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Finding the Needle and the Haystack: New Insights into Locating Bog Turtles (Glyptemys muhlenbergii) and their Habitat in the Southeastern United States

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FINDING THE NEEDLE AND THE HAYSTACK: NEW INSIGHTS INTO LOCATING BOG TURTLES (GLYPTEMYS MUHLENBERGII) AND THEIR HABITAT IN THE SOUTHEASTERN UNITED STATES

A Thesis
Presented to
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Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
Wildlife and Fisheries Biology

by
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Accepted by:
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ABSTRACT

Because rare and cryptic species can be difficult to locate, distribution maps for these species are often inaccurate or incomplete. Bog Turtles (Glyptemys muhlenbergii) are emblematic of this challenge. In fact, 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 within the southern range. Therefore we examined ways to better locate Bog Turtle habitat and Bog Turtles within that habitat. First we determined a detection probability for a standardized trapping method so we could effectively survey for Bog Turtles at sites with unknown occupancy status. A species distribution model (SDM) was then used to identify potentially suitable Bog Turtle habitat within the species’ southern range. The SDM was ground-validated, using our trapping method, to assess its ability to locate suitable Bog Turtle habitat. At a local scale we then analyzed wetlands occupied and unoccupied by Bog Turtles to examine differences in their habitat characteristics and site history. We had a 0.19 average probability of detecting a turtle at a site during one trapping event, implying 15 trapping events at a site would minimize the probability of Bog Turtles being at a site but going undetected to 5%. Ground-validation of the SDM with this trapping method showed that the SDM greatly over-predicted the amount of suitable habitat. For example, of 196 wetlands in Georgia and South Carolina identified as suitable by the SDM and ground-validated, only 22 met criteria for suitable Bog Turtle habitat, and trapping of 17 of those suitable wetlands revealed only 2 to be occupied by Bog Turtles. At the local scale, a discriminant analysis showed that wetlands with Bog
Turtles were distinguishable from those without based on area of the wetland, percent of the wetland that has emergent vegetation, percent of the wetland that is flooded by beaver or lake presence, and water pH. These results suggest that future work should focus on better understanding local scale characteristics distinguishing Bog Turtle wetlands, as current data resolution does not enable a SDM to be effective.
DEDICATION

I dedicate this thesis to Thomas Floyd and Grover Brown.

This project all began six years ago with Thomas Floyd of the Georgia Department of Natural Resources giving me a chance to work with Bog Turtles. Thomas has not only been instrumental with the field work portion of the project but has become one of my most valued mentors and friends. No years of schooling could have taught me about what it really means to try and save an endangered species on-the-ground like working with Thomas did. I created some truly unpleasant field work for us, and although he didn’t have to, Thomas stuck with me through it all. I will forever be thankful that I had the incredible luck to work with such an amazing person.

Grover Brown has also stuck with me throughout this project, helping out with three years of field work. No one else would be crazy enough to face the challenges we faced, all in the name of turtles. With no one else would I rather share a laugh, catch a turtle, or go on an adventure. His optimism and friendship are what help me through life’s hurdles.

Finally I would like to say that everything I did was for Bog Turtles. I am grateful that I get a thesis out this work, but every second was really about trying to further Bog Turtle conservation. The blood, sweat, and tears would never have been worth it otherwise. They’re a tremendous annoyance to study, but I do not want to live in a world without them, and will gladly donate more blood, sweat, and tears to fight for a world that is more than just skyscrapers and pigeons.
ACKNOWLEDGMENTS

This project would not have been possible without the help of many people. First there are the people who have always believed in me and encouraged a young girl with big dreams: my advisor, Dr. Kyle Barrett, my Riverbanks Zoo family – especially Scott Pfaff and Kathy Vause, my friends at the Turtle Survival Alliance, and my parents – Johannes and Claudia Stratmann. Dr. John Maerz helped me initially design the project and take it to some cool places like Washington D.C. Dr. Nate Nibbelink and Dr. Jena Hickey helped guide the initial stages of the species distribution model work. I would also like to thank my committee members, Dr. Robert Baldwin and Dr. Michael Dorcas for their involvement. Then there are all the people who helped with field work, despite the fact that it often was not fun: Grover Brown, Briana Cairco, Maddy Fesite, David Hutto, Meaghan Miranda, Todd Pierson, Danielle Sexton, Claudia Stratmann, Kathy Vause, and Sydney Wells. I am also indebted to all the wonderful landowners who let me explore the wetlands on their property and taught me about the history of the area. Funding and support was generously provided by the Bern W. Tryon Funding for Southern Bog Turtle Population Research, Clemson University, the Georgia Department of Natural Resources, Riverbanks Zoo and Garden, and the South Carolina Department of Natural Resources.
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CHAPTER

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CHAPTER ONE

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

Abstract. — Because rare and cryptic species can be difficult to locate, distribution maps 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 a species’ range that currently has no known occurrence records.
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 the species 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 America’s smallest and rarest species of chelonian (Ernst and Lovich 2009). The species’ range is split into two regions, a Northern range reaching from New York and Massachusetts south to Maryland and Delaware and a Southern range predominantly found 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; globally they are considered one of the 40 most endangered turtles (USFWS 1997; 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 (Chase et al. 1989; Tryon 1990). These wetlands are a rare features within the landscape, in part due to past drainage efforts for farming (Weakley and Schafale 1994). It is in this muck of these rare wetlands where Bog Turtles spend most of their time, making this small (maximum shell length of 11.5cm), 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 and individuals, the State Wildlife Action Plans 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; GA DNR 2005; NCWRC 2005; SC DNR 2005; 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 states’ goals of locating new populations.
Species distribution modeling (SDM) techniques are one way to map species habitat associations, and they have greatly increased in popularity as user-friendly geographic information systems (GIS) and easily accessed 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 the required 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 (see Rodríguez et al. 2006 for an overview), to decrease sampling effort when searching for rare species (Singh et al. 2009), to locate rare species [plants (Guisan et al. 2006; Williams et al. 2009; Le Lay et al. 2010; Buechling and Tobalske 2011), endemic insects (Rinnhofler et al. 2012), a cryptic mammal (Jackson and Robertson 2011), a bat (Rebelo and Jones 2010), and salamanders (Apodaca et al. 2012; Chunco et al. 2013; Peterman et al. 2013)], to define areas for re-introduction (McKenna et al. 2013), and prioritize conservation areas (Gogol-Prokurat 2011; Hunter et al. 2012). 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 the wetland by woody vegetation, invasive plant
species, and loss of habitat connectivity leave 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; Feaga et al. 2012; Feaga et al. 2013; 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) have too few occurrence records to build a strong state level model. In addition, by using all known occurrence records in the south, we increase the likelihood of providing an accurate 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 specimen. They were considered a northern species 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 range (Tryon 1990). This late discovery in the south is emblematic that the task is ongoing to find new populations that will establish a specific, thorough knowledge of the Bog Turtle range (USFWS 2001; GA DNR 2005; NCWRC 2005; SC DNR 2005; VA DGIF 2005). The task is complicated by the fact that we are now searching for populations after there has been much time for humans to alter the landscape 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 pressure are high (Wear and Bolstad 1998). For this reason, we restrict 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. 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).
FIGURE 1. Number of Bog Turtle localities by county for the southern portion of the Bog Turtle range. The light gray polygon represents all counties with known bog turtle localities plus a 25 km buffer. This region was used as the area of interest for the species distribution model.
Choice of species distribution model. — There are many potential modeling techniques to examine species habitat selection and distribution (Johnson et al. 2004; 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 machine-learning approach to species distribution modeling called maximum entropy (Maxent; Phillips et al. 2006), which has been shown to perform better than other presence-only models (Elith et al. 2006) 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 species’ range. By comparing the environment in areas with known Bog Turtle populations to the environment available to it (i.e. the background points), Maxent identifies species’ preferences 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 patches.

Occurrence records. — All presence data were obtained from the Georgia Department of Natural Resources, South Carolina Department of Natural Resources, North Carolina Wildlife 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 close 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 years, 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 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 randomly sampled. 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 in close proximity 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 (all anurans, all chelonians, several species of squamata (worm snake - *Carphophis amoenis*, ring-necked snake - *Diadophis punctatus*, 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/](http://www.herpnet.org/) [Accessed 22 November 2013]), BISON ([Biodiversity Information Serving Our Nation. Available from http://bison.usgs.orl.gov/#home](http://bison.usgs.orl.gov/#home) [Accessed 1 December 2013]), and GBIF ([Global Biodiversity Information Facility. Available from http://www.gbif.org/](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.
Predictor variables. — A 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. 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. Elevation data were obtained from the USGS Digital Elevation Model (DEM; Available from http://eros.usgs.gov/#/Guides/dem [Accessed 8 September 2013]) and were then used with the ArcGIS tool Focal Statistics to calculate topographic relief 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). Climatic variables (seasonality (BIO4) and maximum temperature of warmest month (BIO5)) were obtained from the WorldClim database (Available from www.worldclim.org/bioclim [Accessed 8 September 2013]) at a resolution of 1 km². We used land cover data from the 2011 National Land Cover Database (NLCD; Available from www.mrlc.gov/nlcd2011.php [Accessed 8 September 2013]) to characterize developed areas, pasture and hay fields, and wetlands. 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). Since known Bog Turtle localities are represented by points and extracting the data directly below a point can be an inaccurate representation of the larger area the wetland covers, we used the Focal Statistics tool to calculate the percent land cover of interest (e.g. percent pasture/hay) in the surrounding hectare. 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 and the National Wetlands Inventory (NWI; Available from http://www.fws.gov/wetlands/ [Accessed 8 September 2013]) and the USGS National Hydrography Dataset (Available from http://nhd.usgs.gov/ [Accessed 8 September 2013]), respectively. 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: percent organic matter, percent clay, and percent hydric soils. Soils data were obtained from 2015 Soil Survey Spatial and Tabular Data (SSURGO 2.2) and gaps were filled using the larger grain but more geographically complete U.S. General Soil Map (STATSGO2) (Available from http://websoilsurvey.nrcs.usda.gov/ [Accessed 8 September 2013]). All 12 environmental variables were resampled to the cell size of the smallest available data (30 m x 30 m) and were processed in ArcGIS 10.1. A Pierson’s correlation test was done in R version 3.1.1 (R Development Core Team 2014) on all 12 environmental variables. BIO4 and BIO5 each correlated with elevation (r = -0.70 and -0.98, respectively), but not with each other. Since elevation is a much finer-grain data set and addresses geographic distribution,
whereas climate addresses thermal tolerances, we kept all three. No other variables exhibited strong correlations (all r values < 0.70).

*Model Output Processing.* — 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 which areas we would examine on-the-ground. First, our ground-validation 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). 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.

At prioritized sites, we evaluated the quality of the habitat for Bog Turtles by following the Phase 1 survey guidelines established by the United States 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*), wither rod (*Viburnum nudum* L. var. *cassinoides*), royal fern (*Osmunda regalis*), cinnamon fern (*Osmunda cinnamomea*), red chokeberry (*Aronia arbutifolia*), turtle head (*Chelone glabra*); (5) large area of open canopy; (6) proximity to a stream; (7) active or historic beaver activity. Wetlands that met USFWS standards were those surveyed 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 un-baited, custom-made traps of galvanized welded-wire are set in shallow rivulets of water that could act as potential travel corridors for Bog Turtles (see Chapter 2). 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 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 1). Each model was driven by different environmental variables and thus produced different suitability maps (Fig. 2). In the RP model, distance to wetland, maximum temperature of warmest month, elevation, and topographic relief had the highest percent contributions (22.8%, 19.3%, 17.4%, and 10.8% respectively). In the TG model, distance to wetland, percent pasture/hay, percent developed area, and distance to stream had the highest contributions (30.7%, 29.3%, 17.1%, and 10.8% respectively). 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 1.** Overview of the SDM’s classification success. The Maxent models had high accuracy in correctly classifying the known Bog Turtle localities as suitable habitat. Known bog turtle localities 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.

<table>
<thead>
<tr>
<th>Site Suitability</th>
<th># Localities</th>
<th>Percentage (%) of All Localities (out of 72)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Combined Model</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>suitable in both models</td>
<td>52</td>
<td>72.2%</td>
</tr>
<tr>
<td>suitable in only one model</td>
<td>14</td>
<td>19.4%</td>
</tr>
<tr>
<td>unsuitable in both models</td>
<td>6</td>
<td>8.3%</td>
</tr>
<tr>
<td><strong>Random Points Model</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>suitable</td>
<td>56</td>
<td>77.8%</td>
</tr>
<tr>
<td>unsuitable</td>
<td>16</td>
<td>22.2%</td>
</tr>
<tr>
<td><strong>Target Group Model</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>suitable</td>
<td>62</td>
<td>86.1%</td>
</tr>
<tr>
<td>unsuitable</td>
<td>10</td>
<td>13.9%</td>
</tr>
</tbody>
</table>
Figure 2. Maxent logistic output for (a) the random points model and (b) the target group model. Warmer colors indicate higher suitability. Models are based off of the same presence points but the random points model uses 10,000 random generated points as background points, while the target group model uses ~2000 points derived from herpetofauna occurrences as its background points.
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).

**Figure 3.** Binary (suitable/unsuitable) model results for the random points (purple) and the target group (green) models. Black areas were considered suitable in both models.
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 this narrows to 316 wetlands designated as suitable by both models and 34 wetlands 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 113 were examined on the ground in Georgia and 83 in South Carolina. Nine of the 113 sites in Georgia were considered potential Bog Turtle habitat and were trapped. In South Carolina 13 of the 83 sites were considered potential Bog Turtle habitat, 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 about 10 to be 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 suggest that Maxent greatly over predicted the amount of suitable habitat. Of the nine trapped sites in Georgia, five were on public property and four were on private property. Of the eight trapped sites 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, three of the eight sites trapped were only deemed suitable by a single model. These sites were targeted based on their close 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 habitat specialist. Past studies have demonstrated success with this approach (Guisan et al. 2006; Williams et al. 2009; Le Lay et al. 2010; Rebelo and Jones 2010; Buechling and Tobalske 2011; Jackson and Robertson 2011; Apodaca et al. 2012; Rinnhofer et al. 2012; Chunco et al. 2013, Peterman et al. 2013); however, we found that the modeled distribution greatly over-predicted 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 areas of close proximity. 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 in presence points (Phillips and Dudík 2008). This target group (TG) model was substantially different from the standard random points background (RP) model (Fig. 2). 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) (Fig. 2). In the target group model, pasture/hay held the most information, with suitability increasing with 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. The actual importance of this habitat type may be over-emphasized and is probably due to the fact that 51% of Bog Turtle presence localities (37 out of 72) were associated with pasture/hay whereas only 10% (186 out of 1967) of the target group points were. The importance of pastures and 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 ultimately maintain quality Bog Turtle habitat. 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 used NLCD and NWI 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, 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 m x 30 m was the finest grain available (NLCD, DEM), with soil and climate environmental layers being particularly coarse. These large scale data sets used are also minimally ground-validated and have their own errors, which when combined with the lack of fine-scale resolution may mean that data are simply not fine enough resolution to pick-up small features like small wetlands within the larger landscape. Until finer resolution wetland and environmental data are available, there would be no way to improve the SDM. Two other factors that might explain the difficulty of building a SDM for Bog Turtles were brought to our attention by the fact that 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 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 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 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 amidst rocky
seeps as alternative refugia. The reporting of Somers and colleagues (2007) demonstrate
that this 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 site’s
history 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).

**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. 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. 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 cooperi*), four-toed salamanders (*Hemidactylium scutatum*), and golden-winged warbler (*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 since a model that better identifies suitable habitat will not be available until a complete wetland layer and finer-grained environmental layers become available and even those improvements may not alter the model’s utility if site history drives the distribution of the species. Conservation efforts for many species (e.g. flatwoods salamanders, pine barren tree frogs, gopher frogs) 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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CHAPTER TWO

DO HABITAT CHARACTERISTICS AND HISTORICAL DISTURBANCE PREDICT BOG TURTLE (GLYPTEMYS MUHLENBERGII) HABITAT OCCUPANCY AT THE FRINGE OF THEIR SOUTHERN RANGE?

Abstract. — Distinguishing between sites that a species does and does not occupy can enhance population discovery and management. For Bog Turtles (Glyptemys muhlenbergii), these differences are poorly understood and it was thus the objective of our study to determine whether wetland characteristics and site history can effectively distinguish wetlands occupied by Bog Turtles from those not occupied. We measured wetland characteristics and evaluated historical aerial photographs for eight occupied and 17 unoccupied wetlands in Georgia and South Carolina. Confidence of site occupancy was determined using results of trapping surveys in wetlands known to be occupied. These data minimized the probability that Bog Turtles were present but not detected at sites classified as unoccupied. After determining site status, we used a discriminant analysis to evaluate the ability of wetland environments and historical characteristics to predict occupancy status. Wetlands with Bog Turtles are distinguishable from those without based on area of the wetland, percent of the wetland that has emergent vegetation, percent of the wetland that is flooded by beaver or lake presence, and water pH. These promising results warrant further testing in other parts of the Bog Turtle range. In addition, this work produces the first quantifiable and repeatable method to survey for Bog Turtles, which will allow surveyors to have confidence that they are trapping sites with sufficient effort to detect even small populations of Bog Turtles.
INTRODUCTION

Ecology is often defined as the study of the distribution and abundance of organisms (Andrewartha and Birch, 1954). Indeed, the distribution of organisms is not a trivial study (Hutchinson, 1957; MacArthur and Wilson, 1967; Levins, 1969; Hubbell, 2001). Where a species is located within the landscape is confounded by several factors: (1) a species’ habitat needs (Hutchinson, 1957); (2) historical biogeographical processes such as a species’ ability to colonize a particular area (MacArthur and Wilson 1967, Levins 1969); (3) effects of past disturbances (Dupouey et al., 2002; Lunt and Spooner, 2005; Piha et al., 2007); and (4) stochastic events (Hanski 1998). Understanding what drives the distribution of a species can be very important to finding new populations and better conserving known populations through effective habitat restoration and maintenance. Finding new populations has been a particular challenge for the conservation of North America’s smallest and perhaps rarest chelonian, Bog Turtles (Glyptemys muhlenbergii). This challenge is amplified because biologists have an incomplete understanding of what drives the species’ distribution.

Bog Turtles are both rare and cryptic, and as a result they are a challenge to locate both within the landscape and within wetlands (Tryon, 1990; Somers and Mansfield-Jones, 2008). As their name suggests, they are deemed habitat specialist, confined to habitat that is known by a multitude of names: marsh, swamp, wet meadow, spring-fed wetland, seepage, bog, and fen (Tryon, 1990; Rosenbaum and Nelson, 2010). The common denominator is that these wetlands, at least the portions used by Bog Turtles, are usually shallow with a soft substrate of muck, open-canopied, and spring-fed (USFWS,
Wetland drainage, succession to forest, beaver (*Castor canadensis*) activity, invasive species, and land use change (e.g. use for pasture) have all altered Bog Turtle-inhabited wetlands such that they can actually take many forms. As a result, it is not unusual to find the species in habitat that currently appears marginal if not unsuitable. For example, Tesauro and Ehrenfeld (2007) have shown that wetlands in livestock pastures can be quite suitable while Sirois and colleagues (2014) have shown that populations persist (albeit while declining) in response to beaver activity and invasive species. The study by Sirois and colleagues (2014) also shows that Bog Turtle population growth can be enhanced by sound habitat management, so even identifying marginal habitats that are occupied can yield conservation benefits. In this context, determining what characterizes suitable habitat for Bog Turtles, or rather, what distinguishes wetlands occupied by Bog Turtles from those unoccupied, is not a trivial question. The need for such knowledge is great because 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 (USFWS, 2001; GA DNR, 2005; NC WRC, 2005; SC DNR, 2005; VA DGIF, 2005). Surveys for the species are extremely time consuming; therefore, surveys are only going to be cost effective when those wetlands most likely to be suitable for Bog Turtles are identified. Visual/probing surveys (called ‘Phase 2 Surveys’ in USFWS, 2006) require a minimum of 4 surveys of 3-6 person-hours per acre of wetland with 3 to 6 days between surveys (USFWS, 2006). Trapping surveys, based on recommendations in Somers and
Mansfield-Jones (2008), require the deployment of 20 traps per hectare for 20 days. Given how time consuming surveys are, it is often necessary to prioritize such that only those sites with the most potential to have Bog Turtles are ever evaluated in detail. Therefore both identifying wetlands to survey and prioritizing which to survey would greatly benefit from understanding if and how wetlands occupied by Bog Turtles differ from those that are unoccupied. To-date only two studies have explicitly and quantitatively compared wetlands occupied by Bog Turtles and those unoccupied. Myers and Gibbs (2013) conducted a study in Southeastern New York using 65 Bog Turtle-occupied wetlands. Their research focused on environmental variables available in GIS. In their study Bog Turtle wetlands were larger in area, contained a greater proportion of emergent and shrub-shrub vegetation, were located in larger watersheds, had more stream connections, and were more often over carbonaceous rock than randomly chosen wetlands within the same area. Feaga and colleagues (2012, 2013) examined 12 wetlands in southwest Virginia and showed that wetlands occupied by Bog Turtles had higher mean water tables and surface saturation then unoccupied wetlands. Yet, these hydrologic characteristics are time consuming and difficult to carry out making them unpractical for quick wetland assessments. On the other hand, those wetland characteristics examined by Myers and Gibb (2013) could be used to quickly assess the ‘Bog Turtle potential’ of a wetland, but their study depends heavily on the assumption that the unoccupied wetlands they used were truly unoccupied. Even if we assume unoccupied wetlands were truly unoccupied, then it still remains to be seen if their study findings transfer to other portions of the Bog Turtle range.
The Bog Turtle range covers a broad area of the eastern United States, and differences across a latitudinal gradient have been identified. For example, the species’ distribution appears in part to be determined by thermoregulatory requirements. Thus in the southern portion of their range, Bog Turtles are a montane species while they are found close to sea level in the northern portion (Tryon, 1990; Rosenbaum and Nelson, 2010). The change in latitude also comes with a change in underlying geology which ultimately affects wetland chemistry and vegetation (Moorhead and Rossell, 1998). These landscape-scale changes in the setting of Bog Turtle wetlands thus warrant studies in both the southern and northern portion of the range to ensure that trends are consistent. In addition, the study by Myers and Gibbs (2013) seems atypical as they were looking at wetlands $13.93 \pm 64.49$ ha (mean $\pm 95\%$ confidence interval) while most studies across the range describe Bog Turtle wetlands as less than 2 ha (Tryon, 1990; Buhlmann et al., 1997). This discrepancy might be due to differences in definitions used among studies (entire wetland complex area vs. area used by Bog Turtles) or the fact that the Myers and Gibbs (2013) study used National Wetland Inventory (NWI) wetlands which tend to be larger wetlands (Leonard et al., 2012).

In addition these two studies do not consider history of the wetlands, and recent studies have shown that past land use history can affect present day distribution of species (Dupouey et al., 2002; Lunt and Spooner, 2005; Piha et al., 2007). This is especially relevant for Bog Turtles as the shallow, open canopy wetlands they favor were heavily targeted in past drainage efforts, converting wetlands to pastures and agricultural fields (Tryon, 1990; Morrow and Rossell, 1998). In many cases, when maintenance of
ditches or tiles was abandoned or drainage was incomplete, wetlands were able to recover or persist in a degraded state. On the other end of the spectrum, lack of disturbance can lead to encroachment of wetlands by woody vegetation, which ultimately makes the wetland unsuitable for Bog Turtles (Tryon, 1990; USFWS, 2001; Ernst and Lovich, 2009). Together this creates a continuum of wetlands in different stages of degradation, some of which may still be suitable for Bog Turtles. Thus knowledge of current and past disturbances and their duration may be important in predicting if a wetland, even though it looks degraded, could still be occupied by Bog Turtles. This influence of site history on Bog Turtle presence at a site has been minimally explored in the Bog Turtle literature.

Given the aforementioned gaps in knowledge it is the objective of our study to determine whether habitat characteristics at a site and site history can effectively distinguish wetlands occupied by Bog Turtles from those that are not. Specifically we focused on wetlands at the fringe of the southern range, in Georgia and South Carolina, where little is known about the distribution of Bog Turtles. To-date there are eight extant, three historical, and two introduced populations of Bog Turtles in Georgia. In South Carolina there are only five known sightings of Bog Turtles, none of which have ever been connected to a population. Better understanding of occupied habitats will promote identification of new populations and allow for better management of occupied sites within these states and the range as a whole.
MATERIALS AND METHODS

Site Selection and Description. — We surveyed 17 wetlands in Georgia and eight in South Carolina (Fig. 1). All surveyed sites were within the Blue Ridge physiogeographic region. Eleven of the Georgia sites had been identified and surveyed by the Georgia Department of Natural Resources (GA DNR) before 2014. The remainder of the sites were selected with the help of a species distribution model (SDM), which identified potential areas of suitable Bog Turtle habitat in the southern portion of the Bog Turtle range (see Chapter 1). The wetlands chosen by the SDM and used in this study all met suitable Bog Turtle habitat criteria according to USFWS (2001).
FIGURE 1. Map of the study area within northern Georgia and South Carolina, USA. We trapped 17 wetlands across four counties in Georgia and eight wetlands across three counties in South Carolina. Trapping was confined to the Blue Ridge physiogeographic region of each county.

Survey Method: Trapping. — A key part of our ability to examine differences between wetlands occupied by Bog Turtles and those that are not, is confidence in designating a wetland as unoccupied by Bog Turtles. Although we can easily show a species occurs at a site, we can rarely prove its absence. Instead, we quantified the detection probability of our Bog Turtle survey method and used this to calculate the
probability that Bog Turtles was present at a site but went undetected (Maerz et al., in press).

Bog Turtles have historically been surveyed using either visual and probing surveys (USFWS, 2006) or un-baited traps (USFWS, 2006; Somers and Mansfield-Jones, 2008). Although visual and probing surveys are most frequently used (e.g., US Fish and Wildlife Service recommends such surveys prior to trapping), trapping-based methods are easier to standardize across sites, and unlike visual and probing surveys, they are not affected by time of day or weather.

Trapping is generally conducted according to the recommendations given by Somers and Mansfield-Jones (2008) of setting 20 traps per hectare for 20 days (a 20-20 rule). The study promoting this rule is based only on two Piedmont populations in North Carolina, and no detection probabilities were associated with the guidelines. Additionally, although the method recommends a trapping density and duration, it does not describe the arrangement of traps, which actually determines density and thus the replicability of the method. Trap arrangement is crucial because traps are not baited and strictly catch turtles within the travel corridor where traps are placed. Given the lack of detail in the Somers and Mansfield-Jones (2008) study, we felt it was important to create and validate our own trapping strategy. This would better allow for standardized trapping effort across sites and better promote replication among study efforts.

The objective of our trapping method was to detect a population of Bog Turtles at a site. Each wetland of interest was examined for an area within it deemed most suitable for trapping and Bog Turtles. These areas: (1) had small rivulets of water flowing over a
mucky substrate, or other potential travel corridors (e.g. small mammal tunnels in the vegetation, ditches); (2) had a substrate that was somewhat firm so the bottom of the trap was only covered by 1-2 inches of water and turtles were more likely to attempt to enter the trap than dive under it; and (3) were not so thickly covered in vegetation as to prevent traps from being set. Open canopy was preferred to closed canopy, though canopy cover does not appear to be a strict regulator of habitat use. Trapping areas were not always contiguous within the wetland. Trapping took place between late April and mid-July of 2014. Specifically, determination of trapping location and trap placement occurred in late April to May when vegetation was still low and travel corridors were most apparent.

Once a suitable trapping area was delineated, the area was gridded into 5 m by 5 m grid cells and one trap was placed in the most suitable travel corridor within each grid cell (Fig. 2). Set traps were placed such that they were filled with 1-2 inches of water to keep the animals cool and hydrated. Each trap was covered with vegetation to prevent turtles from direct exposure to sunlight. By gridding the suitable area, we avoided clumping traps in certain areas and we were forced to assess the entire trappable habitat, maximizing number and length of travel corridors trapped.

With the permission of the Georgia Department of Natural Resources (GA DNR) and South Carolina Department of Natural Resources (SC DNR), all sites evaluated in this study were trapped using this method. One trapping event consisted of a 48 hour period. We deployed a total of 536 traps over 23 sites. The two other sites used in this study were trapped in previous years using the same method.
Figure 2. A schematic of the trapping method used in this study. Trapping takes place in the part of the wetland that is most suitable for Bog Turtles and where trap placement can be accommodated. A gridding method is used to thoroughly examine available trapping habitat and facilitate unbiased, even trap placement. In some grid cells there are no appropriate places to set a trap and thus none are set. In some sites the main movement corridors might be ditches. The trapping portion of the wetland may also be split into several distinct sections, if there is unsuitable habitat between suitable sections.

Determining Site Status (Occupied/Unoccupied). — Data obtained from trapping occupied wetlands in 2014 was used to calculate a detection probability for our trapping method. Data were analyzed in Program MARK version 7.1 (White and Burnham, 1999) using the Occupancy Estimation option. Due to limited data (eight sites, 29 survey occasions) we examined only two different models. In both models $P_{si}$
(occupancy) was set to be constant across sites, as we know all sites to be occupied, while $p$ (probability of detecting a Bog Turtle at a site during a given trapping event) was set constant in one model and allowed to vary by site in the other. The model allowing detection to vary by site had the most support, and was therefore used to calculate how the probability that the species is present but undetected ($1-p$) decreases with increasing survey effort (Table 1). This enabled us to calculate probability that Bog Turtles were present but never detected at sites considered unoccupied (Table 2).

Two sites were not trapped in 2014. Site G (0.46 ha) was trapped in 2010 (10 traps/65 days), 2011 (20 traps/44 days), and 2012 (16 traps/54 days). Trapping in 2010 occurred before our method was refined and thus was at a lower density, with traps set opportunistically. One Bog Turtle was captured in 2010 but subsequent surveys resulted in no recaptures or new captures. This site is therefore transiently occupied but was grouped with occupied sites in all analyses. Site N (15.48 ha) has been trapped periodically since 1992 and 12 turtles are known from the site. We trapped it in 2010 (22 traps/65 days) and captured two individuals and again in 2011 (26 traps/61 days) and captured four individuals six times. In 2012-2014 flooding by beaver made the site impossible to trap; however, based on previous captures, the site was considered occupied. Finally, it should be noted that two of the sites considered unoccupied (sites CC and J) have introduced populations of Bog Turtles and were thus used to help determine detection probability, but because no non-introduced Bog Turtle has ever been captured at the site, they are categorized with the unoccupied sites for the purpose of the analysis.
Table 1. Detection probabilities for occupied Georgia wetlands to calculate required trapping effort. Eight sites with Bog Turtle populations were trapped in Georgia using a trap density of 1 trap/25m$^2$. Here we report the probability of detecting a Bog Turtle at a site during one trapping event (a 48 hour period). By taking the inverse (the probability that Bog Turtles are present at the site but not detected during a trapping event) we determined how long a site must be trapped before there is only a ≤ 10% or ≤5% chance that Bog Turtles are present at the site but were not detected (highlighted in gray).

<table>
<thead>
<tr>
<th># days</th>
<th># of trapping events</th>
<th>probability Bog Turtles are present, but not detected</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>1</td>
<td>0.59 0.69 0.76 0.83 0.86 0.90 0.93 0.97</td>
</tr>
<tr>
<td>4</td>
<td>2</td>
<td>0.34 0.48 0.58 0.68 0.74 0.80 0.87 0.93</td>
</tr>
<tr>
<td>6</td>
<td>3</td>
<td>0.20 0.33 0.44 0.57 0.64 0.72 0.81 0.90</td>
</tr>
<tr>
<td>8</td>
<td>4</td>
<td>0.12 0.23 0.33 0.47 0.55 0.65 0.75 0.87</td>
</tr>
<tr>
<td>10</td>
<td>5</td>
<td>0.07 0.16 0.25 0.39 0.48 0.58 0.70 0.84</td>
</tr>
<tr>
<td>12</td>
<td>6</td>
<td>0.04 0.11 0.19 0.32 0.41 0.52 0.65 0.81</td>
</tr>
<tr>
<td>14</td>
<td>7</td>
<td>0.02 0.07 0.14 0.27 0.35 0.47 0.61 0.78</td>
</tr>
<tr>
<td>16</td>
<td>8</td>
<td>0.01 0.05 0.11 0.22 0.31 0.42 0.56 0.76</td>
</tr>
<tr>
<td>18</td>
<td>9</td>
<td>0.01 0.04 0.08 0.18 0.26 0.37 0.53 0.73</td>
</tr>
<tr>
<td>20</td>
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<td>0.02 0.06 0.15 0.23 0.34 0.49 0.70 0.13</td>
</tr>
<tr>
<td>22</td>
<td>11</td>
<td>0.02 0.05 0.12 0.20 0.30 0.46 0.68 0.10</td>
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<tr>
<td>24</td>
<td>12</td>
<td>0.01 0.04 0.10 0.17 0.27 0.42 0.66 0.09</td>
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<tr>
<td>26</td>
<td>13</td>
<td>0.01 0.03 0.09 0.15 0.24 0.39 0.63 0.07</td>
</tr>
</tbody>
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<table>
<thead>
<tr>
<th></th>
<th>RC</th>
<th>BT</th>
<th>WC</th>
<th>E</th>
<th>H</th>
<th>J</th>
<th>FL</th>
<th>CC</th>
<th>Average</th>
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<tbody>
<tr>
<td>p (detection probability)</td>
<td>0.41</td>
<td>0.31</td>
<td>0.24</td>
<td>0.17</td>
<td>0.14</td>
<td>0.10</td>
<td>0.07</td>
<td>0.03</td>
<td>0.19</td>
</tr>
<tr>
<td>1-p</td>
<td>0.59</td>
<td>0.69</td>
<td>0.76</td>
<td>0.83</td>
<td>0.86</td>
<td>0.90</td>
<td>0.93</td>
<td>0.97</td>
<td>0.81</td>
</tr>
<tr>
<td># captures (recaptures)</td>
<td>14(6)</td>
<td>4(5)</td>
<td>2(5)</td>
<td>2(3)</td>
<td>5(0)</td>
<td>2(1)</td>
<td>1(1)</td>
<td>1(0)</td>
<td></td>
</tr>
<tr>
<td># days</td>
<td># of trapping events</td>
<td>probability Bog Turtles are present, but not detected</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>--------</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.01       0.02       0.07       0.13       0.22       0.37       0.61</td>
<td>0.06</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>30</td>
<td>15</td>
<td>0.02      0.06       0.11       0.19       0.34       0.59</td>
<td>0.05</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>32</td>
<td>16</td>
<td>0.01      0.05       0.09       0.17       0.32       0.57</td>
<td>0.04</td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>40</td>
<td>20</td>
<td></td>
<td></td>
<td>0.02      0.05       0.11       0.24       0.50</td>
<td>0.02</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>42</td>
<td>21</td>
<td>0.02      0.04       0.10       0.22       0.48</td>
<td>0.01</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>54</td>
<td>27</td>
<td>0.01      0.02       0.05       0.15       0.39</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>64</td>
<td>32</td>
<td></td>
<td>0.01      0.03       0.10       0.33</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>82</td>
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<tr>
<td>130</td>
<td>65</td>
<td></td>
<td></td>
<td></td>
<td>0.01      0.10</td>
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<tr>
<td>166</td>
<td>83</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.05</td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>
Table 2. Trapping effort invested at 23 sites in Georgia and South Carolina from late April to mid-July of 2014. For sites in which no Bog Turtles were captured and sites were considered unoccupied, we show the probability Bog Turtles are actually present at those sites but were not detected. Estimates are given for the lowest and highest detection probabilities we observed in our occupied sites, as well as the average detection probability.

<table>
<thead>
<tr>
<th>Site</th>
<th>Area (ha)</th>
<th># Traps Set</th>
<th>Area Trapping Represents* (m²)</th>
<th>Days Trapped</th>
</tr>
</thead>
<tbody>
<tr>
<td>Occupied Sites</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RC</td>
<td>1.57</td>
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<td>700</td>
<td>58</td>
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<td>E</td>
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<td>58</td>
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<td>WC</td>
<td>1.02</td>
<td>15</td>
<td>375</td>
<td>58</td>
</tr>
<tr>
<td>HAM</td>
<td>1.96</td>
<td>32</td>
<td>800</td>
<td>82</td>
</tr>
<tr>
<td>BT</td>
<td>1.59</td>
<td>19</td>
<td>475</td>
<td>82</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Unoccupied Sites</th>
<th>Probability Bog Turtles are Present but were Not Detected</th>
</tr>
</thead>
<tbody>
<tr>
<td>TR</td>
<td>0.13</td>
</tr>
<tr>
<td>OSSHS</td>
<td>2.96</td>
</tr>
<tr>
<td>AH</td>
<td>1.67</td>
</tr>
<tr>
<td>WAT</td>
<td>0.09</td>
</tr>
<tr>
<td>288</td>
<td>10.60</td>
</tr>
<tr>
<td>WOOD</td>
<td>0.23</td>
</tr>
<tr>
<td>A</td>
<td>0.62</td>
</tr>
<tr>
<td>BRO</td>
<td>3.12</td>
</tr>
<tr>
<td>TB</td>
<td>1.15</td>
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<tr>
<td>CC</td>
<td>0.28</td>
</tr>
<tr>
<td>J</td>
<td>0.63</td>
</tr>
<tr>
<td>HOL</td>
<td>0.23</td>
</tr>
<tr>
<td>P</td>
<td>0.86</td>
</tr>
<tr>
<td>WW</td>
<td>0.12</td>
</tr>
<tr>
<td>BURN</td>
<td>0.68</td>
</tr>
<tr>
<td>M</td>
<td>2.70</td>
</tr>
<tr>
<td>S</td>
<td>0.49</td>
</tr>
</tbody>
</table>

*Area trapped = # traps * 25m² as the method was to divide the trapping area into 5 m x 5 m grid cells and assign one trap to each grid cell (1 trap/25 m²)
Habitat Characteristics. — We evaluated 11 habitat characteristics hypothesized to influence Bog Turtle occupancy during fall 2014. The first five were related to soil properties (percent organic matter, percent sand, percent silt, percent clay, and soil pH). Bog Turtles spend much of their time within the first 10 cm of muck in a wetland (Pittman and Dorcas, 2009), and thus may select for certain soils that are easier to move through (Feaga et al., 2013). We used a composite soil sampling approach, generally following the method of Feaga et al. (2013). Composite sampling involved using an 8 cm diameter, 16.5 cm long bucket auger to collect 10 soil samples in areas covered by water from random locations within the perimeter of the wetland. We created a single sample from each wetland by mixing all subsamples and removing any pieces of vegetation, large roots, or woody debris. Samples were air dried and then sent to the University of Georgia Cooperative Extension’s Soil, Plant, and Water Laboratory for analysis for percent organic matter, percent sand, percent silt, percent clay, and soil pH. Organic matter is determined by the loss on ignition method for 3 hours at 360°C and results are given as percent by weight. Soil pH is calculated by placing 20 cm³ of soil in a 3-ounce wax-paper cup with 20 ml of 0.01 molar calcium chloride solution, which is allowed to equilibrate for at least 15 minutes. The soil pH is then measured using a LabFit AS-3000 Dual pH Analyzer. Since this method uses 0.01 molar calcium chloride, as it gives more consistent readings when soil salts are low and between sampling periods, instead of deionized water, 0.6 is added to the measured value to make it comparable to the traditional method.

In addition to determining soil pH, we also recorded water pH at all of our sites, as southern mountain fens tend to be acidic (Moorhead and Rossell, 1998). pH of a wetland determines the vegetation community which in turn determines its faunal community (Weakley and Schafale, 1994; Moorhead and Rossell, 1998). Water pH was measured using a YSI with a
600r sonde (YSI, Yellow Springs, OH). As pH can vary within a site, three readings were taken randomly within the wetland and then averaged.

The remaining habitat characteristics describe the structure of the wetland. We used a GPS (Garmin GPSmap 62sc) to delineate the perimeter of the wetland, based mainly on presence of wetland indicative vegetation and topography. Myers and Gibbs (2013) found wetland area to be an important factor distinguishing occupied from unoccupied wetlands. Like Myers and Gibbs (2013) we also divided the wetland into the three relevant wetland categories described by Cowardin et al. (1979): palustrine emergent (PEM), palustrine scrub-shrub (PSS), and palustrine forested (PFO). Unlike Myers and Gibbs (2013) who got their data from NWI, we delineated these different wetland types on-the-ground using a GPS, as most wetlands were too small to use aerial imagery to accurately characterize the different parts of the wetland. In this process we also delineated the area influenced by beaver flooding, as beaver flooding has been shown to negatively impact Bog Turtle populations (Sirois et al., 2014).

Measuring the Influence of Site History. — To examine the effect of site history on current use of wetlands by Bog Turtles we used historical aerial imagery. Aerial images have been taken since the late 1930s and thus it was our goal to collect at least one photograph of each of our study wetlands per decade, beginning with the 1940s. The photos were obtained either through EarthExplorer (USGS, Available from http://earthexplorer.usgs.gov/ [Accessed 21 January 2015]) or the University of Georgia Map Library, where hard copies of the images were scanned. Quality of the imagery varied throughout the decades, but all of our wetlands were distinct enough to easily locate in all images without georeferencing. We were strictly interested in condition of the wetland, rather than surrounding land use, as Bog Turtles tend to stay within one wetland, with only few individuals ever documented moving away from or between sites.
(Lovich et al., 1992; Carter et al., 1999; Morrow et al., 2001; Pittman and Dorcas, 2009). We therefore would expect within-wetland disturbances to have the greatest impact on Bog Turtles.

Four within-wetland disturbances were of interest to us: (1) wetland drainage, especially when it resulted in the conversion of the wetland to a pasture or agricultural field; (2) encroachment by woody vegetation leading to a closed canopy state; (3) beaver activity; and (4) flooding due to lake creation or maintenance. We identified the presence or absence of these disturbances within each decade from 1940 to 2014 and used that information to create an index of historical disturbance. This index ranges from 0 to 100, with higher numbers indicating more disturbance.

To create this index each disturbance was given a point value from 0 to 3. These point values were determined based on what we know about how these disturbances affect Bog Turtles. Wetland conversion to pasture can cause loss of habitat, but if the wetland does not completely disappear and there is presence of livestock, Bog Turtle populations can thrive (Buhlmann et al., 1997; Tesauro and Ehrenfeld, 2007). Yet creation of pasture also implies attempts at drainage of the wetland. Wetlands can be drained using either ditches or tiles, both of which lower the water table, often completely draining the wetland. While other turtle species have been shown to persist in ditches (Yagi and Litzgus, 2012; O’Bryan, 2014), tiling re-routes all water underneath the surface leaving no wet refugia like ditching does. Thus we would expect tiling to be much worse for wetland species than ditching. Although ditching and tiling continue to affect the wetland for many decades, wetlands can recover if these drainage systems are not maintained and fill in over time. Based on the above rationale, conversion of >75% of the wetland to pasture was given a value of 1. Another point was added for evidence of ditching, and 2 points were added for evidence of tiling. Beaver activity, like creation of pasture, can also be damaging as well as beneficial. Flooding can create temporary loss of habitat and promote
invasive species, negatively affecting populations (Sirois et al., 2014). On the other hand, by killing trees, the flooding can also open-up wetlands that have slowly succeed to a closed canopied state, creating open-canopied wetlands suitable for Bog Turtles once beaver leave and the flooding stops (Weakley and Schafale, 1994; Buhlmann et al., 1997; Moorhead and Rossell, 1998). Thus beaver activity during a decade was also given a value of 1. Encroachment of the wetland by woody vegetation is another common problem that occurs due to lack of disturbance (USFWS, 2001). Encroachment by woody vegetation such as alder (Alnus serrulata) and red maple (Acer rubrum) creates a positive feedback cycle where presence of woody vegetation lowers the water table through transpiration, making it more suitable for other types of woody vegetation which continue to remove water from the wetland (Moorhead and Rossell, 1998). Thus a prolonged closed canopy state can ultimately make the wetland unsuitable for Bog Turtles due to lack of sunlight and a low water table. Sites where >75% of the area was closed canopied, were assigned a value of 1. The last category, lake influence, reflects the fact that many lakes may have once been larger Bog Turtle habitats that were dammed for energy, recreation, or control structure purposes. Such activity would most likely, relegate Bog Turtles to the margins of the flooded region. Thus we were interested to see if they could indeed persist in these types of habitat. Often these lake influenced sites experience considerable erratic flooding, which is an unsuitable condition for a semiaquatic turtle like a Bog Turtle, so we assigned a value of 3 points to areas subject to fluctuating lake levels. Ultimately, these point assignments were meant to make minimal assumptions and were limited to disturbances that could be easily seen in aerial images.

To assign an index value to a given wetland, each decade was assigned the appropriate number of points for each disturbance and then points were summed across decades. Majority
open pasture and majority closed canopy are mutually exclusive. Pastures can revert to wetlands over time but once ditched or tiled these structures continue to affect the wetland and thus we continue to add points for these activities in all subsequent decades after initial drainage attempts. If both beaver and lake influence were present, the dominant disturbance was chosen. A ditched or tiled pasture cannot also be a beaver wetland and in the unlikely case that there is a beaver wetland in a forest, we would not be able to tell. This meant that for each decade there could be a maximum of four points (if a site was a ditched and tiled pasture). Since there were occasional gaps in availability of aerial imagery, we standardized across sites by dividing total number of points earned by total number of possible points (4*number of decades of imagery) and multiplying by 100. Thus our index ranged from 0 to 100 with 0 indicating no disturbance and 100 indicating maximum disturbance. In addition we also calculated how long a site has had to recover from disturbance. Examples of recovery from disturbance include a pasture reverting back to a wetland state, a pasture no longer being mowed or maintained, beaver leaving a site, or a lake being drained.

**Discriminant Analysis.** — Information on habitat characteristics and historical disturbance were analyzed using a discriminant analysis (DA). A DA identifies which combination of environmental variables distinguish groups of interest. The influence of variables by themselves and in conjunction with each other are relevant to the final results. It is often considered a reverse ANOVA because the environmental variables are the independent variables and the groups the dependent variables. DA not only determines which combination of environmental variables predict group membership, but can also be used to predict which group a site belongs to, given its environmental characteristics (McCune and Grace, 2002).
Data used in a DA must meet several assumptions. First the predictor variables cannot correlate (assumption of non-multicollinearity). We ran a Pierson’s correlation test on all variables, keeping those with $|r|<0.70$. Percent clay and percent sand were correlated ($r = -0.85$) so we removed percent sand. We then standardized the remaining variables using the `scale()` function in R. Next, we tested data for homogeneity of variance/covariance using the approach of Anderson (2001) which relies on the `betadisper()` and `permutest()` functions in the R package vegan version 2.0-10 (Oksanen et al., 2013). As variances were equal ($p = 0.31$) we then tested for multivariate normality. We evaluated normality by (1) examining a linear model of the predictor variables and plotting a histogram of the residuals; (2) a Shapiro-Wilkes tests for each of the group/predictor variable combinations; and (3) Q-Q plots for each variable. All approaches suggested the majority of the data did not differ substantially from bivariate normality. With assumptions met, we ran the DA using the `lda()` function in MASS package (Venables and Ripley, 2002), with sites categorized as described under Methods: Determining Site Status. All analyses were run in R version 3.1.1 (R Development Core Team 2014).

**RESULTS**

Data gathered in the mark/recapture study were best represented by an occupancy model that let detection ($p$) vary by site, while keeping occupancy ($\Psi$) constant. Detection probabilities varied greatly from site-to-site, ranging from $p = 0.03$ to $p = 0.41$ (Table 1). The lowest detection probability occurred at a site with only 3 individuals, only one of which was caught in 2014. Yet a small number of individuals at a site did not always result in low detection probabilities, as years of trapping has shown that there are only 2 individuals at WC but these individuals were recaptured frequently enough to have a high detection probability. For a site
with an average detection probability \( p=0.19 \) it would take 15 trapping occasions (30 days) before there is only a 5% chance that Bog Turtles are present but were not captured (Table 1).

Examination of the habitat characteristics showed that there were no pairwise differences between occupied and unoccupied sites (Table 3). The historic disturbance index also did not show any obvious differences between occupied and unoccupied sites (Table 3). It is interesting to note that 6 out of 10 occupied wetlands were pastures at one point in their history and 8 out of 10 have evidence of past drainage efforts. Site H was even tiled, with no evidence of a wetland until 1984, but that site has recovered sufficiently to hold one of the larger populations of Bog Turtles in Georgia to-date. Site BT could only be identified as a forest until 1980 when a power line cut is evident for the first time, giving the impression that this site is only suitable because the power line installation opened the canopy.

Despite a small sample size and the fact that there were no apparent trends in the variables by themselves, the discriminant analysis shows that the sites do group as a function of occupancy status in reduced environmental space (Figure 3). The DA was able to correctly classify 22 out of 25 sites. Area of the wetland, percent of the wetland that can be classified as PEM, percent of the wetland that is flooded by beaver activity or lake, and water pH contributed the most to distinguishing between the groups, respectively.
**Table 3.** Mean and range of the wetland characteristics used in the discriminant analysis.

Results are divided into those for wetlands occupied by Bog Turtles \((n = 8)\) and for those unoccupied \((n = 17)\). %PEM, PSS, and PFO refer to the wetland classification of Cowardin et al. (1979) and represent the percent of the wetland that is considered palustrine emergent (PEM), palustrine scrub-shrub (PSS), and palustrine forested (PFO). % flooded refers the percentage of the total area that is influenced by flooding due to beaver activity or fluctuating lake levels. A detailed description of the historical disturbance index and years of recovery variable can be found in the *Methods* section.

<table>
<thead>
<tr>
<th>Wetland Characteristic</th>
<th>Occupied Range</th>
<th>Occupied Mean</th>
<th>Unoccupied Range</th>
<th>Unoccupied Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>% organic matter</td>
<td>5.71 – 17.78</td>
<td>11.18</td>
<td>5.1 – 19.03</td>
<td>9.72</td>
</tr>
<tr>
<td>% silt</td>
<td>24 – 42.1</td>
<td>33.75</td>
<td>18 – 50.1</td>
<td>34.40</td>
</tr>
<tr>
<td>% clay</td>
<td>12 – 36.3</td>
<td>23.14</td>
<td>4.2 – 56.2</td>
<td>21.78</td>
</tr>
<tr>
<td>Water pH</td>
<td>5.66 – 6.67</td>
<td>6.10</td>
<td>5.20 – 6.58</td>
<td>5.93</td>
</tr>
<tr>
<td>% PEM</td>
<td>0 – 88.29</td>
<td>48.23</td>
<td>0 – 88.67</td>
<td>24.53</td>
</tr>
<tr>
<td>% PSS</td>
<td>0 – 57.00</td>
<td>24.52</td>
<td>0 – 100</td>
<td>57.01</td>
</tr>
<tr>
<td>% PFO</td>
<td>0 – 51.03</td>
<td>27.26</td>
<td>0 – 86.59</td>
<td>18.46</td>
</tr>
<tr>
<td>% flooded area (ha)</td>
<td>0.46 – 15.48</td>
<td>3.09</td>
<td>0.09 – 10.60</td>
<td>1.56</td>
</tr>
<tr>
<td>historical disturbance index</td>
<td>3.13 – 81.25</td>
<td>39.04</td>
<td>10.71 – 96.43</td>
<td>45.59</td>
</tr>
<tr>
<td>years of recovery</td>
<td>0 – 68</td>
<td>34.63</td>
<td>0 – 68</td>
<td>39.76</td>
</tr>
</tbody>
</table>
**Figure 3.** Results of the discriminant analysis on occupied ($n = 8$) and unoccupied ($n = 17$) Bog Turtle wetlands in Georgia and South Carolina, USA. Our analysis consisted of only two groups, resulting in only one linear discriminant and thus we simply plot the discriminant scores for each site. Misclassified sites are marked in red and indicated by an arrow.
DISCUSSION

Locating new populations of Bog Turtles is important to effectively conserve this species (USFWS, 2001; GA DNR, 2005; NC WRC, 2005; SC DNR, 2005; VA DGIF, 2005), but we understand very little about how wetlands occupied by Bog Turtles differ from those that are unoccupied (Feaga et al., 2012, 2013; Myers and Gibbs, 2013). To fill this gap, we used local habitat characteristics and information on site history to try and distinguish between wetlands occupied by Bog Turtles and those that are not. We examined 25 wetlands for this study, 8 occupied and 17 unoccupied. Habitat characteristics examined in isolation did not vary as a function of occupancy status (Table 3). When evaluated in a multivariate framework, a subset of these habitat variables become important in distinguishing among occupied and unoccupied sites. Area of the wetland, percent of the wetland that can be classified as PEM, percent of the wetland that is flooded by beaver activity or lake, and water pH contributed the most to distinguishing between the groups. Generally occupied sites have little beaver flooding, have a larger portion of the wetland that is PEM, and are least a hectare in size. Water pH only ranges from 5.16 to 6.67, with an average of 6.00 for the occupied sites and 5.89 for the unoccupied sites, and it is difficult to imagine that Bog Turtles would be responding to such differences changes in pH. Site history only ranked 7th in importance in distinguishing between groups. This variable may have greater importance if we were able to consider abundance instead of simply occupancy, as many of our occupied sites vary widely in both historical disturbance and the total number of turtles captured. Often less disturbed and degraded sites have larger populations (Table 4).
**Table 4.** Overview of occupied Bog Turtle wetlands within Georgia, USA. Descriptions are given to emphasize distinguishing features of wetland history and habitat and how they relate to abundance. We approximate abundance by number of individual turtles observed since 2010, when formal trapping efforts began.

<table>
<thead>
<tr>
<th>Site</th>
<th># Turtles Observed Since 2010</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>RC</td>
<td>21</td>
<td>Small (&lt;1 ha) fen with no past history of disturbance</td>
</tr>
<tr>
<td>E</td>
<td>9</td>
<td>Affected by extensive ditching in the past and present-day beaver activity but a recovering fen.</td>
</tr>
<tr>
<td>H</td>
<td>9</td>
<td>Despite being a ditched and tiled pasture in the past, this is now a well recovered fen fed by springs located within the former pasture. There is also an active beaver presence.</td>
</tr>
<tr>
<td>BT</td>
<td>7</td>
<td>A series of seeps running down a hillside under a power line cut amidst forest. As this site used to be forested, it appears the power line cut made the area open enough for Bog Turtles. The seeps pool in a few of the flatter areas and create pockets of muck used by the turtles, although the turtles also use the seeps and creeks flowing through the forested part of the hillside.</td>
</tr>
<tr>
<td>N</td>
<td>4</td>
<td>Large (&gt;15 ha) wetland, more alluvial than groundwater fed, now heavily influenced by beaver. The only past disturbance was channeling and ditching of the two creeks within the wetland.</td>
</tr>
<tr>
<td>W</td>
<td>3</td>
<td>A remnant fen, completely encroached by woody vegetation. Turtles have not been seen at this site since 2011.</td>
</tr>
<tr>
<td>FL</td>
<td>2</td>
<td>The majority of this wetland has been a field since the 1940s, with turtles only known to be present in one deep, 2 m wide ditch.</td>
</tr>
<tr>
<td>WC</td>
<td>2</td>
<td>An opening amidst forest service land with turtles inhabiting 5 ditches with very shallow mud. The land separating the ditches is of upland soils and is not boggy.</td>
</tr>
<tr>
<td>G</td>
<td>1</td>
<td>Fen in an active cow pasture with a history of extensive and persistent ditching and tiling that has continued to present-day.</td>
</tr>
</tbody>
</table>
Bog Turtles appear to occupy a wide range of habitat types, as the sites in this study were drastically different (Table 4), and sites that meet all suitable Bog Turtle habitat criteria (USFWS, 2001) are often unoccupied (e.g. HOL, WW, CC, J). Bog Turtles may be opportunistically using any shallow, open-canopied mucky area (as some of our sites can hardly be classified as wetlands). Observed occupancy patterns are potentially confounded by Bog Turtle habitat selection, Bog Turtles dispersal ability, the effects of past disturbances, and stochastic events. Qualitative assessments of site suitability (i.e., USFWS, 2001) can be misleading and occupancy prediction is further hampered by turtle dispersal and stochastic events. Nevertheless, a quantitative analysis of habitat characteristics was sufficient to distinguish between occupied and unoccupied sites. If our results are transferable across states, habitat characteristics could be measured and evaluated in the context of our linear discriminant function. Such an approach would be very useful in cases were prioritization of survey efforts must occur due to limited resources. Taking habitat measurements is much less time consuming than properly surveying a wetland and could be used to identify the most promising sites (i.e. those the DA classifies as occupied). This approach would also be useful in the northern populations where any potential Bog Turtle wetland must be assessed before any building activity or land use alteration can occur (Somers and Mansfield-Jones, 2008). Bog Turtle surveys are only possible during periods of heightened turtle activity which occur between mid-April and July (USFWS, 2001), but requests for wetland assessment can come at all times of the year, often with pressure for assessment to occur quickly (Somers and Mansfield-Jones, 2008). In cases like these, since habitat measurements can be collected
year-around, wetlands could be pre-assessed using our DA approach. Using the DA to predict site occupancy would provide quantitative evidence that a more detailed site assessment is necessary or suggest that a given site is not likely to warrant allocation of limited time and resources.

Not only have we provided a way to potentially better identify Bog Turtle wetlands, but we have also established a method of surveying that will allow anyone surveying for Bog Turtles to quantify the probability that a site is unoccupied. Arguably even small Bog Turtle populations contribute to the species’ conservation (Shoemaker and Gibbs, 2013), so it is vital to know with some certainty that a site truly is unoccupied if no turtles are captured during survey efforts. Although our method is resource intensive, it can be tailored to the amount of resources available by adjusting what level of certainty is deemed acceptable regarding probability of detection. It should also be noted that the detection probabilities we observed were based on small populations; in fact, most of the sites had five or fewer individual captures (Table 1). In states where populations tend to be much larger (>10 individuals), the maximum detection probability we observed could be used and much less trapping effort would be required. The maximum detection probability we identified ($p = 0.41$) would suggest 12 days of surveys without a detection means the probability of Bog Turtles being present but undetected at a site is only 4%. Because detection probability varies by site, we strongly encourage determining locality-specific detection probability for whatever survey method is used. We acknowledge that trapping may not be possible at all sites, just as probing is not possible at our sites. But if surveys are being used to evaluate probability of species
absence at a site, then results are not truly meaningful or justifiable until detection probability is known and can be used to quantify probability of absence. To-date the majority of Bog Turtle surveys have been conducted assuming that the Phase 2 (probing/visual surveys) and 3 (trapping) surveys according to USFWS guidelines are sufficient, but until detection probability is available for these methods, one can never really be sure of their efficacy and if their efficacy holds across the range of the species and different habitat types. This does not invalidate these guidelines, but it does suggest they need to be re-evaluated to ensure sufficient resources are being used, especially given the value of even small populations. Our survey method is transparent, flexible, and quantifiable. The combination of our survey technique, which allows for exact calculation of needed survey effort, and our manner of assessing habitats through a DA will allow researchers to efficiently and justifiably allocate limited resources in the most promising wetlands for Bog Turtles.

**LITERATURE CITED**


