LOCATING SUITABLE HABITAT FOR A RARE SPECIES: EVALUATION OF A SPECIES DISTRIBUTION MODEL FOR BOG TURTLES (*GLYPTEMYS MUHLENBERGII*) IN THE SOUTHEASTERN UNITED STATES

THERESA S. M. STRATMANN^{1,2,4}, KYLE BARRETT¹, AND THOMAS M. FLOYD³

¹Department of Forestry and Environmental Conservation, Clemson University, 261 Lehotsky Hall, Clemson, South Carolina 29634, USA

²Current address: Senckenberg Biodiversity and Climate Research Centre (BiK-F) and Department of Biological Sciences

at the Goethe University, Senckenberganlage 25, 60325 Frankfurt am Main, Germany

³Wildlife Resources Division, Georgia Department of Natural Resources, 116 Rum Creek Drive, Forsyth, Georgia 31029, USA ⁴Corresponding author, e-mail: theresastrat@gmail.com

Abstract.—Because rare and cryptic species can be difficult to locate, distribution maps for such species are often inaccurate or incomplete. Bog Turtles (*Glyptemys muhlenbergii*) are emblematic of this challenge. Conducting surveys of known, historical, and potential Bog Turtle habitat is a specific need stated in the Bog Turtle Northern Population Recovery Plan and in most Comprehensive Wildlife Conservation Strategies of states in the southern population. To address this need, we constructed a species distribution model for the southern population of Bog Turtles and ground-validated the model to assess its ability to locate suitable Bog Turtle habitat. Our final model identified 998,325 ha of potentially suitable habitat. On-the-ground evaluation of habitat identified as potentially suitable was carried out at 113 wetlands in Georgia and 83 in South Carolina. Of these, only nine wetlands met criteria for suitable Bog Turtle habitat in Georgia and 13 in South Carolina. Trapping efforts at the nine Georgia sites and eight of the South Carolina sites showed Bog Turtles to be present at two of the Georgia sites. This ground-validation effort demonstrates that the species distribution model greatly over-predicts the amount of suitable habitat for Bog Turtles. Nonetheless, this manner of searching for rare and cryptic species does avoid the typical biases of haphazard searches and helps identify habitat on private property. Given these findings, the model is most useful when the area of interest is small, such as a county within the range of a species that currently has no known occurrence records.

Key Words.--endangered species; habitat suitability; Maxent; model validation; South Carolina; Georgia; wetland

INTRODUCTION

Conservation efforts for rare and cryptic species are often hampered by an incomplete understanding of their distribution (Guisan et al. 2006). There are the extreme cases, such as Zhou's Box Turtle (Cuora zhoui), where species are known only from specimens that appear in markets, with no wild populations known to scientists (Zhao et al. 1990; McCord and Iverson 1991). Yet the challenge of finding populations of rare and cryptic species is not solely a problem for the understudied ecosystems of the world. Searches for new populations of rare and cryptic species and efforts to better understand their geographic ranges occur regularly within the United States (Yozzo and Ottmann 2003; Campbell et al. 2010; Graham et al. 2010; Sheldon and Grubbs 2014), and many of these searches are for herpetofauna (Apodaca et al. 2012; Groff et al. 2014; Lindeman 2014; Pierson et al. 2014; Searcy and Schaffer 2014). In particular, efforts to study and conserve the Bog Turtle (Glyptemys muhlenbergii) capture the challenges faced in these search endeavors, as its use of a rare habitat and its cryptic habits make locating

populations on the landscape and individuals within a wetland especially challenging.

Endemic to the Eastern United States, Bog Turtles are the smallest and rarest species of chelonian in the USA (Zappalorti 1978; Ernst and Lovich 2009). The range of the species is split into two regions, a Northern range reaching from New York and Massachusetts south to Marvland and Delaware and a Southern range predominantly in the Appalachian region, reaching from southern Virginia to northern Georgia. In the northern portion of their range, Bog Turtles are listed as Threatened under the U.S. Endangered Species Act; whereas, they are listed as Threatened by Similarity of Appearance in the southern portion (U.S. Fish and Wildlife Service [USFWS] 1997); globally they are considered one of the 40 most endangered turtles (Turtle Conservation Coalition 2011). Within their range, Bog Turtles are confined to small, isolated, open-canopy, spring-fed wetlands characterized by shallow rivulets flowing over ankle to hip-deep muck (Zappalorti 1976a, b; Chase et al. 1989; Tryon 1990). These wetlands are rare features within the landscape, in part due to natural succession and past drainage efforts for farming

(Weakley and Schafale 1994). It is in the muck of these rare spring-fed wetlands where Bog Turtles spend most of their time, making this small (maximum shell length of 11.5 cm), mud-colored turtle very difficult to find within a wetland (Ernst and Lovich 2009). The fact that they tend to occur in small populations (< 50 individuals) lessens their detection probability even more (Rosenbaum et al. 2007). Because of the difficulties associated with finding Bog Turtle habitat Comprehensive and individuals, the Wildlife Conservation Strategies of Georgia, South Carolina, North Carolina, and Virginia, and the Bog Turtle Northern Population Recovery Plan all emphasize surveying for new populations in unexplored areas as part of their conservation strategy (USFWS 2001; Georgia Department of Natural Resources [GA DNR] 2005; North Carolina Wildlife Resources Commission [NCWRC] 2005; South Carolina Department of Natural Resources [SC DNR] 2005; Virginia Department of Game and Inland Fisheries [VA DGIF] 2005). Although there are guidelines on how to assess whether a site is suitable for Bog Turtles and how to survey for Bog Turtles within potentially suitable sites (USFWS 2001; Somers and Mansfield-Jones 2008), there are no suggestions on how to locate potential habitat within the greater landscape. Without guidelines, searches for this rare habitat tend to be haphazard and will naturally be biased towards roads and easily accessible areas, providing no way to assess habitat on private lands or far from the road. Thus there is a need to map suitable habitat for Bog Turtles to efficiently and strategically achieve goals of state wildlife agencies for locating new populations (USFWS 2001).

Species distribution modeling (SDM) techniques are one way to map species habitat associations, and they have greatly increased in popularity as integration with user-friendly geographic information systems (GIS) has become easier and remotely sensed data have become more available (Johnson et al. 2012). At the root of all these techniques is the idea that environmental conditions in places a species is known to occur can provide information on species-specific habitat requirements, and then new areas with similar environmental conditions can then be found on the landscape. The end product is a habitat description or map that highlights potentially suitable areas for the species. Such maps are now being used for conservation planning (Rodríguez et al. 2007; Gogol-Prokurat 2011; Hunter et al. 2012), to decrease sampling effort when searching for rare species (Singh et al. 2009), to locate rare species of plants (Guisan et al. 2006; Williams et al. 2009; Le Lay et al. 2010; Buechling and Tobalske 2011), endemic insects (Rinnhofer et al. 2012), a cryptic species of mole (Jackson and Robertson 2011), a bat (Rebelo and Jones 2010), and salamanders (Apodaca et al. 2012; Chunco et al. 2013; Peterman et al. 2013), and to define

areas for re-introduction (McKenna et al. 2013). Because SDMs have demonstrated utility for rare species, including those with only a few known localities, we decided to apply the approach toward more efficiently and strategically locating suitable Bog Turtle habitat.

We propose this SDM approach at a time when it is more important than ever to survey for new populations of Bog Turtles. Habitat loss, alteration, and degradation are the main threats facing Bog Turtles (USFWS 2001). A century of past ditching and draining efforts, encroachment of wetlands by woody vegetation, invasive plant species, and loss of habitat connectivity leaves us trying to understand Bog Turtle habitat selection in an altered landscape (Tryon 1990; Buhlmann et al. 1997; USFWS 2001; Ernst and Lovich 2009). It is not uncommon to see this long-lived turtle persisting in degraded habitat it selected long-ago. We must therefore search for Bog Turtles before this habitat degradation becomes prohibitive in identifying habitat and understanding habitat selection.

Our objective is to address the problems associated with Bog Turtle habitat detection by constructing a SDM for the species and ground-validating the model to assess its ability to locate suitable Bog Turtle habitat. This represents the first attempt to understand Bog Turtle distribution and habitat selection at a regional scale, as all previous attempts have been narrowly focused at the state level or home range scale (Chase et al. 1989; Carter et al. 1999; Morrow et al. 2001; Pittman and Dorcas 2009; Myers and Gibbs 2013). This regional scale approach was applied to the southern portion of the Bog Turtle range. This is an area where a regional model might be particularly useful as three states (South Carolina, Georgia, and Tennessee, USA) have too few occurrence records to build strong state level models. In addition, by using all known occurrence records in the south, we increase the likelihood of providing a more complete depiction of environmental characteristics the species tolerates in the south, which should generate a more accurate model (Elith et al. 2011).

MATERIALS AND METHODS

Study site.—Bog Turtles were first scientifically described in 1801 from a Pennsylvania, USA, specimen. They were considered a species of northern North America until 1917 when an individual was found in North Carolina, but other states were not added to the southern range until the 1960s when Bog Turtles were found in Virginia (Tryon 1990). The range of Bog Turtles in the south did not take its current form until 1986 when the species was discovered in Tennessee, the last state to be added to the current range (Tryon 1990). This late discovery in the south is emblematic that the task is ongoing to find new populations that will



FIGURE 1. Number of Bog Turtle (*Glyptemys muhlenbergii*) localities by county for the southern portion of the Bog Turtle Range (dark gray polygons). The light gray polygon represents all counties within a 25-km buffer around counties known to be occupied. The mapped region was used as the area of interest (i.e., background) for the species distribution model.

establish a specific, thorough knowledge of the Bog Turtle range (USFWS 2001; GADNR 2005; NCWRC 2005; SCDNR 2005; VADGIF 2005). The task is complicated by the fact that we are now searching for populations after extended periods of human alteration of landscapes through wetland drainage and other means. The need to find new populations is most pressing in the south, where research on the species is not as extensive and developmental pressures are high (Wear and Bolstad 1998). For this reason, we restricted our study to the southern range of Bog Turtles, which occurs in northern Georgia, northern South Carolina, western North Carolina, eastern Tennessee, and southwestern Virginia, USA. For modeling purposes, we considered the study area to be all counties with known Bog Turtle localities plus an additional 25 km buffer (Fig. 1); however, due to an error we did not buffer Franklin County, Virginia. The one point within this county is in close proximity to the western counties and thus this oversight does not interfere with the purpose of the buffer. The purpose of the buffer is to allow the SDM to examine areas just outside of the core area. As the omitted county buffer represents a very small part of the overall range it is not likely to greatly influence conclusions and has no bearing on groundvalidation efforts which occurred far south of the area in question.

Choice of species distribution model.—There are many potential modeling techniques to examine species habitat selection and distribution (Elith et al. 2006; Satter et al. 2007; Singh et al. 2009; Buechling and Tobalske 2011; McKenna et al. 2013); however, many of the available tools require knowledge of both presence and absence at a suite of sites. Because Bog Turtles are rare and extremely difficult to locate, robust absence data are unavailable, and we were restricted to presence-only modeling techniques. We chose to use a machinelearning approach to species distribution modeling called maximum entropy (Maxent; Phillips et al. 2006), which has been shown to perform very well relative to other presence-only options (Elith et al. 2006), is easily interpretable, and works well with small datasets (Hernandez et al. 2006). Maxent (version 3.3.3k) compensates for absence data by randomly selecting points (i.e., background points) from the study area to characterize the range and variation of the environmental variables available within the range of a species. By comparing the environment in areas with known Bog Turtle populations to the environment available to it (i.e., the background points), Maxent identifies preferences of species for certain ranges of environmental variables. The direction and strength of these preferences allows for predictions on the probability of suitable conditions in unsurveyed areas. The ultimate product is a map, dividing the study area into suitable and unsuitable data included all anurans, all chelonians, several species of squamata (Worm Snake, *Carphophis amoenus*, Ring-

Occurrence records.—All presence data were obtained from the Georgia Department of Natural Resources, South Carolina Department of Natural North Carolina Wildlife Resources. Resources Commission, Virginia Department of Conservation and Recreation, and Tennessee Department of Environment and Conservation through data use agreements. Data were provided as GPS points or polygons. All polygons were assigned a point representing their center and then combined with the point data into a single shapefile using ArcGIS 10.1 (ESRI, Redlands, California, USA). This original data set of 172 localities consisted of all extant and historical sites cataloged within each state (Fig.1).

Historical localities, locations in proximity to other known locations, and non-random species surveys can all introduce biases into the assessment of habitat suitability (Phillips et al. 2009; Kramer-Schadt et al. 2013). We applied three data filters to reduce these biases in the data. First, we kept only sites last visited and confirmed as extant in the past 30 y, a time period that approximates the life-span of the species (Ernst and Lovich 2009). Second, when several localities are clumped in a small area, the habitat characteristics of that area become over-represented and can bias the model. For sites that occurred in clusters, we performed a single data reduction exercise. Specifically, we randomly eliminated sites, until no site was within 5 km of another (Barrett et al. 2014; Sutton et al. 2015). Boria et al. (2014) and Kramer-Schadt et al. (2013) both have shown that addressing this bias can result in large differences in model performance. The first and second filters reduced our data set from 172 to 72 occurrence records. The third filter addresses the fact that species are rarely sampled randomly. Locality records can easily become spatially biased, for example, toward roads and certain geopolitical areas that are more sampled than others (Funk and Richardson 2002; Graham et al. 2004; Rondinini et al. 2006; Beck et al. 2014). Bog Turtle records, like records for many other species, likely suffer this bias. Most sites are close to roads and developed areas, and locality data suggest that some states have invested much more search effort than others (Fig. 1). This kind of bias can be accounted for by adjusting how background points are chosen. We made this adjustment using a target background approach, in which background data are acquired from species that are collected with similar biases as the target species (Phillips and Dudík 2008; Phillips et al. 2009). To build our target group background data set, we acquired locality data from other reptiles and amphibians to capture the behavior of the sampling agent (i.e., herpetologists). Species we included for background

of squamata (Worm Snake, Carphophis amoenus, Ringnecked Snake, Diadophis punctatus, Eastern Fence Lizard, Sceloporus undulatus, and Ribbon Snake, Thamnophis sauritus), and all salamanders in the genera Desmognathus, Plethodon, Eurycea, Gyrinophilus, Pseudotriton occurring in the range of interest. Occurrence records were obtained from HerpNet (Available from http://www.herpnet.org/ [Accessed 22 November 2013]), BISON (Biodiversity Information Serving Our Nation. Available from http://bison. usgs.ornl.gov/#home [Accessed 1 December 2013]), and GBIF (Global Biodiversity Information Facility. Available from http://www.gbif.org/ [Accessed 22 November 2013]), and any duplicate points were removed. The study area was divided into three equal areas and points were randomly removed from areas until the distribution of points was approximately even among the three areas. After filtering in this manner, 1,967 background points remained. This is a small but sufficient number of background points (Phillips and Dudík 2008), but we also built a model using a background layer with 10,000 randomly generated points (Phillips et al. 2006), as Phillips and Dudík (2008) show a larger number of points can improve model performance. Thus, we produced two models, a random points (RP) model, and a target group (TG) model.

variables.—A Predictor Maxent model uses environmental characteristics related to the natural history of a species to make predictions about potentially suitable habitat. We focused on 12 environmental variables (Table 1). The first set of environmental variables, elevation, topographic relief, temperature seasonality (standard deviation of monthly temperatures), and maximum temperature of warmest month, all relate to the montane, ectothermic nature of this turtle. Topographic relief was calculated with the ArcGIS tool Focal Statistics as the standard deviation of elevation within a 1-ha moving window. One hectare was chosen for this and all other moving window analyses as most bogs are smaller than a hectare (Lee and Nordon 1996; Buhlmann et al. 1997). Developed areas, pasture and hay fields, and wetlands were chosen as the relevant land cover variables. We specifically selected the pasture and hay field category to address the fact that the wetlands these species occupy tend to occur in flat areas in the mountains that are often ditched and drained for agricultural or development purposes (Tryon 1990; Moorhead and Rossell 1998). We hypothesized that developed areas are likely to represent unsuitable habitat, but hay fields and pastures browsed by livestock often remain wet and can support viable Bog Turtle populations (Tesauro and Ehrenfeld 2007). Because known Bog Turtle localities are represented by points and extracting the data directly below a point can be an

TABLE 1. The source of data and their biological relevance for 12 environmental characteristics used to build the species distribution model of the Bog Turtle (*Glyptemys muhlenbergii*). All data were accessed 8 September 2013. An asterisk (*) denotes a variable is characterized within a 1-ha moving window.

Environmental Characteristic	Source	Biological Relevance	
Elevation Topographic Relief (standard deviation of elevation)* Temperature Seasonality (standard deviation of monthly temperatures)	USGS Digital Elevation Model (DEM) - Available from http://eros.usgs.gov/#/Guides/dem WorldClim database - Available from www.worldclim.org/bioclim	Montane, ectothermic nature of turtle.	
Maximum Temperature of Warmest Month			
Percentage Developed Land* Percentage Pasture or Hay Fields* Percentage Wetland*	National Land Cover Database (NLCD) - Available from www.mrlc.gov/nlcd2011.php	To rule out flat but unsuitable areas. Land cover that could contain suitable habitat.	
Distance to Nearest Wetland	National Wetlands Inventory (NWI) - Available from http://www.fws.gov/wetlands/	Connectivity to other wetlands.	
Distance to Nearest Stream	USGS National Hydrography Dataset - Available from http://nhd.usgs.gov/		
Percentage Organic Matter Percentage Clay	Survey Spatial and Tabular Data (SSURGO 2.2). Gaps were filled using the larger grain but more geographically complete U.S. General Soil Map		
Percentage Hydric Soils	(STATSGO2) - Available from http://websoilsurvey.nrcs.usda.gov/	conductive for burrowing.	

inaccurate representation of the larger area the wetland covers, we used the Focal Statistics tool to calculate the percentage land cover of interest (e.g., percentage pasture/hay) in the surrounding hectare. This was only a problem for the land cover variables which were at a much finer scale than the average Bog Turtle wetland size, the other environmental variables were at a much coarser scale and captured the size of the wetland and surrounding area. We did not include the National Wetland Inventory (NWI) database as a predictor variable in the model, as this dataset is notorious for missing the small wetlands that typify Bog Turtle habitat (Leonard et al. 2012). By not restricting the model to known wetland localities, we hoped to identify potential habitat in previously unconsidered locales.

As a species with high site fidelity that historically existed in a metapopulation structure (Buhlmann et al. 1997), connectivity is important, so we also included distance to nearest wetland and stream as modeled environmental variables. Distance to nearest wetland and stream were calculated using Euclidean distance. Finally, because this species spends much of its time within the first 10 cm of organic wetland muck (Pittman and Dorcas 2009) and must be able to move through the soil, we also used information on soils: percentage organic matter, percentage clay, and percentage hydric soils. We resampled all 12 environmental variables to

the cell size of the smallest available data ($30 \text{ m} \times 30 \text{ m}$) and we processed them in ArcGIS 10.1. We made a Pearson's correlation test in R version 3.1.1 (R Development Core Team 2014, Vienna, Austria) on all 12 environmental variables. BIO4 and BIO5 each correlated with elevation (r = -0.70 and -0.98, respectively), but not with each other. Despite this we kept elevation in the model. While temperature is the more likely mechanistic driver of distribution from a historical standpoint, elevation is a more important driver in recent times because it reflects places where developmental pressures may accumulate more slowly (Napton et al. 2010). No other variables exhibited strong correlations (all r values < 0.70).

Model processing.—Maxent was run using the auto features option, which attempts to fit a range of functions including linear, quadratic, product, threshold, and hinge features. We withheld 10% of points for evaluating model quality. We ran the model 10 times, and all results shown are the average of the10-fold cross-validation.

To select potential Bog Turtle habitat, we examined the Maxent logistic output in the context of 11 different default thresholds, used to categorize values as suitable (at or above threshold value) or unsuitable (below threshold value). For each of our models (RP and TG), we used the most restrictive threshold (maximum test sensitivity plus specificity and equal training sensitivity and specificity, respectively) in an effort to restrict the model to the most promising sites. We then examined the intersection of the two models to evaluate areas considered unsuitable by both, suitable by both, and, suitable by one model but not the other.

Model ground-validation.—To evaluate the predictive power of the species distribution model, we conducted on-the-ground surveys of sites modeled to be potentially suitable by both models of Bog Turtle habitat. Resources were not available to ground validate the model across the entire southern range. We therefore made a series of decisions to prioritize the areas that we would examine on-the-ground. First, our groundvalidation assessed only errors of commission (i.e., areas incorrectly identified as suitable habitat). Next, we narrowed our focus to Georgia and South Carolina, where demand to find new populations was highest and resources were readily available. In Georgia, the model identified 88,038 ha of potentially suitable habitat to survey; whereas, 12,635 ha were identified in South Carolina. We further narrowed our search to the Blue Ridge physiogeographic region of each state, as all Bog Turtle records except for 17 in North Carolina fall within this physiogeographic region. A lack of high-quality color infrared imagery made it difficult to assess in ArcGIS whether suitable areas were also wet areas. To ensure we would spend resources traveling to actual wetlands, we clipped the suitability map to all National Wetlands Inventory (NWI) wetlands in the palustrine emergent (PEM), palustrine scrub-shrub (PSS), or palustrine forested (PFO) categories (following Cowardin et al. 1979). The NWI does not capture all wetlands (Leonard et al. 2012) but was sufficient for a first round of ground-validation. Finally, we had to consider accessibility to sites. Therefore, of the sites remaining, we prioritized those sites on public land within 1 km of a road and sites on private property within 20 km of a Bog Turtle occurrence record. With this strategic search, we were able to test the hypothesis that sites modeled as suitable are actually occupied by Bog Turtles. Given this hypothesis, the decisions we made to sample those areas that could be reasonably accessed did not bias our field surveys. With unlimited time and money we would have taken our unbiased habitat model and assessed both errors of commission and omission, yet given the difficulties of working on private lands, the costs of driving through a large geographic extent, and the logistical challenges of trapping remote areas, we made a series of decisions to take a first pass at validating the model in way that was practical.

At prioritized sites, we evaluated the quality of the habitat for Bog Turtles based on indicator soils,

vegetation, and hydrology, as outlined in the Phase 1 survey guidelines established by the U.S. Fish and Wildlife Service (USFWS 2006). Characteristics of interest are: (1) presence of mucky areas of more organic than alluvial characteristics; (2) presence of small rivulets of water flowing over a muddy substrate; (3) presence of springs or seep heads; (4) presence of sphagnum (Sphagnum spp.), rushes (Juncus spp.), sedges (Carex spp.), Alder (Alnus serrulata), Red Maple (Acer rubrum), Bog Rose (Rosa palustris), Multiflora Rose (Rosa multiflora), Withe Rod (Viburnum nudum L. var. cassinoides), Royal Fern (Osmunda regalis), (Osmunda cinnamomea), Cinnamon Fern Red Chokeberry (Aronia arbutifolia), and Turtle Head (Chelone glabra); (5) large area of open canopy; (6) proximity to a stream; and (7) active or historic North American Beaver (Castor canadensis) activity. We surveyed wetlands that met USFWS standards for Bog Turtles.

Traditional techniques to survey for Bog Turtles include trapping surveys and visual/probing surveys (USFWS 2006). To maximize detection probability, we used a trapping method similar to that described by Somers and Mansfield-Jones (2008) but at a much higher trap density (1 trap /25 m²). With this method unbaited, custom-made traps of galvanized welded-wire are set in shallow rivulets of water that could act as potential travel corridors for Bog Turtles (Stratmann 2015). Traps were open from mid-May to mid-July 2014 and checked every-other day. Based on trapping efforts at other sites in the region known to be occupied, we estimate that this trapping duration means there is a very low probability (average = 0.03) that turtles are present but were not detected (Stratmann 2015).

RESULTS

Both the random points (RP) and target group (TG) background models had high AUC values (RP model = 0.88, TG model = 0.91) and correctly classified a majority of the known Bog Turtle localities (Table 2). Each model was driven by different environmental variables and thus produced different suitability maps In the RP model, distance to wetland, (Fig. 2). maximum temperature of warmest month, elevation, and topographic relief had the highest percentage contributions (22.8%, 19.3%, 17.4%, and 10.8%, respectively; Table 3). In the TG model, distance to wetland, percentage pasture/hay, percentage developed area, and distance to stream had the highest contributions (30.7%, 29.3%, 17.1%, and 10.8%, respectively; Table 3). Jackknife tests show that maximum temperature of the warmest month holds the most information by itself for the RP model, whereas in the TG model it is percent pasture/hay.

TABLE 2. The Maxent models had high accuracy in correctly classifying the known Bog Turtle (*Glyptemys muhlenbergii*) localities as suitable habitat. Known Bog Turtle localities (n = 72) and their classification (suitable or unsuitable) are presented for each of the three different models: random points (RP), target group (TG), and a model which combines the RP and TG models.

Site Suitability	No. locations correctly classified (percent)				
Combined Model					
suitable in both models	52 (72.2%)				
suitable in only one model	14 (19.4%)				
unsuitable in both models	6 (8.3%)				
Random Points Model					
suitable	56 (77.8%)				
Target Group Model					
suitable	62 (86.1%)				

For the RP model, the most conservative threshold was the maximum test sensitivity plus specificity. This translates to 1,219,828 ha of suitable habitat and 6,995,533 ha of unsuitable habitat across the area of interest. For the TG model, the most conservative threshold was the equal training sensitivity and specificity threshold. This resulted in 3,074,811 ha of suitable habitat and 5,140,550 ha of unsuitable habitat. When both models were combined 998,325 ha were considered suitable (Fig. 3).

Of the area considered suitable by both models, 88,038 ha and 12,635 ha occurred in Georgia and South Carolina, respectively. When limited to PSS, PEM, or PFO NWI wetlands in the Blue Ridge physiogeographic region, 316 wetlands were designated as suitable by both models and 34 wetlands were designated as suitable by only one model but not the other in Georgia. In South Carolina 109 wetlands were designated as suitable by both models and 87 wetlands designated as suitable by one model but not the other. Of these wetlands, we examined 113 on the ground in Georgia and 83 in South Carolina. Nine of the 113 sites in Georgia met USFWS criteria for suitable Bog Turtle habitat and we trapped these. In South Carolina, 13 of the 83 sites met criteria; although, we were only able to gain permission to trap at eight of the sites in South Carolina. Therefore, for about every 100 wetlands searched, we found that only 10 met the USFWS criteria for suitable Bog Turtle habitat. Although wetlands deemed unsuitable for Bog Turtles according to USFWS guidelines cannot be counted as absences, the high number of wetlands not matching these guidelines would at least suggests that Maxent greatly over predicted the amount of suitable habitat. Of the nine sites we trapped in Georgia, five were on public property and four were on private property. Of the eight

sites we trapped in South Carolina, three were on public property and five were on private property. In South Carolina, because we were denied access to five promising wetlands, we trapped at three of the eight sites only deemed suitable by a single model. These sites were targeted based on their proximity to known occurrences. Of the 17 sites trapped, we discovered Bog Turtles at two of the sites in Georgia. One site was a spring-fed wet meadow with open canopy and active beaver presence and is the only known extant population of Bog Turtles in Rabun County. The other was an extremely atypical site located on the slope of a hill under a power line right of way. Seeps run down the hill and pool in several places to create areas of very shallow muck (< 30 cm). This is only the second Bog Turtle population found in Towns County.

DISCUSSION

The objective of our study was to determine if species distribution modeling could be a useful tool to find habitat for a rare and cryptic species. Although past studies have demonstrated success with this approach, we found that the modeled distribution greatly overpredicted the amount of suitable habitat for Bog Turtles and was thus difficult to use in a resource-efficient manner.

Model differences.--We built two SDMs to address biases in our data. Known Bog Turtle populations are biased towards roads and easily accessible areas, and the discovery of one population in an area tends to focus future search efforts in nearby areas. We dealt with this bias by filtering our locality points and modeling available habitat from a target group background of other reptile and amphibian localities, which presumably share any biases held by the presence points (Phillips and Dudík 2008). This target group (TG) model was substantially different from the standard random points background (RP) model. As was expected, the RP model was biased toward areas of known occurrence; whereas, the TG model made stronger predictions in less-sampled areas (Phillips et al. 2009). In the target group model, pasture/hay held the most information; suitability increased with an increasing percentage of pasture/hay land cover. Consequently, the model indicated suitable habitat in areas of pasture/hay in the Piedmont region that the RP model did not consider. During ground-validation, we examined many pastures, as NWI wetlands often showed up in this land cover type. Nonetheless, we believe wetlands in pasture/hay areas were over-emphasized in the model because 51% of Bog Turtle presence localities (37 out of 72) were associated with pasture/hay, but only 10% (186 out of 1967) of the target group points were associated with this land use type. The importance of pastures and

Stratmann et al.—A species distribution model for Bog Turtles.



FIGURE 2. Maxent logistic output for (a) the random points model and (b) the target group model of Bog Turtles (*Glyptemys muhlenbergii*). Warmer colors indicate higher suitability. Models are based off of the same presence points but the random points model uses 10,000 randomly generated points as background points, while the target group model uses about 2,000 points derived from herpetofauna occurrences as its background points.

TABLE 3. The percentage contribution and permutation importance of variables used in Maxtent for the Random Points and Target Background
models for Bog Turtles (Glyptemys muhlenbergii). Permutation importance is the drop in training AUC when the values of a variable for training
presence and background data are randomly permuted and the model is reevaluated using the permutated data. Variables of higher importance
result in larger drops in AUC.

	Random Points Model		Target Background Model	
	Percentage	Permutation	Percentage	Permutation
Variable	Contribution	Importance	Contribution	Importance
Distance to Wetland	22.8	16.0	30.7	34.4
Maximum Temperature of Warmest Month	19.3	29.8	2.0	1.1
Elevation	17.4	9.8	0.4	1.6
Topographic Relief	10.8	25.6	5.6	12.2
Percent Hydric Soil	9.1	0.9	1.3	0.1
Distance to Stream	8.6	8.9	10.8	24.8
Percent Organic Matter	3.6	1.1	0.6	0.4
Percent Pasture/Hay	3.0	1.1	29.3	2.0
Percent Developed Land	2.8	4.6	17.1	20.8
Percent Clay	1.8	1.8	0.8	0.5
Percent Wetland	0.6	0.0	0.6	0.0
Temperature Seasonality	0.2	0.5	0.7	2.0

hayfields to Bog Turtles is well established (Tesauro and Ehrenfeld 2007). Throughout the Appalachians, farmers have converted wetlands to pastures or hay fields through ditching and draining. When these efforts fail and some part of the wetland remains, the site is kept as an emergent wetland through grazing activities, which occasionally provides quality Bog Turtle habitat (Zappalorti 1976b, 1997). Yet it is not the pasture/hay land cover that initially made the site suitable; conditions for wetland formation must be present. This complicated mix of geomorphology, historic land alteration, and current land use (i.e., grazing) highlights the importance of our duel-modeling approach and ground validation for model output.

Ground validation.-The distribution model highlighted many areas that were not wetlands. There appear to be four main reasons why the SDM was not as restrictive as we had hoped. First, identifying small wetlands across large extents is difficult in general (Pitt et al. 2011; Leonard et al. 2012). We did not expect our model to only identify wetlands. Instead, we aimed to determine if a model generated from available remote sensing data would be sufficient to identify Bog Turtle It appears key missing data (e.g., better habitat. hydrologic and soil maps) do considerably limit the effectiveness of the SDM. We did incorporate the available NLCD and NWI wetland data to identify wetlands but NWI is notorious for missing small wetlands (Leonard et al. 2012), and many NWI wetlands we visited no longer have standing water in them and are barely distinguishable as wetlands. As remote sensing continues to improve, especially with the availability of LiDAR (Light Detection And Ranging), this problem may diminish and enable us to restrict the model to specific areas of interest (e.g., Peterman et al. 2013). Second, high resolution environmental data are lacking.

Wetlands tend to be small features (1-3 ha) within the greater landscape. In our model, $30 \text{ m} \times 30 \text{ m}$ was the finest grain available (NLCD, DEM), with soil and climate environmental layers being particularly coarse. These large scale data sets are also minimally groundvalidated and have their own errors, which when combined with the lack of fine-scale resolution may mean that data are simply not at a fine enough resolution to pick-up small features like small wetlands within the larger landscape. Until finer resolution wetland and environmental data are available, it will be difficult to improve this aspect of the SDM. Two other factors that might explain the difficulty of building a SDM for Bog Turtles were brought to our attention: we have trapped many wetlands that meet established USFWS criteria for good Bog Turtle habitat without detecting Bog Turtles, but know of populations in sites that would never be considered suitable under USFWS criteria because they are so unusual or degraded. This seems to hint at two things. One, unusual sites might suggest that Bog Turtles are less habitat specialists than thought, with main requirements being shallow water, winter refugia. and open canopy. For example, the new Bog Turtle locality in Towns County is very different from typical Bog Turtle habitat as it is situated on a slope, has very shallow muck, is very rocky, and is more a series of hillside seeps that occasionally puddle than a typical wetland. Although the model deemed it as suitable, we only trapped this area because of claims that a Bog Turtle had been seen at the site. Radio-telemetry at the site has shown that with little mud available, individuals use cavities under shrub root clumps amid rocky seeps as alternative refugia. This observation could be explained by the fact that moving spring water is more important to hibernating Bog Turtles than the depth of the mucky soil (Ernst et al. 1989; Zappalorti 1997). The reporting of Somers and colleagues (2007) demonstrate that this

Stratmann et al.—A species distribution model for Bog Turtles.



FIGURE 3. Binary (suitable/unsuitable) model results for the random points (purple) and the target group (green) models of habitat suitability for Bog Turtles (*Glyptemys muhlenbergii*) in the southeastern United States. Black areas were considered suitable in both models. Green or purple areas are considered suitable in only one model.

unusual use of habitat is not unprecedented. On the other hand, for degraded sites, site history (e.g., past ditching and draining efforts, past beaver influence, canopy cover over the years) may play a larger role than current habitat characteristics in explaining where turtles persist or have sought refugia. Some historically drained wetlands may have had time to recover and now appear suitable, but a recolonization event would be needed if those draining efforts initially extirpated Bog Turtles. Other wetlands may have been recently or minimally drained, enabling Bog Turtles to persist despite apparent habitat degradation. Thus, a SDM could highlight wetlands suitable for Bog Turtles based on environmental characteristics, but a detailed knowledge of the history of the site would be required to determine its true suitability. Other studies have shown that incorporating information on site history can enable better predictions of species occurrence and patterns of biodiversity (Dupouey et al. 2002; Lunt and Spooner 2005; Piha et al. 2007). Site history would also be one way to parse suitable but unoccupied sites from those suitable and occupied. Suitable sites may have all the habitat characteristics required by a species, but may still be unoccupied due to historical disturbance events, loss of connectivity, extirpation, competition, and predation, which would need to be added to a model to better understand the realized distribution of a species (Guisan and Thuiller 2005).

Recommended uses of the model.—When rare and cryptic species are targeted for management and conservation action, finding suitable habitat and new populations can represent an overwhelming task, especially when the species occurs across large spatial extents. Species distribution models can highlight a subset of possible search environments and by using such models to guide search efforts, we can strategically search for populations, prioritizing where to invest resources. Using a SDM to guide searches for suitable habitat is strategic in the sense that it eliminates typical search bias and examines the entire area of interest. All potential areas of interest are known and thus a strategic plan can be made to examine as many wetlands as possible. We had to make a series of choices on where to search based on time and budget constraints, but ideally all areas could be examined. Searches for habitat driven by information from a SDM would avoid biasing searches along or close to roads or previously searched locales, while drawing attention to difficult to access areas, like those on private property. This is especially important considering 80% of known Bog Turtle localities and 91.6% of suitable habitat occur on private

property. In South Carolina, we were able to examine much of the publically owned land, and subsequently concluded if Bog Turtles still exist in the state, they most likely occur only on private property. In South Carolina and Georgia, the publically owned land is often the most topographically intense in the state because these areas were not valuable as agricultural lands. Yet Bog Turtles, like agriculture, thrive in the valleys, which puts the species in direct conflict with agricultural developments. The SDM emphasizes these associations and offers a platform for large-scale conservation planning that will undoubtedly need to incorporate a number of stakeholders.

A regionally based SDM such as the one we created is particularly valuable for Georgia, South Carolina, and Tennessee, which have too few Bog Turtle records to build locally-based SDMs for Bog Turtles. In addition, in these states the need to find new populations is the greatest and the amount of area to search is the smallest. Collectively, these conditions mean over-prediction is less of a logistical problem. The large area modeled as suitable errs on the side of inclusion, which may be wise given our discovery of a Bog Turtle population in atypical habitat. Practical model application would likely require narrowing the focus to wetlands for survey, as was done in this study. Once this list is created, a long-term plan of action based on available resources becomes more realistic. For states like North Carolina and Virginia where the area modeled as suitable is much larger, this approach may be less feasible. Nevertheless, these states may choose to focus on areas where gaps in the range remain to be filled.

It should also be noted, that although a SDM may not always identify populations of the target species, it more often identifies suitable but unoccupied habitat. This suitable habitat could be used as a re-introduction site for Bog Turtles, or other mountain fen specialists (Tryon 2009). For example, our SDM identified two sites in Georgia that are now being considered as out-planting sites for Swamp Pink (Helonias bullata) and pitcher plants (e.g., Sarracenia purpurea). These wetlands could now also be surveyed for other species of concern within the state (e.g., Bog Lemmings, Synaptomys Hemidactylium Four-toed Salamanders, cooperi, scutatum, and Golden-winged Warblers, Vermivora chrysoptera).

The ground-based survey process is extremely time intensive (USFWS 2001; Somers and Mansfield-Jones 2008). Finding new populations of Bog Turtles will always represent a significant investment and state agencies must seriously consider if population discovery is where they should direct resources earmarked for this species. Such considerations are especially pertinent because a model that better identifies suitable habitat will not be available until a complete wetland layer and finer-grained environmental layers become available;

however, even those improvements may not alter the utility of the model if site history drives the distribution of the species. Conservation efforts for many species (e.g., flatwoods salamanders, Ambystoma cingulatum and bishopi), Pine Barren Treefrogs, Hyla andersonii, Gopher Frogs, Lithobates capito) pose the same logistical challenges because the species is rare on the landscape, difficult to detect even in suitable habitat, and greatly affected by land-use change. For these species the answer may simply be that until wetland and environmental data become more fine scale, finding new populations will be resource intensive, and as long as these data are unavailable, it may be more prudent to prioritize resources for restoration efforts and conservation of known populations.

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THERESA STRATMANN is currently a Ph.D. student at the Senckenberg Biodiversity and Climate Research Centre (BiK-F) and Department of Biological Sciences at the Goethe University in Frankfurt, Germany. This work was part of her undergraduate research at the University of Georgia and her Master's project at Clemson University. Theresa is interested in how we can combine ecology, math, and modeling to better approach today's challenging conservation problems. She is a former co-chair of the Southeast Partners in Amphibian and Reptile Conservation (SEPARC). (Photographed by Grover Brown).

KYLE BARRETT is an Ecologist in the Department of Forestry and Environmental Conservation at Clemson University. He is broadly interested in the influence of large-scale anthropogenic disturbances, such as urbanization and climate change, on the diversity and distribution of vertebrates. Kyle enjoys working on projects that have relevance to basic ecology and management/policy decision making. He received his Ph.D. from Auburn University. (Photographed by Shannon Barrett).

THOMAS M. FLOYD is a Wildlife Biologist in the Nongame Conservation Section of the Wildlife Resources Division, Georgia Department of Natural Resources. He received his BSFR from the University of Georgia and his MS from Clemson University (2003). Thomas is involved in the conservation of reptiles and amphibians including species of conservation concern within the State of Georgia, USA. Conservation efforts include population monitoring and species status assessments of rare herpetofauna, and habitat restoration and management including the implementation of prescribed fire. Thomas's research pursuits include species biogeography, techniques for the survey of elusive species, effects of land management and habitat degradation on herpetofauna, human dimensions in wildlife, and natural resources policy including policy analysis, drafting of laws and regulations for wildlife species conservation, and the development of incentives for private landowners in the conservation of endangered species. (Photographed by Matthew Kaurt).