0.000 | 65.738 | 1.004 |
| Dist2rds | Distance to roads | −0.003 | 0.001 | 33.808 | 0.997 |
| %clay | Percentage of clay in the first soil layer | −0.152 | 0.011 | 178.898 | 0.859 |
| Transportation | A land cover category consisting of roads, railways and runways | 1.751 | 0.303 | 33.409 | 5.761 |
| Utility swaths | Vegetated linear features maintained for transmission lines and gas pipelines | 2.327 | 1.159 | 4.030 | 10.246 |
| Clearcut | Areas that have been clear-cut within the past 5 years, as well as areas of sparse vegetation | 2.684 | 0.297 | 81.627 | 14.643 |
| Decid | Deciduous forests, which contain at least 75% deciduous trees in the canopy, deciduous mountain shrub/scrub areas, and deciduous woodlands | 1.913 | 0.284 | 45.404 | 6.776 |
| Evergreen | Forests with at least 75% evergreen trees, pine plantations, and evergreen woodlands | 1.004 | 0.269 | 13.972 | 2.729 |
| Mixed | Forests with mixed deciduous/ coniferous canopies, natural vegetation within the fall line and coastal plain ecoregions, mixed shrub/scrub vegetation, and mixed woodlands | 1.800 | 0.276 | 42.418 | 6.048 |
| Pasture | Pastures and non tilled grasses | 3.987 | 0.357 | 124.857 | 53.915 |
| Row crop | Agricultural row crops, orchards, vineyards, groves, and horticultural businesses | 2.435 | 0.562 | 18.793 | 11.416 |
| Constant | Constant in the logistic regression equation | −0.757 | 0.279 | 7.349 | 0.469 |

* B = Beta coefficient; SE = standard error; Wald = Wald statistic; Exp (B) = exponential function of B

VALIDATION OF THE MODEL FOR THE FIVE-COUNTY REGION

A map (Fig. 2) of the predicted probabilities for the presence of gopher tortoise burrows in the region was created to assess how well the model performed in predicting gopher tortoise habitat outside Fort Benning. Reference data were collected on 42 sites in the study area. The burrow status on the ground was compared to the model-predicted probability (Table 4). The land use recorded in the region helped in understanding the reasons for varying predictions.

TABLE 3.—Observed and predicted number of gopher tortoise burrows at Fort Benning

| | Observed | | |
|---|---|---|---|
| Predicted | No burrow | Burrow | Total |
| No burrow | 789 | 226 | 1015 |
| Burrow | 211 | 774 | 985 |
| Total | 1000 | 1000 | 2000 |

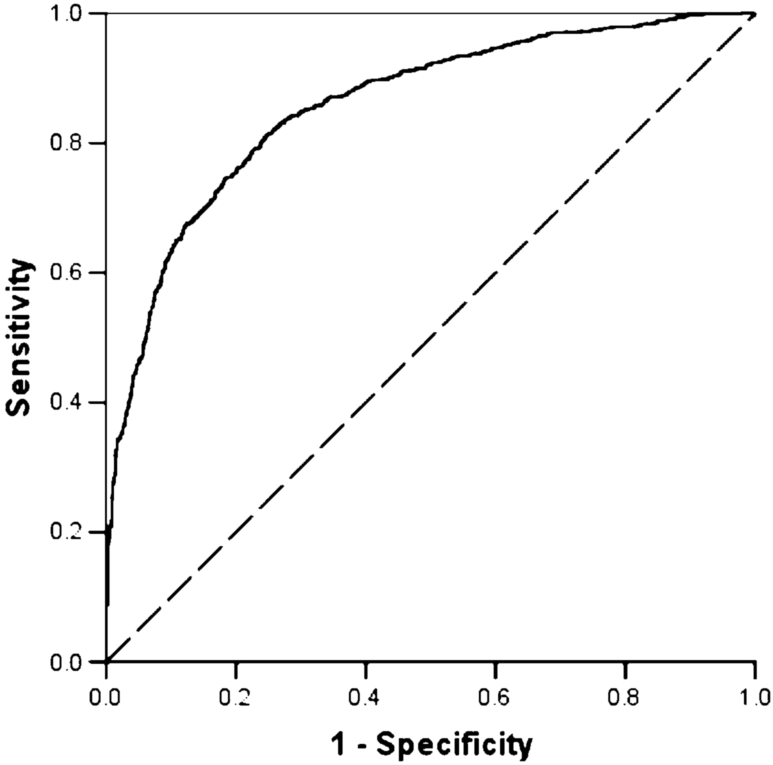


FIG. 3.—Receiver operating characteristics (ROC) curve for model prediction within Fort Benning

The difference between the predicted measures and the actual conditions in parts of the five-county region was tested using different cut–off values (Fig. 4). At a cut–off of 0.5, which is the typical center point threshold, the sensitivity of the model, which indicates the positive predictive power of a model, was 100%. But the specificity or negative predictive power of the model was 48.57%, which showed that the model overestimated possible gopher tortoise habitats. At a cut–off of approximately 0.8, the overall accuracy, the burrow presence and burrow absence predictive values were maximum (Fig. 4). The sensitivity, specificity and overall accuracy of the model at that threshold were 71.43%, 80% and 78.57, respectively (Table 5). Hence, a cut–off value of 0.8 was considered the appropriate threshold for this analysis.

## DISCUSSION

Regression analysis provided an appropriate means to determine the influence of environmental variables on the ability to predict gopher tortoise habitat. In a logistic regression, the beta (B) coefficient does not provide much direct interpretation of the effect of each variable on the probability of the dependent variable occurrence. However, the exponential function of B [Exp(B)] indicates a change in odds of the probability of occurrence of the dependent variable.

TABLE 4.—Data collected in regions around Fort Benning listed by predicted probability

| Location number | Burrow | Burrow status | Predicted probability | Land use |
|---|---|---|---|---|
| 1 | Present | Two abandoned burrows | 0.96 | Native sandhill habitat, mixed pine, xeric |
| 2 | Absent | Not a good habitat—no foraging vegetation | 0.95 | Lawn, open area (pasture) |
| 3 | Present | Two active burrows | 0.94 | Power lines (utility lines) |
| 4 | Present | One active burrow | 0.92 | Sand pine forests, open, savannah-like canopy |
| 5 | Present | Two abandoned burrows | 0.91 | Native sandhill habitat, open canopy |
| 6 | Absent | Possible habitat | 0.85 | Planted longleaf and loblolly pine forests |
| 7 | Absent | Not a good habitat—human intervention | 0.77 | Pasture, houses (lawns), mowed fields |
| 8 | Absent | Possible habitat | 0.69 | Hardwood to the north, planted pine to the south |
| 9 | Absent | Possible habitat | 0.68 | Planted pine to the southeast, thinned planted pine to the northeast |
| 10 | Present | Two abandoned burrows | 0.56 | Young longleaf pine forests with sparse understory |
| 11 | Absent | Not a good habitat | 0.48 | Edge of planted pine and riparian hardwood |
| 12 | Absent | Not a good habitat—wetland | 0.37 | Mesic hardwood forests, next to two ponds |
| 13 | Absent | Not a good habitat—wetland | 0.29 | Wetland with a creek nearby and also next to riparian hardwood forests |

## INFLUENCE OF VARIABLES

The effect of each variable on the occurrence of a gopher tortoise burrow can have several interpretations, based on our model. The probability of finding a burrow decreased as the clay percentage in the top soil layer increased. This result is logical, because gopher tortoises require well-drained sandy soils to dig burrows. Regions with clay soils are not suitable habitat because of respiratory limitations and difficulty of burrowing (Wilson *et al.*, 1997).

The probability of a burrow being present increased when the land cover was a transportation corridor; a utility swath; a clear-cut or sparse region; deciduous, evergreen or mixed forest; a pasture, or a row crop. This effect was most significant for pastures and clear-cut or sparse regions. This result is in agreement with a previous observation from scrub and flatwoods in Florida that gopher tortoise habitat is associated with high herbaceous cover providing food for tortoises (Breininger *et al.*, 1994).

Contrary to the expectation that road-influenced mortality causes a decline in gopher tortoise population, the probability of finding a burrow decreased as the distance from the road increased. This association of gopher tortoises with roads occurred at Fort Benning but was also observed elsewhere, such as at Camp Shelby, MS (Hal Balbach, U.S. Army Engineer Research and Development Center, pers. comm., 22 March 2004). Such a pattern was

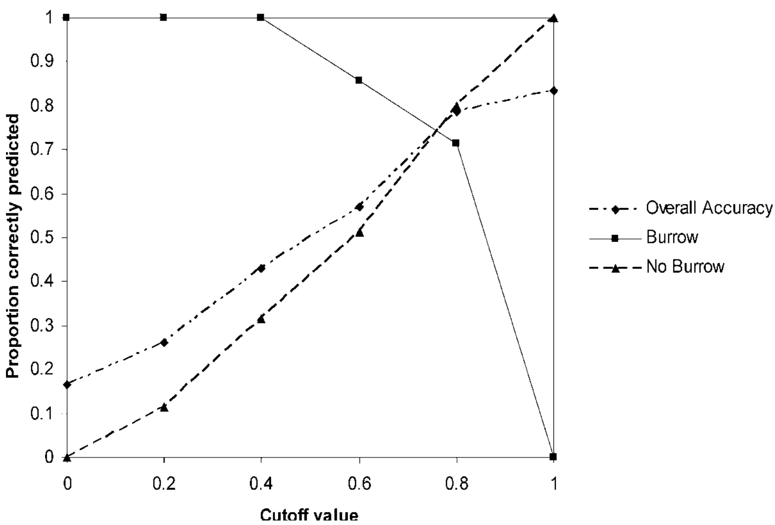


FIG. 4.—Prediction accuracies at different cut–offs (by definition, the extreme points indicate either a complete prediction of burrows at 0, or a complete absence of burrows at 1)

consistent with the positive relationship between gopher tortoise burrow probability and the presence of a transportation land-cover class. Road edges often have herbaceous cover and low tree cover, as well as a sunny exposure that may be favored by tortoises, and this association of burrows with roads has been observed in other species such as the desert tortoise (*Gopherus agassizii*) (Boarman *et al.*, 1997; Lovich and Daniels, 2000). Further, roads and trails occur along ridge tops and avoid wetland areas since such regions represent a stable path with low erosion and reduced requirements for fill (Hugh Westbury, Fort Benning, GA, pers. comm., 03 January 2005). Since gopher tortoises also avoid wetlands and clayey regions (Kushlan and Mazzotti, 1984), regions along the roads are favorable for burrowing. In some cases, gopher tortoises are forced into marginal habitats (such as those near roads) because fire suppression has resulted in canopy closure and in land-use changes that are unfavorable for the gopher tortoise (McCoy *et al.*, 1993). Alternatively, tortoises may burrow near roads to avoid predation by species that avoid roads. For example, it has been hypothesized that prairie dog colonies are found at high densities in urbanized areas because predator densities are low (Johnson and Collinge, 2004).

The probability of finding a burrow increased as the distance to streams increased. Some authors have suggested that gopher tortoises like to burrow in moist soils (McRae *et al.*,

TABLE 5.—Observed and predicted gopher tortoise burrows around Fort Benning

| | Observed | | |
|---|---|---|---|
| Predicted | No burrow | Burrow | Total |
| No burrow | 28 | 2 | 30 |
| Burrow | 7 | 5 | 12 |
| Total | 35 | 7 | 42 |

1981; Means, 1982), but in our study area, gopher tortoises avoided moist regions for burrowing, consistent with observations by Kushlan and Mazzotti (1984).

EVALUATION OF MODEL

The overall accuracies of the model within and outside Fort Benning were 78.15% and 78.57%, respectively. There are several possible explanations for the approximately 22 % of false predictions from the gopher tortoise habitat model both within and outside the installation. Since locations of burrows within Fort Benning are clearly known, the predictions within the installation were analyzed relative to certain characteristic information, such as detailed soil data, land–use data and forest inventory data that is available only for Fort Benning.

First, the model predicted a higher probability of a burrow being present in a pasture, but the definition of pasture land from remote sensing imagery is ambiguous. Areas identified as pasture land within Fort Benning included areas managed as wildlife openings. Such regions supported gopher tortoise burrows, but in the region surrounding Fort Benning, pasture land supported animal grazing or hay cultivation. Furthermore, grazing land may not support gopher tortoise burrows because of disturbance by livestock and/or the removal of tortoises by humans. Such misclassifications occurred for locations 2 and 7 (Table 4), where although the model predicted a high probability of gopher tortoise burrow presence (0.95 and 0.77), no burrows were observed owing to the use of land for pastures.

Second, slope was a parameter initially entered in the model, but it was not retained as a significant variable. However, other topographic parameters, like elevation, could be of importance, since gopher tortoise burrows were more common along ridges than flat terrain. But it is unclear whether topographic features could be useful at a 30-m resolution for the relatively flat or gently sloping areas of central Georgia.

The locations of false positive predictions were analyzed for Fort Benning and showed that about 31% of falsely predicted regions lay in areas of high military use (training areas, ranges, etc.). The military uses were not categorized as such in the satellite images; rather, areas used actively by troops were classified as clear-cut regions, pastures, forests, etc. It is likely that these locations did not support gopher tortoise burrows because of the intense military activities.

About 10% of the false positive prediction regions in Fort Benning lay in areas with tree basal areas $>70\ m^2/ha$. Such areas are unsuitable for gopher tortoise burrows since Florida gopher tortoises are known to abandon areas with tree basal areas $\geq 70\ m^2/ha$ and areas with $\geq 1400$ trees/ha (Aresco and Guyer, 1999). A high basal area is related to high tree density and high canopy cover. Mature gopher tortoises also abandon areas with greater than 50% tree canopy (Wilson *et al.*, 1997). This behavior explains about 10% of the false predictions in Fort Benning.

Mature individuals are known to abandon habitat patches of $<2$ ha (Wilson *et al.*, 1997). Approximately 19% of the predicted habitats were in regions that were less than 2 ha in area. The size of a patch is not included in the model as a predictor variable, and hence, such small areas, though not suitable and sustainable habitats for gopher tortoises, were predicted as potential habitats. This might be a significant factor, but it conflicts with our attempt to build on land-cover data based on landsat imagery.

Finally, the model considered the percentage of clay in the upper soil layer (0 to 5 cm). However, gopher tortoise burrows are up to 2 m deep and, thus, soil conditions below the first soil layer may also affect ease of burrowing.

Even though the model prediction of gopher tortoise habitat might be improved with additional data, better refinement of land-use categories, or finer resolution, we present this version in Eq. (1), because it can easily be adopted by resource managers, and it uses data that are readily available. The use of this approach should help managers better identify potential sites of gopher tortoise burrows. A field visit or the use of recent aerial images in conjunction with the model predictions is warranted if actions are planned that would irrevocably jeopardize the suitability of a site for gopher tortoise habitat. The model can be used to alert resource managers to potential gopher tortoise sites, to monitor changes in potential habitat, to plan field surveys for gopher tortoise, and to guide habitat restoration efforts.

## CONCLUSIONS

This study developed a quantitative habitat model for the gopher tortoise using the extensive data available on a military installation and extended it across the surrounding private lands. The model indicated that the probability of finding a gopher tortoise burrow increased when soils contain a low percentage of clay; the distance to a road is low; the distance to a stream is high; and land cover is a transportation cover, utility swath, clear-cut or sparse region, a deciduous, evergreen or mixed forest, a pasture or a row crop. The model may best be used as a planning tool to identify areas of importance for restoration, conservation, relocation, etc.

Natural resource management and military activities at Fort Benning are designed to avoid jeopardizing federal- or state-listed species. Conserving the habitat of rare species is of great importance to planners and developers at Fort Benning and in the surrounding regions in order to avoid the constraints on management that would occur if habitat were to become rare. The habitat model developed here will aid planning activities of resource managers and become part of a more comprehensive simulation model of environmental impacts in the region (RSim) (Dale *et al.*, 2005; Dale *et al.*, *in press*). One of the main indicators of the environmental effects of development is the response and alteration of the habitats of focal species. The gopher tortoise model will be an important component in RSim, enabling it to project impacts of changes in land use and cover on gopher tortoise habitat. The approach of developing a model based on the extensive data on public lands and then testing it on private lands illustrates how our understanding of habitat can be used across a variety of land ownerships.

*Acknowledgments.*—The assistance of Rusty Bufford with spatial data and Mark Thornton with data on gopher tortoise burrows at Fort Benning is appreciated. Hugh Westbury provided logistic support. Roger Birkhead informed us of certain references. Discussions with Hal Balbach and Deborah Epperson were also quite helpful in developing this project. The project was funded by a contract from Strategic Environmental Research and Development Program (SERDP) project CS-1259 to Oak Ridge National Laboratory. Oak Ridge National Laboratory is managed by the UT-Battelle, LLC, for the U.S. Department of Energy under contract DE-AC05-00OR22725.

## LITERATURE CITED

AEBISCHER, N. J., P. A. ROBERTSON AND R. E. KENWARD. 1993. Compositional analysis of habitat use from animal radio tracking data. *Ecology,* **74**:1313–1325.

ALEXY, K. J., K. J. BRUNJES, J. W. GASSETT AND K. V. MILLER. 2003. Continuous remote monitoring of gopher tortoise burrow use. *Wildlife Society Bulletin,* **31**:1240–1243.

ALLDREDGE, J. R., D. L. THOMAS AND L. L. MCDONALD. 1998. Survey and comparison of methods for study of resource selection. *Journal of Agricultural, Biological and Environmental Statistics,* **3**:237–253.

ARESCO, M. J. AND C. GUYER. 1999. Burrow abandonment by gopher tortoises in slash pine plantations of the Conecuh National Forest. *Journal of Wildlife Management,* **63**:26–35.

AUFFENBERG, W. AND R. FRANZ. 1982. The status and distribution of the gopher tortoise (*Gopherus* *polyphemus*), p. 95–216. *In:* R. B. Bury (ed.). North American tortoises: conservation and ecology. Wildlife Research Report 12, U. S. Fish and Wildlife Service.

BOARMAN, W. I., M. SAZAKI AND W. B. JENNINGS. 1997. The effect of roads, barrier fences, and culverts on desert tortoise populations in California, USA, p. 54–58. *In:* J. Van Abbema (ed.). Proceedings: Conservation, Restoration and Management of Tortoises and Turtles—An International Conference. New York Turtle and Tortoise Society.

BOGLIOLO, M. D., W. K. MICHENER AND C. GUYER. 2000. Habitat selection and modification by the Gopher Tortoise, Gopherus polyphemus, in Georgia Longleaf pine forest. *Chelonian Conservation and Biology,* **3**:699–705.

BOYCE, M. S., P. R. VERNIER, S. E. NIELSON AND F. K. A. SCHMIEGELOW. 2002. Evaluating resource selection functions. *Ecological Modelling,* **1537**:281–300.

BREININGER, D. R., P. A. SCHMALZER AND C. R. HINKLE. 1994. Gopher tortoise (*Gopherus polyphemus*) densities in coastal scrub and slash pine flatwoods in Florida. *Journal of Herpetology,* **28**:60–65.

CEDERBAUM, S. B., J. P. CARROLL AND R. J. COOPER. 2004. Effects of alternative cotton agriculture on avian and arthropod populations. *Conservation Biology,* **18**:1272–1282.

COLLINGE, S. K., K. L. PRUDIC AND J. C. OLIVER. 2003. Effects of local habitat characteristics and landscape context on grassland butterfly diversity. *Conservation Biology,* **17**:178–187.

CONNER, L. M., M. D. SMITH AND L. W. BURGER. 2003. A comparison of distance-based and classification-based analysis of habitat use. *Ecology,* **84**:526–531.

DALE, V. H., M. ALDRIDGE, T. ARTHUR, L. BASKARAN, M. BERRY, M. CHANG, R. EFROYMSON, C. GARTEN, C. STEWART AND R. WASHINGTON-ALLEN. In press. Bioregional Planning in Central Georgia, A special issue on "The Future of Bioregions and Bioregional Planning" in the journal *Futures.*

———, D. DRUCKENBROD, L. BASKARAN, M. ALDRIDGE, M. BERRY, C. GARTEN, L. OLSEN, R. EFROYMSON AND R. WASHINGTON-ALLEN. 2005. Vehicle impacts on the environment at different spatial scales: observations in west central Georgia. *Journal of Terramechanics,* **42**:383–402.

——— AND P. D. PARR. 1998. Preserving DOE's research parks. *Issues in Science and Technology,* **XIV**:73–77.

DIEMER, J. E. 1986. The ecology and management of the gopher tortoise in the southeastern United States. *Herpetologica,* **42**:124–133.

DODD, C. K. AND R. A. SEIGEL. 1991. Relocation, repatriation and translocation of amphibians and reptiles—are they conservation strategies that work? *Herpetologica,* **48**:402–407.

DONNELLY, R. AND J. M. MARZLUFF. 2004. Importance of reserve size and landscape context to urban bird conservation. *Conservation Biology,* **18**:733–745.

EFROYMSON, R. A., V. H. DALE, L. BASKARAN, M. CHANG, M. ALDRIDGE AND M. BERRY. 2005. Planning transboundary ecological risk assessments at military installations. *Human and Ecological Risk Assessment,* **11**:1193–1215.

EUBANKS, J. O., W. K. MICHENER AND C. GUYER. 2003. Patterns of movement and burrow use in a population of gopher tortoises (*Gopherus polyphemus*). *Herpetologica,* **59**:311–321.

FIELDING, A. H. AND J. F. BELL. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation,* **24**:38–49.

FOODY, G. M. 2002. Status of land cover classification accuracy assessment. *Remote Sensing of Environment,* **80**:185–201.

FRANK, P. A. AND J. N. LAYNE. 1992. Nests and daytime refugia of cotton mice (*Peromyscus gossypinus*) and golden mice (*Ochroromys nuttalli*) in south central Florida. *American Midland Naturalist,* **127**:21–30.

GROVES, C. R., L. S. KUTNER, D. M. STOMS, M. P. MURRAY, J. M. SCOTT, M. SCHAFALE, A. S. WEAKLEY AND R. L. PRESSEY. 2000. Owning up to our responsibilities: who owns lands important for biodiversity? p. 275–300. *In:* B. A. Stein, L. S. Kutner and J. S. Adams (eds.). Precious heritage: the status of biodiversity in the United States. Oxford University Press, New York.

HANOWSKI, J. M., G. J. NIEMI AND D. C. CHRISTIAN. 1997. Influence of within-plantation heterogeneity and surrounding landscape composition on avian communities in hybrid poplar plantations. *Conservation Biology,* **11**:936–944.

HERMANN, S. M., C. GUYER, J. H. WADDLE AND M. G. NELMS. 2002. Sampling on private property to evaluate population status and effects of land use practices on the gopher tortoise, Gopherus polyphemus. *Biological Conservation,* **108**:289–298.

HOSMER, D. W. AND S. LEMESHOW. 1989. Applied logistic regression. John Wiley and Sons, New York. 1 p.

HUBBARD, H. G. 1893. The Florida land tortoise—Gopher, Gopherus polyphemus. *Science,* **22**:57–58.

JOHNSON, W. C. AND S. K. COLLINGE. 2004. Landscape effects on black-tailed prairie dog colonies. *Biological Conservation,* **115**:487–497.

JONES, J. C. AND B. DORR. 2004. Habitat associations of gopher tortoise burrows on industrial timberlands. *Wildlife Society Bulletin,* **32**:456–464.

KANE, S. AND R. KEETON. 1998. Fort Benning: the land and the people. Southeast Archeological Center, National Park Service, Tallahassee, Florida.

KEATING, K. A. AND S. CHERRY. 2004. Use and interpretation of logistic regression in habitat-selection studies. *Journal of Wildlife Management,* **68**:774–789.

KUSHLAN, J. A. AND F. J. MAZZOTTI. 1984. Environmental effects on a coastal population of gopher tortoises. *Journal of Herpetology,* **18**:231–239.

LAGO, P. K. 1991. A survey of arthropods associated with gopher tortoise burrows in Mississippi. *Entomological News,* **102**:1–13.

LANDERS, J. L., D. H. V. LEAR AND W. D. BOYER. 1995. The longleaf pine forests of the southeast: requiem or renaissance? *Journal of Forestry,* **93**:39–44.

LESLIE, M., G. K. MEFFE, J. L. HARDESTY AND D. L. ADAMS. 1996. Conserving biodiversity on military lands: a handbook for natural resources managers. The Nature Conservancy, Arlington, Virginia.

LEUNG, P. S. AND L. T. TRAN. 2000. Predicting shrimp disease occurrence: artificial neural networks vs. logistic regression. *Aquaculture,* **187**:35–49.

LOVICH, J. E. AND R. DANIELS. 2000. Environmental characteristics of desert tortoise (*Gopherus agassizii*) burrow locations in an altered industrial landscape. *Chelonian Conservation and Biology,* **3**:714–721.

MANLY, B. F. J., L. L. MCDONALD, D. L. THOMAS, T. L. MCDONALD AND W. P. ERICKSON. 2002. Resource selection by animals: statistical design and analysis for field studies, 2nd ed. Kluwer Academic Publishers, Boston, Masachussets. p. 1–15.

MANN, L. K., A. W. KING, V. H. DALE, W. W. HARGROVE, R. WASHINGTON-ALLEN, L. POUNDS AND T. A. ASHWOOD. 1999. The role of soil classification in geographic information system modeling of habitat pattern: threatened calcareous ecosystems. *Ecosystems,* **2**:524–538.

———, P. D. PARR, L. R. POUNDS AND R. L. GRAHAM. 1996. Protection of biota on nonpark public lands: examples from the U.S. Department of Energy Oak Ridge Reservation. *Environmental Management,* **20**:207–218.

MANN, W., P. DORN AND R. BRANDL. 1991. Local distribution of amphibians: the importance of habitat fragmentation. *Global Ecology and Biogeography Letters,* **1**:36–41.

MCCOY, E. D. AND H. R. MUSHINSKY. 1992. Studying a species in decline: gopher tortoises and the dilemma of correction factors. *Herpetologica,* **48**:402–407.

———, H. R. MUSHINSKY AND D. S. WILSON. 1993. Patterns in the compass orientation of gopher tortoise burrows at different spatial scales. *Global Ecology and Biogeography Letters,* **3**:33–40.

MCRAE, W. A., J. L. LANDERS AND J. A. GARNER. 1981. Movement patterns and home range of the gopher tortoise. *American Midland Naturalist,* **106**:165–179.

MEANS, D. B. 1982. Responses to winter burrow flooding of the gopher tortoise (*Gopherus polyphemus*). *Herpetologica,* **38**:521–525.

MILLER, D. A. AND R. A. WHITE. 1998. A conterminous United States multi-layer soil characteristics data set for regional climate and hydrology modeling. *Earth Interactions,* **2**:1–26.

MOFFATT, S. F., S. M. MCLACHLAN AND N. C. KENKEL. 2004. Impacts of land use on riparian forest along an urban-rural gradient in southern Manitoba. *Plant Ecology,* **174**:119–135.

NATURESERVE. 2004. Species at risk on DoD installations. http://natureserve.org/prodServices/speciesatRiskdod.jsp.

NOSS, R. F. 1989. Longleaf pine and wiregrass: keystone components of an endangered ecosystem. *Natural Areas Journal,* **9**:211–213.

PEARCE, J. AND S. FERRIER. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling,* **133**:225–245.

PEARLSTINE, L. G., S. E. SMITH, L. A. BRANDT, C. R. ALLEN, W. M. KITCHENS AND J. STENBERG. 2002. Assessing state-wide biodiversity in the Florida Gap analysis project. *Journal of Environmental Management,* **66**:127–144.

RAMSEY, E. W., G. A. NELSON, D. ECHOLS, AND S. K. SAPKOTA. 2002. The National Vegetation Classification Standard applied to the remote sensing classification of two semiarid environments. *Environmental Management,* **29**:703–715.

RIVARD, D. H., J. POITEVIN, D. PLASSE, M. CARLETON AND D. J. CURRIE. 2000. Changing species richness and composition in Canadian national parks. *Conservation Biology,* **14**:1099–1109.

RUSSELL, K. R., D. H. VAN LEAR AND D. C. GUYNN. 1999. Prescribed fire effects on herpetofauna: review and management implications. *Wildlife Society Bulletin,* **27**:374–384.

SAUNDERS, D. A., R. J. HOBBS AND C. R. MARGULES. 1991. Biological consequences of ecosystem fragmentation—a review. *Conservation Biology,* **5**:18–32.

SCOTT, J. M., F. W. DAVIS, R. G. MCGHIE, R. G. WRIGHT, C. GROVES AND J. ESTES. 2001. Nature reserves: do they capture the full range of America's biological diversity? *Ecological Applications,* **11**:999–1007.

STEFFAN-DEWENTER, I. 2003. Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conservation Biology,* **17**:1036–1044.

SWETS, J. A. 1988. Measuring the accuracy of diagnostic systems. *Science,* **240**:1285–1293.

THOMPSON, J. R., M. D. ANDERSON AND K. N. JOHNSON. 2004. Ecosystem management across ownerships: the potential for collision with antitrust laws. *Conservation Biology,* **18**:1475–1481.

TREXLER, C. J. AND J. TRAVIS. 1993. Nontraditional regression analysis. *Ecology,* **74**:1629–1637.

USFWS (U.S. FISH AND WILDLIFE SERVICE). 1999. Fort Benning Terrestrial Resources Inventory Report 1995–1999. U.S. Fish and Wildlife Service, West Georgia Field Sub-Office, Fort Benning, Georgia.

WILSON, D. S., H. R. MUSHINSKY AND R. A. FISCHER. 1997. Species profile: Gopher tortoise (*Gopherus polyphemus*) on military installations in the southeastern United States. Technical report SERDP-97-10. U.S. Army Corps of Engineers.

WINTON, B. R. AND D. M. LESLIE. 2004. Density and habitat associations of barred owls at the edge of their range in Oklahoma. *Southeastern Naturalist,* **3**:475–482.

WITZ, B. W., D. S. WILSON AND M. D. PALMER. 1991. Distribution of Gopherus polyphemus and its vertebrate symbionts in three burrow categories. *American Midland Naturalist,* **126**:152–158.

SUBMITTED 25 APRIL 2005 ACCEPTED 2 NOVEMBER 2005