Wetland hydrology and soils as components of Virginia bog turtle (*Glyptemys muhlenbergii*) habitat

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Abstract

Reptile populations are in decline worldwide, with turtle species showing some of the largest drops in population. The bog turtle (*Glyptemys muhlenbergii*) is considered one of the rarest North American turtle species, and this rarity is made more severe by anthropogenic factors. The wetland habitats that are used by bog turtles contain seepage areas and soil saturation that are characteristic of specific types of wetlands, suggesting that bog turtle rarity may in part be attributed to narrow habitat requirements. In this dissertation, I have sought to spatially and temporally characterize the hydrology and soils of wetlands that are used by bog turtles in an effort to determine how these factors are related to the species' habitat requirements, movement, and activity.

In Chapter 1, I evaluated hydrology over a continuous 28-month period using shallow groundwater wells in six wetland fens known to be used by bog turtles for breeding and six apparently similar, but unused, wetlands. The saturated surface area near wells was measured and correlated with depth to the water table. Overall, water tables remained high, with mean monthly depth to the water table for all 12 wetlands remaining > -35 cm (depth below surface datum is negative). Bog turtle breeding wetlands had significantly higher mean water tables and surface saturation than wetlands where no turtles were encountered, particularly during and after the two-year drought occurring in 2007 and 2008. Findings of Chapter 1 suggest that relatively small differences in water table hydrology can affect bog turtle biology and use of wetlands.

Bog turtles access soils and move through them to thermoregulate, find cover, and hibernate. Most wetlands used by bog turtles are also grazed by livestock that can modify soil strength. In Chapter 2, I identified dominant soil series and sampled surface soils from wetlands used by bog turtles and similar, but unused, wetlands. Samples were analyzed for organic carbon content and particle size distribution. Organic carbon content was greater in areas that were always wet (10%) than temporarily wet areas (5%). Somewhat higher organic carbon contents

were present in wetlands that were used by bog turtles (8.8%) than wetlands where turtles were never encountered (5.7%). Soil textures were sandy loams and silt loams on all the study wetlands. Based on measurements of soil strength made with a static cone penetrometer, bog turtles selected wetland locations with low-strength soils. The mean and variability of soil strength were no different between grazed and ungrazed areas. The physical qualities of surface soils in bog turtle wetlands are dependent on consistently high water tables.

In Chapter 3, I described three field studies in which I deployed temperature loggers to measure and contrast ambient air and soil temperatures to turtle carapace temperatures during activity and hibernation. I used temperature signatures to evaluate the timing and cues of spring emergence and to recognize thermoregulatory activities during periods of turtle activity. Mean daily turtle temperatures (n=16 turtles) during the coldest portion of two winters ranged between 1.3°C and 6.1°C, with one turtle experiencing 14 continuous days at temperatures between -1°C and 0°C when ambient temperatures dipped below -10°C. Water tables remained within 10 cm below the soil surface throughout the winter, preventing freezing temperatures for shallow hibernating turtles. Soil temperatures at 10 cm depth were a primary cue for spring emergence. Daily mean summer turtle temperature (n=8) was 20.8°C. My findings indicated that the presence of water near the surface and the ability for turtles to submerge themselves in mud are important for thermoregulation.

In Chapter 4, I used radio telemetry to evaluate bog turtle activity (distance moved / hour), linear range, and the pathways used for dispersal. I also investigated bog turtle activity during sampling periods with either wet or dry hydrology. Mixed model analysis indicated that turtles were much less active between 18:30 and 09:30 relative to the daytime and that turtles were most active during times when hydrology was categorized as wet during 2008 when moderate to severe drought was the dominant condition. Sex was not a factor in turtle activity. Bog turtle paths during large movements (≥ 80 m) were mostly contained to areas within 80 m of USGS 7.5' quadrangle mapped streams. Turtles made large movements more frequently during dry conditions. Results suggested that drying conditions can stimulate bog turtles to either remain inactive in sparsely available saturation or to move long distances to find wetter conditions. Future conservation efforts should focus on allowing safe dispersal among habitats by reducing obstructions and risks to travel near streams.

In chapter 5, I used GIS-derived data to compare land cover, stream order, topographic wetness index inverse, presence of hydric soils, and presence of National Wetland Indicator (NWI) wetlands on bog turtle occupied wetlands (n=50) to the same variables on apparently unoccupied (n=48) wetlands or random areas (n=74) along streams. Occupied areas differed from random areas in having near zero values of the topographic wetness index inverse (indicating areas with low slopes and large upstream drainage areas that are more prevalent in wet portions of the landscape), the presence of > 50% low vegetation typical of non-forested agricultural areas, and presence of 3rd order streams. I used significant regression coefficients to create a GIS layer of high quality bog turtle habitat over the landscape, and tested this layer with bog turtle field survey data collected in 2009 independently of model building data. The resulting model has the potential to quickly rule out large portions of the landscape as potential bog turtle habitat.

Finally, in Chapter 6, I provided general recommendations for managing bog turtle habitats in Southwestern Virginia. Managing bog turtle wetlands must emphasize the maintenance of high water tables, while avoiding inundation. Maintaining connectivity among wetlands used by bog turtles is an important aspect to consider when developing bog turtle conservations plans associated with development and other land use changes. Educating landowners and enforcing existing wetland laws are imperative for effective bog turtle management in Southwestern Virginia.

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Introduction

Chapter 1: Water table depth, surface saturation, and hydrologic drought response in bog turtle (*Glyptemys muhlenbergii*) wetlands

Introduction

Reptile populations are in a decline worldwide, with turtle species showing some of the largest drops in population (Gibbons et al. 2000). The bog turtle (*Glyptemys muhlenbergii*) is considered one of the rarest North American turtle species, and is listed as federally threatened because of apparent declines in the northern portion of its range (Copeyon 1997; see Figure 1 for range description). In the southern portion of its range, federally threatened status applies because of similarity of appearance to the northern population. The bog turtle is listed as state endangered in every state where it occurs.

The bog turtle is considered a rare species, and this rarity is made more severe by anthropogenic factors. Species rarity can be defined as having a small range, a low density, very specific habitat requirements, or any combinations of these three (Rabinowitz 1981). The first two measures of rarity seem to apply to the bog turtle based on previous research and natural history studies. The bog turtle has a patchy distribution within its overall disjunct range (Lee and Norden 1996, Rosenbaum et al. 2007). The low population density of bog turtles is evident in both the northern and the southern range. In Virginia, most wetlands where bog turtles are found support fewer than 20 individuals (Buhlmann et al. 1997). By 1997, bog turtle populations in the north were known at about 200 sites only, and the number of known sites declined by roughly 50% in approximately 20 years (Copeyon 1997). Only 54% of 143 investigated bog turtle sites in the south were considered capable of supporting viable populations (Herman and Tryon 1997). Many of these sites were considered non-viable because of low population densities and no evidence of breeding or juvenile recruitment, while others had severe habitat alteration. The wetland habitats that are used by bog turtles contain seepage areas and soil saturation that are characteristic of specific types of wetlands, suggesting that bog turtle rarity may also be attributed to narrow habitat requirements. Previous studies have characterized the vegetation in bog turtle wetlands (Carter et al. 1999, Morrow et al. 2001). In an effort to determine how hydrology and soil conditions are related to specific habitat requirements, I have sought to spatially and temporally characterize the hydrology and soils of wetlands used by bog turtles. An additional goal of this study was to see if the patchy distribution of the bog turtle within its range could be explained by narrow habitat requirements.

Wetland hydrology is considered the most important component defining the function and ecology of a wetland (Mitsch and Gosselink 1993). It follows that wetland hydrology is likely a dominant factor driving how bog turtles use their habitats. It is already known that bog turtles select areas within a wetland that are close to water and have deep mud (Carter et al. 1999). Is it conceivable that the same habitat selection processes taking place within wetlands used by bog turtles can explain use or non-use of entire wetlands in the landscape? Wetland soils are related to wetland hydrology, as these soils are formed by the influence of persistent saturation and associated anaerobic conditions. The bog turtle spends much of its time submerged in saturated wetland soils that provide a medium for temperature regulation, shelter from predators, and hibernation (Carter et al. 1999). Is bog turtle use limited to wetlands that offer the specific types of soil conditions that allow formation of deep mud that is easily accessed and moved through by bog turtles?

Wetland hydrology is dynamic because it changes over short and long time scales. For example, immediate vertical fluctuations of the water table in a wetland can occur from short and intense rain events. In contrast, the water table can drop slowly but steadily over a long dry period. Understanding how bog turtles respond to hydrologic change is an important component to understanding how hydrology may limit wetland use by the species. Human activities that drain wetlands, lower water tables, or alter hydrology from former conditions are the most common causes of bog turtle habitat degradation (Buhlmann et al. 1997). Since human activities such as wetland ditching and draining are associated with rapid hydrologic change, understanding the ecology of bog turtles in conditions of normal hydrology and drought can help us recognize how wetland degradation may lead to changes in bog turtle ecology.

Across their entire range, the wetlands used by bog turtles are described as having groundwater-supplied hydrology that results in saturation of surface soils, without deep standing water (Pitts 1978, Bury 1979, Chase et al. 1989, Buhlmann et al. 1997, Carter et al. 1999, Ernst and Lovich 2009). Soil conditions are summarized as being deep, soft, and silty mud that is saturated and contains black organic material (Chase et al. 1989, Buhlmann et al. 1997, Ernst and Lovich 2009). In the southern range, bog turtle wetlands are located primarily in the Blue Ridge Physiographic Province and occur within a landscape matrix of hilly agricultural lands and hardwood forests (Buhlmann et al. 1997). Bog turtle wetlands are usually less than two hectares, and are often overlooked as wetlands because they contain little to no standing water. The agricultural land use in the bog turtle's range means that the species has been influenced by human activities. Most known bog turtle wetlands are currently grazed or were used for this purpose at some time since European settlement (Herman and Tryon 1997). In the Blue Ridge of North Carolina where bog turtles occur, estimates based on draining records, historical accounts of wetland vegetation, and landscape observations indicate that approximately 85% of non-alluvial (little to no surface flooding) wetland areas have been lost to agriculture, road building, and other development activities since 1931 (Weakley and Schafale 1994).

This dissertation focused on how wetland hydrology and soils are related to bog turtle habitat use. I also evaluated how dry and wet periods and long-term drought are related to bog turtle movement and activity. In Chapter 1, I compared water table depth and variability in wetlands used by bog turtles to unused wetlands. In Chapter 2, I determined soil series on the study wetlands, evaluated soil strength using a penetrometer in areas used by turtles, and compared organic carbon and particle size distribution on wetlands used and unused by bog turtles. In both Chapters 1 and Chapter 2, the overall hypothesis is that water table conditions would be higher and of longer duration on wetlands used by bog turtles than on unused wetlands, creating more saturation and altering soil conditions. In Chapter 3, I described how the presence of saturation and soft soils are related to the thermal regime of bog turtles in the summer and the winter. A principal concept of Chapter 3 is that routine bog turtle thermoregulation in winter and summer is reliant upon the consistent presence of water in the upper soils of bog turtle wetlands. In Chapter 4, I evaluated the paths taken by turtles traveling between core habitat areas and described how turtle movements and activity are related to water table height and time of day. I hypothesized that turtles would travel near streams and that more bog turtle activity would occur during wet periods. In Chapter 5, I broadened the spatial scale of the study and used logistic regression to identify the GIS-derived variables that are most associated with bog turtle habitats covering a 1,410 km^2 landscape area. Finally, in Chapter 6, I provided general recommendations to aid in future bog turtle habitat management.

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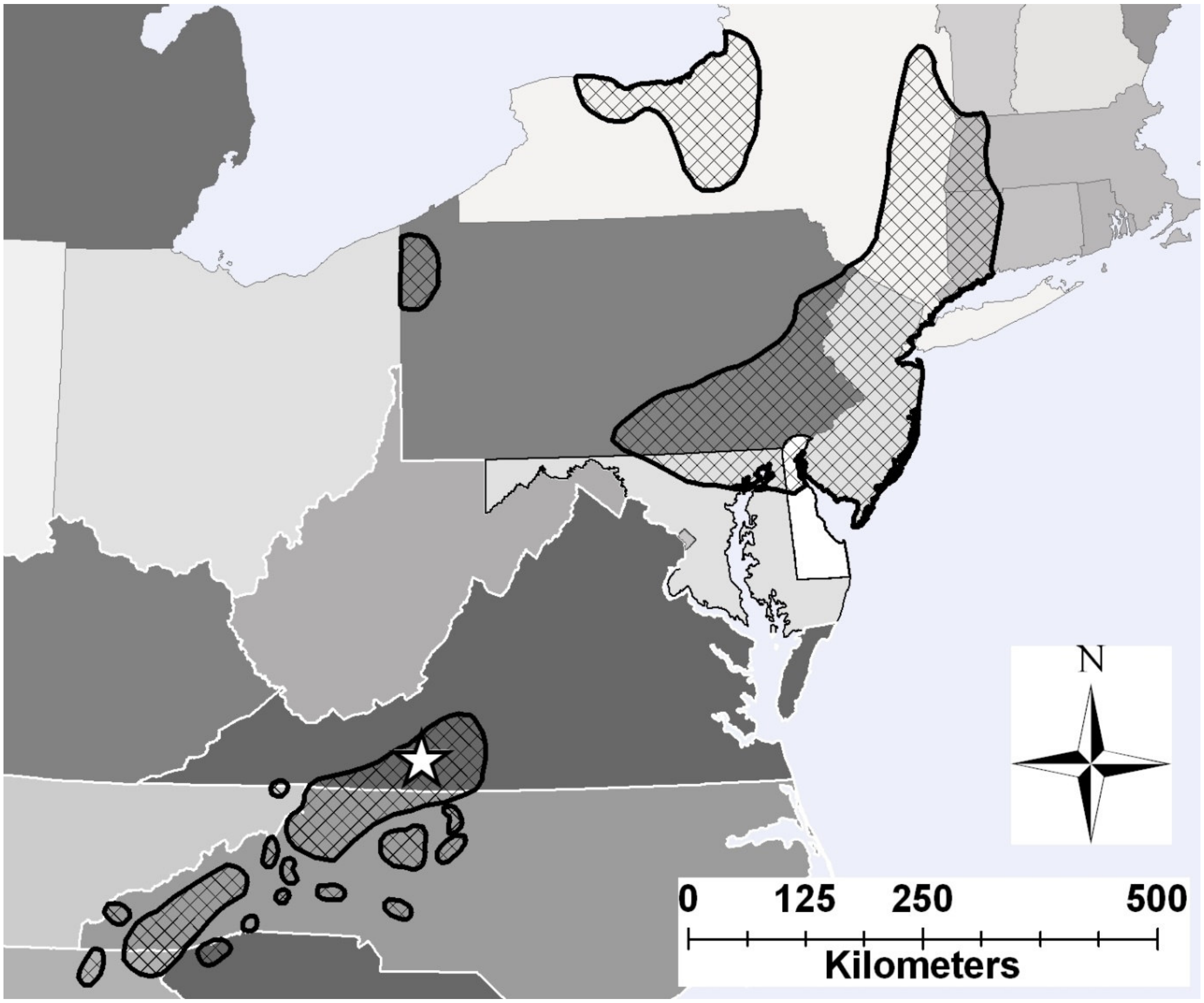

Figure Intro.1. Overall range of the bog turtle (*Glyptemys muhlenbergii*) (Natureserve 2009). Two distinct populations of the bog turtle are recognized. The northern population occurs northward from Maryland, while the southern population occurs southward from Virginia. This study occurred primarily in Virginia in the location depicted by the star.

Chapter 1: Water table depth, surface saturation, and hydrologic drought response in bog turtle (*Glyptemys muhlenbergii*) wetlands

ABSTRACT

The bog turtle (*Glyptemys muhlenbergii*) is known to select wetland areas that are near water pockets with deep mud, but water table dynamics in their habitats have not been well described. I installed and monitored shallow groundwater wells and piezometers in six wetland fens known to be used by bog turtles for breeding and six similar, but apparently unused, wetlands to evaluate hydrology over a continuous 28-month period. Overall, water tables remained high, with mean monthly depth to the water table for all 12 wetlands varying between -1 cm and -35 cm (depth below surface datum is negative). The saturated surface area near wells was measured periodically over the study period and showed a negative correlation with greater (more negative) depths to the water table. Localized upward vertical gradients from groundwater discharge resulted in nearly constant surface saturation in portions of most of the study wetlands. Bog turtle breeding wetlands had significantly higher mean water tables and surface saturation than wetlands where no turtles were encountered. Mean water table (17 cm) and saturation (25%) differentials were greatest between bog turtle breeding wetlands and wetlands where no turtles were encountered during the peak of Southwestern Virginia's 2008 drought. A differential remained even after the resumption of normal rainfall, demonstrating the importance of aquifer recharge and groundwater discharge to bog turtle wetlands. The proportion of months that water tables remained between the soil surface and -15 cm was 86% in bog turtle breeding wetlands and 68% in wetlands where no turtles were encountered. As bog turtles use the top 15 cm of the soil during summer activity and winter dormancy, relatively small differences in water table hydrology can affect their biology and wetland use. Geomorphic positions of study wetlands were primarily groundwater-maintained riparian depressions with hydrologic gradients independent of local stream flow.

***Key Words*:** fen, habitat use, groundwater, monitoring well, drought, Virginia, hydroperiod

INTRODUCTION

The geographic range of the bog turtle (*Glyptemys muhlenbergii*) in the south extends from approximately Roanoke, Virginia to Northern Georgia, primarily along the Blue Ridge

Physiographic Province (Figure 1.1). The hydrologic conditions of bog turtle wetlands are qualitatively described as spring seeps, spring-fed meadows or floodplains with moderate amounts of slow-moving water. These wetlands have interspersed wet and dry pockets, but generally lack areas of deep standing water (Arndt 1977, Bury 1979, Chase et al. 1989, Lee and Norden 1996, Buhlmann et al. 1997). The type of wetlands used by bog turtles has been classified as mountain bogs (Richardson and Gibbons 1993); however, the classification of fen has been the most common (Herman and Tryon 1997, Somers et al. 2000).

Wetland fens are differentiated from other wetland types primarily because their hydrology is dependent on groundwater and secondarily by the types of vegetation and soils resulting from the hydrology (Bedford and Godwin 2003). Fens in the Blue Ridge of Virginia and North Carolina have also been called poor fens to recognize that they are more acidic than other fen types, resulting in vegetation characteristics that are somewhat similar to true bogs (Richardson and Gibbons 1993, Zoltai and Vitt 1995). Many of these fens contain sphagnum moss, which has been associated with bog turtle nesting (Mitchell 1994, Ernst and Lovich 2009). Fens often occur at the break of a slope and in areas with changing topography, thus they display multiple seepage areas and may show both upward and downward vertical gradients within the same wetland system (Amon et al. 2002). As temperate zone fens are usually found on land that is slightly sloped, they generally are not inundated. Because of groundwater inflow, fens generally have smaller water level fluctuations than wetlands that depend on periodic flood events or precipitation (Hunt et al. 1999). Fen recharge areas are difficult to delineate, but it is expected that the larger the recharge area, the more stable the hydrology in a fen (Bedford and Godwin 2003).

In order to interpret how hydrology is related to bog turtle wetland use, more specific hydrologic information is needed in regard to water table persistence and variation in bog turtle habitats. The importance of hydrology cannot be understated, as it is considered the primary influence on the ecology, development, and persistence of wetlands (Mitsch and Gosselink 1993). Fen wetland systems have a significant groundwater component that can be difficult to characterize, but groundwater is related to many other important wetland factors such as saturation in the root zone and surface temperature (Hunt et al. 1999). Important wetland hydrologic variables such as degree of water table fluctuation are not accurately assessed without detailed and objective methods. Indirect evidence of wetland hydrology such as water marks and depth of redoximorphic soil features are difficult to interpret, even among people trained in wetland assessments (Genthner et al. 1998, Whigham et al. 1999). The effects of water level and hydroperiod on turtles and amphibians have been assessed in wetlands with primarily surface water-driven hydrology (Gibbons 1990, Skidds and Golet 2005, Roe and Georges 2008). However, few if any large-scale wildlife studies have been completed in wetlands where soil saturation and not inundation are of primary importance. This effort is worthwhile for the bog turtle because it is rare, federally protected, and occupies wetlands that are under threat by numerous pressures that have the potential to change hydrology (Buhlmann et al. 1997).

The limited realm of the upper 15 cm of soil is where bog turtles spend much of their lives, during both activity and hibernation (Chase et al. 1989, Chapter 3, Chapter 4). Within this realm, the turtles spend much time submerged in saturated soils that provide a medium for temperature regulation and shelter from predators (Carter et al. 1999). Bog turtles use areas with the deepest and softest mud, and are usually found close to water (Carter et al. 1999). The species is more associated with interspersed wet and dry areas than they are with expansive open water areas (Chase et al. 1989). Use of saturated areas is also associated with the wet pockets created by livestock hooves (Tesauro and Ehrenfeld 2007). Associating water table characteristics with surface saturation is an important link between hydrology and bog turtle biology. Detailed surface elevation data has been used successfully in some wetlands to model the extent of saturation (Shaffer et al. 1999). However, this methodology is not practical in most bog turtle wetlands because of the fine-scale variability of elevation and saturation inherent in their habitats. A practical method to estimate saturation may be to manually measure the response of saturation over a range of independent water table depths.

Within the southern range of the bog turtle, there are many wetlands that upon a brief visual inspection appear to have suitable characteristics to support bog turtles; however, bog turtles have been encountered in only a small proportion of these wetlands. Throughout the range of the bog turtle, subtle differences in water table hydrology and surface saturation may be a factor in the spatial pattern of wetlands that are used and unused by the species. It is also important to evaluate hydrology in wetland areas that are currently used by bog turtles, as temporal changes to wetland vegetation and climate can alter hydrology. Identifying hydrology in areas that are selected by bog turtles may also provide a reference model that is useful for habitat managers aiming to recognize good hydrologic conditions. Observing bog turtle wetland hydrology during drought conditions may provide insight into how wetland function can change under different hydrologic regimes.

The purpose of this study was to evaluate water table hydrology and surface saturation in bog turtle wetlands. To achieve this, I measured hydrology conditions over a 28-month period, including three summers, on wetlands used by bog turtles and nearby wetlands unused by bog turtles. I hypothesized that wetlands unused by bog turtles would differ from used wetlands in the following ways: 1) Average depth to the water table will be deeper in unused wetlands, particularly during hot and dry periods when hydrologic budgets are typically at a deficit; 2) Temporal fluctuation of the water table will be more variable in unused wetlands; and 3) Wetlands unused by bog turtles will have a smaller amount of surface saturation than do wetlands used by bog turtles.

METHODS

Study Area

I conducted this investigation on 12 wetlands located in Floyd and Patrick counties within the Southern Blue Ridge sub-province of Virginia (Figure 1.1). Precise wetland locations are not reported because of the federal and state protected status of the bog turtle and the risk of collection and trading. Eleven of the study wetlands drain to the New River and ultimately to the Gulf of Mexico via the Mississippi River. One wetland drains into the Roanoke River and the Atlantic Ocean. The study wetlands drained to several different 3rd and 4th order streams before converging. Wetlands were irregularly shaped with multiple projections and core areas of saturation due to irregularities in surface elevation and also the spatially irregular pattern of seepage areas. Six out of the twelve study wetlands were identified on the U.S. Fish and Wildlife Service's National Wetland Inventory mapping series and are described as palustrine emergent (Cowardin et al. 1979). Valley slopes where wetlands occurred were between 0 and 3%. The longitudinal axes of the study wetlands were not always oriented in the same direction as the valley slope, and wetland slopes along these axes were between 3 and 5%.

Geology in the study region is characterized by coarse grained igneous and metamorphic rocks that create topology consisting of a broad upland plateau with moderate slopes. Average elevations in the area are 725 – 910 m with higher peaks rising above the uplands. Soils in the study wetlands and their vicinity were determined using ArcMap 9.2 (ESRI Redlands, CA, USA) and the Soil Survey Geographic Database (Chapter 2). The hydric Hatboro sandy loam (fine-loamy, mixed, active, nonacid, mesic Fluvaquentic Endoaquepts) is the most common soil series, comprising approximately 50% of the soil coverage in the study wetlands. Other hydric series were also present, including the Kinkora series (fine, mixed, semiactive, mesic Typic Endoaquults) and Nikwasi series (coarse-loamy over sandy or sandy-skeletal, mixed, superactive, nonacid, mesic Cumulic Humaquepts). The most common non-hydric soil series present in the vicinity of the wetland sites were the Ashe (coarse-loamy, mixed, active, mesic Typic Dystrudepts), Delanco (Fine-loamy, mixed, semiactive, mesic Aquic Hapludults), Edneyville (coarse-loamy, mixed, active, mesic Typic Dystrudepts), and Myersville (fine-loamy, mixed, active, mesic Ultic Hapludalfs) (Soil Survey Staff 2009).

Prior to beginning this study, I worked with the Virginia Department of Game and Inland Fisheries (VDGIF) and National Park Service (NPS) to identify a set of study wetlands known to support bog turtles ("used wetlands") and another set of study wetlands without bog turtles ("unused wetlands"). Ecological surveys designed to determine whether a species is occupying a defined habitat area have inherent error associated with non-detection of the species when the species is truly present. This error is related to the rarity of the species, how the species uses its habitat, how conspicuous the species is, and the density of the species on the survey site (Gu and Swihart 2004). The bog turtle is a species that is difficult to detect in surveys because the animals are small and inconspicuous in their coloration and behavior (Somers and Mansfield-Jones 2008). At the onset of the study, I assigned five wetlands as used and six as unused based on multiple bog turtle surveys since 1987 that were completed and documented by biologists associated with the VDGIF, the NPS, and collaborators. One additional "used" wetland was assigned based on surveys that I completed during the first months of the study in 2007. All six used wetlands contained multiple adult bog turtles and evidence of breeding activities. Nests have been observed at all six used wetlands, and juvenile bog turtles have been captured at five of them during the course of this study (2007-2009). The six unused wetlands were similar in position and slope to the used wetlands and were also dominated by emergent hydrophytic vegetation, contained hydric soils, and contained areas where surface saturation was evident during the growing season. I refer to the initial assignments of used (n=6) and unused (n=6) wetlands as the *a priori* wetland grouping.

I completed additional bog turtle surveys in unused wetlands to reduce the inherent error associated with non-detection and also surveyed in used wetlands to establish realistic expectations of turtle captures given my survey effort and to capture turtles for a radiotelemetry study. During the summer of 2007, I employed hand surveys (peering through vegetation and probing with a wooden stick) for 32 person hours and 106 person hours on *a priori* unused and used wetlands, respectively. No turtles were captured on unused wetlands, while hand surveys on used wetlands resulted in a capture rate of 2.6 turtles per 10 person-hours searched (expected total captures on unused wetlands = 8.3 turtles). More survey hours were applied on used than on unused wetlands because of the need to capture turtle subjects for other research objectives.

I also used traps to survey for bog turtles. Traps consisted of a rectangular prism-shaped cage with two doors. Doors were hinged at the top of the cage so that they could swing inward but not out. No spring-loaded device was used. Traps were set without bait and were placed in approximately 5 to 10 cm of water or wet mud and covered with vegetation to prevent overheating of captured turtles. Set traps were placed between the stems of herbaceous vegetation where bog turtles move through wetlands. During the summers of 2007 and 2008, I trapped for 10,536 trap hours and 16,296 trap hours on *a priori* unused and used wetlands, respectively. No turtles were captured on unused wetlands, while trap surveys on used wetlands resulted in a capture rate of 2.3 turtles per 1,000 trap hours (expected total captures on unused wetlands = 24.3 turtles). Because all of the study wetlands (with exception of one completely forested wetland) were dominated by herbaceous vegetation, there is no reason to assume large differences in detection probability between these two groups of wetlands. Regardless of whether bog turtles may sometimes occur on the "unused" wetlands, there were lower densities of turtles there than on the "used" wetlands.

At the end of the study, the bog turtle use status of the *a priori* wetlands groups was modified to incorporate new information observed from 2007 through 2009. In the summer of 2008, a concurrent radiotelemetry study (Chapter 4) revealed that one adult male bog turtle moved approximately 300 m from a used wetland to an *a priori* unused wetland. This turtle returned to the used wetland after approximately three months and did not revisit the unused wetland in 2009. In June 2009, a juvenile male bog turtle was encountered by chance (not an organized survey) while visiting the wetland to measure water levels in the only completely forested *a priori* unused wetland. This turtle remained in the wetland until the spring of 2010 when it began to move several hundred meters downstream before radiotelemetry contact was lost. This unused wetland, located approximately 2,700 m from the nearest known used wetland, had been surveyed for bog turtles with no success by National Park Service biologists numerous times in the decade before this study. For the remainder of this analysis, I refer to the two *a priori* "unused" wetlands where singular occurrences of bog turtles were recorded as "transiently used wetlands." I emphasize the importance of reproduction at the *a priori* "used" wetlands by referring to them as "breeding wetlands." Finally, I use the term "wetlands with no turtle encounters" to refer to the *a priori* "unused" wetlands where turtles were never encountered throughout the entire course of this study. Together, the three groups of wetlands with bog turtle use statuses of "wetlands with no turtle encounters" (n=4), "transiently used wetlands" (n=2), and the initial *a priori* used "breeding wetlands" (n=6), comprise the *post hoc* wetland grouping (see Appendix A.1 for corresponding VDGIF site numbers). This classification scheme differs from the often used definition of occupancy where a single occurrence implies presence. I justify using *post hoc* wetland groupings and the term "transiently used wetlands" because they imply that although bog turtles may occasionally use a wetland, a viable population is not supported unless breeding also occurs. I emphasize that the primary purpose of this study was to evaluate hydrology on wetlands that could support reproduction of bog turtles.

All study wetlands were currently or historically used for agriculture within the last 15 years with exception of one wetland that supported a mature forest. The study wetlands were situated along a narrow ellipse that spanned 24 km. The median distance between successive wetlands along the ellipse was 1,250 m. The shortest distance between study wetlands was 35 m, and these were separated by the two-lane, frequently travelled Blue Ridge Parkway. The second shortest distance between wetlands was 120 m. The longest distance between an unused and any used wetland (not necessarily a wetland included in this hydrology study) was approximately 2,700 m, which is within the known dispersal distance of bog turtles (Carter et al. 2000).

I estimated wetland size using ArcMap 9.2, aerial photography, and first-hand knowledge of existing landmarks from site visits such as fence lines, tree lines, and farm structures. Each wetland was between 0.1 and 1.2 ha in size with a mean and median size of approximately 0.5 ha. A wetland was considered a discrete study site when it was bounded by greater than 100 m of non-wetland, was bounded by the convergence of hydrology into a stream, or was separated from another site by a road. The latter condition was often accompanied by an increase in slope, dense forest cover, or a road where a culvert was present. Some wetlands were contiguous upstream or downstream with areas containing forested riparian areas that had high-canopy cover. Forested areas were primarily non-wetland, but could contain small areas of forested wetland. Wetland sizes and other detailed characteristics are provided in Appendix A (Table A.1).

Rainfall Conditions

I used the Copper Hill, Floyd, Willis, and Woolwine weather stations (National Weather Service 2010) to gauge rainfall during the study and to summarize long-term conditions before the study. Weather stations generally surrounded the study wetlands and were between three and 18 km from the closest wetland (Figure 1.1). Long-term rainfall averages also included the Rocky Knob station, which is no longer in operation, but was operational between 1940 and 1975 and was near the study area. I considered precipitation to be uniform over the entire study area, although localized precipitation from small storm cells are common in the summer. Monthly and annual precipitation data were plotted and compared to the long-term average (56 to 73 years depending on station) monthly and annual precipitation data.

The severity of drought was examined using the Palmer Hydrological Drought Index (PHDI) developed by the National Weather Service. Data were downloaded for Region six for the years 1895-2009 (National Climatic Data Center 2010). The PHDI is similar to, but differs from the more frequently used Palmer Drought Severity Index (PDSI) in that it measures the long-term hydrological moisture supply rather than severity of wet and dry spells associated with short-term weather patterns. The PHDI index ranges from -6 to 6 and the more extreme the PHDI value, the more extreme the dry or wet period. Negative values indicate dry conditions, with values between -3.0 to -4.0 indicating severe drought and values greater than -4.0 indicating extreme drought. Similar adjectives are attached to positive PHDI values that are associated with wet periods.

Hydrology Characterization

In the spring and early summer of 2007, I installed 51 shallow groundwater monitoring wells on 12 wetlands to measure depth to the water table. Each wetland had three to eight groundwater wells. More wells were used in wetlands where seeps resulted in complex wetland shapes and multiple core saturated areas. I placed wells generally along the wetland's longitudinal gradient and in the most saturated areas as these locations could characterize the hydroperiod of the wetland during the driest seasons and during drought. I avoided installing wells in or directly adjacent to streams conveying channelized flow. I only placed wells in areas of sufficiently deep soil (>60 cm) so that the well could provide data during dry periods and withstand potential trampling by grazing livestock.

Wells were constructed of 3.8-cm outside diameter PVC pipe with factory-cut 0.025-cm horizontal slots spaced at 0.5 cm over the entire length from the bottom end cap to the top of the riser. Boreholes used for well installation were dug using an 8.9-cm diameter mud auger. The annular space between the pipe and borehole was filled with medium-grade (0.25 to 0.5 mm diameter) sand. Well depth was determined by refusal on bedrock or large gravel, or by 140 cm depth, whichever was shallower. I stood on top of plywood platforms with approximate 45-cm holes in the center while digging boreholes and setting the wells to minimize disturbance to the wetland. The depth of organically enriched soil and the depth where gravel and cobble layers began were recorded at the time of well installation.

Depth to the water table was determined with a tape measure and flashlight. I referenced all depths of the water table as the distance from the local ground surface to the measured water surface in the well. Depth from the surface datum was negative. I measured groundwater wells on 135 events between 11 June 2007 and 11 September 2009, encompassing a period of 28 months. Water table depth was measured in water table wells every two to three days from May – August, every two weeks from September – October, and approximately once each month in November – April. Sampling events were more frequent during the summer because the depth to the water table was more variable at this time. The sampling rate was a balance between my limited resources to make hand measurements of groundwater wells and my desire to provide the best estimate of the actual depth to water table using non-continuous data (Hunt et al. 1999, Shaffer et al. 2000).

Four piezometers were installed in 2008. One piezometer was used in Breeding Wetland 1 (VDGIF Site 1) and three were used in Breeding Wetland 4 (VDGIF Site 18,2). Each piezometer was situated within 0.5 m of a monitoring well. I chose to install the piezometers in three locations where groundwater seepage was apparently occurring, while the 4th piezometer was installed at a well location where surface water appeared to infiltrate into the ground following rain events. Each piezometer tube and monitoring well pair created a piezometer nest that was used to determine the direction of vertical flow at a location. Piezometers were made by joining 3.8-cm diameter factory-cut 0.025-cm horizontal slotted PVC used for water table wells to solid 3.8-cm diameter PVC. Piezometers were installed to various depths based on refusal on rock; however, all piezometers were between 36 and 50 cm from the soil surface. The space between the PVC pipe and borehole was filled with medium-grade sand to 10 cm below the soil surface and the remaining volume was filled with bentonite. Water levels in the piezometers were measured at the same time as groundwater wells. Hydraulic head in piezometers were measured over 53 events from 22 August 2008 to 11 September 2009, encompassing a 14 month period. I calculated the head differential, or vertical gradient (VG), between the water level in the piezometer and the water table to find evidence for vertical flow. I calculated the head gradient at a piezometer nest by dividing the height difference between the water levels in the piezometer and the adjacent groundwater well by the length difference between the piezometer intake screen and the water table in the fully-screened groundwater well. A positive VG, with the water in the piezometer higher than the water in the well, would indicate an upward movement of water that is consistent with a gaining or discharge area. A negative VG would indicate downward movement of water that is consistent with a losing or recharge area.

Surface Saturation

Surface microtopography at the study wetlands was irregular because of the combined effects of variation in the height of the underlying parent material, hummocks resulting from plant growth, and voids and mounds caused by the hooves of grazing livestock (Chapter 2). As a result, surface saturation was variable throughout the wetlands. On six events between 29 August 2008 and 11 September 2009, I estimated the amount of saturated surface in the wettest portions of each wetland by measuring saturation in the vicinity of all groundwater wells. Using point intercept methods, measurements were made at 1 m increments out to 5 m in each of the cardinal directions from every groundwater well. Points were recorded as saturated or unsaturated. A location was defined as saturated if it consisted of open water or soil that was wet enough to drip by gravity if suspended, or similarly if a small hole created in the soil by the end of a broomstick immediately filled with water. Groundwater monitoring wells were measured concurrently with estimation of surface saturation to build a relationship between the variables.

Statistical Methods

Yearly PHDI data were calculated by average monthly PHDI data over years. The probability of exceeding a given yearly PHDI value was calculated using the cumulative distribution function on the normally-distributed PHDI yearly data.

I used graphical methods and descriptive statistics to summarize the water table data collected by the monitoring wells and piezometers. Depths to the water table recorded from measurement events were averaged over months for statistical analyses. Averaging water table depth over months not only stabilized the variability inherent in the event data, but it also enabled a more concise analysis that was not biased toward the months when more event measurements were made. I used a linear mixed model (PROC MIXED, SAS Institute, Cary, NC) to test for statistical differences between used and unused wetlands over the 28 months of the study. I tested both *a priori* "used wetlands" and "unused wetlands" and *post hoc* "breeding wetlands" and "wetlands with no turtle encounters." An autoregressive covariance structure was used to account for dependence between months. Individual wetlands within groups were modeled as a random effect. Mixed model analysis with autoregressive covariance was also used to compare the degree of surface saturation on used and unused wetlands over six measurement events. The same *a priori* and *post hoc* wetland comparisons were completed for saturation as were completed for depth to water table. The average depth to the water table in summer (June – September) was compared among years (2007 – 2009) using a 1-way fixed-effect ANOVA.

I used Multiresponse Permutation Procedure (MRPP) (Blossom, U.S. Geological Survey, Fort Collins, CO) to test for statistical differences in the variance of depth to the water table between used and unused wetlands over the 28 months of the study. One variance was calculated for each study wetland, and comparisons were made for both *a priori* and *post hoc* wetland groupings. The MRPP is an effective way to test for differences in grouped data when sample sizes are small or distributions of the data are unknown. I used simple linear regression to model the relationship of percent surface saturation present in the vicinity of groundwater wells to the independent water table depth measurements. Unless noted, I completed all statistical analyses using Minitab (Student Release 14, State College, PA). I used an $\alpha \leq 0.1$ to indicate significance.

RESULTS

Rainfall Conditions

Rainfall from 2007 – 2009 was 86, 72, and 97% of the long-term average (122 cm), respectively (Table 1.1). A drought persisted from the end of 2006 before the study through the first two years of the study. According to the distribution of PHDI values from 1895 through 2009, the probability of exceeding the drought conditions during 2007, 2008, and 2009 were 0.08, 0.03, and 0.76, respectively. In other words, only 3% of the years since 1895 were drier than 2008 according to the PHDI. Monthly PHDI values between -3.0 and -4.0 from September 2007 through March 2008 indicated severe drought conditions, while PHDI values between -2.0 and -3.0 from April 2008 through November 2008 indicated moderate drought conditions (Figure 1.2A).

Depth to Water Table

Average depth to the bottom of the 51 groundwater wells (± SD) was 81.1 cm ± 26.7 cm. The average depth to a gravel layer was 54.7 cm ± 16.6 cm. A layer of gravel and cobble material that caused auger refusal was encountered for 30 of the 51 wells. The average depth of refusal on these materials was 62.5 cm ± 7.6 cm. Saprolitic material was encountered while augering wells in three wetlands and was independent of wetland bog turtle use status (two used, one unused). The boundary was gradual between dark-colored organically enriched soil and organically deficient subsoil that lacked structure. The depth of the transition to subsoil was variable among and within study wetlands and occurred at approximately 32 to 55 cm. Few developed horizons were encountered below the surface as the alluvial wetland soils lacked structure and contained little clay (< 10%) based on field texturing.

Over the 28 individual months of record, average depth to the water table (+SE) was -8.0 cm ± 1.0 cm for breeding wetlands (n=6), -6.9 cm ± 1.0 cm for transiently used wetlands (n=2), and -13.7 cm ± 1.1 cm for wetlands with no turtle encounters (n=4) (Figure 1.2B). The range of monthly water table depths was -0.3 to -32.8 cm, -1.0 to -21.3 cm, and -1.7 to -45.4 cm for bog turtle breeding wetlands, transiently used wetlands, and wetlands with no turtle encounters, respectively (Table 1.2). The range of water table depths appeared larger when all 135 measurement events (rather than monthly averages) were considered, and ranged between 0.8 to -46.3 cm, 0.5 to -29.4 cm, and 0.1 to -60.4 cm for bog turtle breeding wetlands, transiently used wetlands, and wetlands with no turtle encounters, respectively.

Mixed model analysis, with bog turtle use status as the main effect over the entire 28 month study period, showed evidence of a difference between depth to water table on *a priori* wetland groups ($F_{1,10}$=3.56, P=0.0883) (Table 1.3). When the two transiently used wetlands were removed from the analysis, I found stronger evidence of a difference between *post hoc* breeding wetlands and wetlands with no turtle encounters ($F_{1,8}$=11.88, P=0.0087). The repeated, among-month effect (within individual wetlands) was significant for both *a priori* and *post hoc* comparisons (P<0.0001). The interaction effect between repeated months and wetland groups was not significant for either *a priori* or *post hoc* comparisons ($P \geq 0.145$).

In summer (June – September), average depth to the water table differed among the three years of the study for *a priori* used wetlands ($F_{2,15}$=13.06, P=0.001) and unused wetlands (df=2,15, F=10.49, P=0.001). Statistical differences among study years were also present when transiently used wetland were removed ($F_{2,9}$=13.03, P=0.002). Depth to water table was the greatest in the summer of 2008, when the grand mean depth of all wetlands was -25 cm. Multiple comparisons using Tukey's critical difference indicated that significant differences occurred between the summer of 2007 and 2008 and 2008 and 2009 for all comparisons among wetlands with different bog turtle use status. No differences were detected between the summers of 2007 and 2009.

Over the course of each study year, the lowest water levels occurred in the month of August, while the highest levels occurred from March to May. A critical water table depth used in the legal identification of wetland hydrology is -30.5 cm (Wetland Training Institute, Inc. 1995). Monthly water levels remained higher than this critical depth for greater than 90% of the study period, and were similar among all wetland groups. A more constraining critical depth related to bog turtle habitat use is -15.0 cm. Most locations of bog turtles in the summer and the winter during hibernation are between -15.0 cm and the surface (Chapter 3 and 4). Study groups with different bog turtle use status showed more variation in regard to this turtle-related metric, with water tables meeting the threshold 86, 96, and 68% of the months for bog turtle breeding wetlands, transiently used wetlands, and wetlands with no turtle encounters, respectively.

Variance in Depth to Water Table Over Time

The among-months variance of depth to the water table in each wetland over the 28-month study indicated how greatly the water table changed over time (Table 1.2 and Figure 1.3). The average among-months variance ($\pm$ SD) for *a priori* used (n=6) and unused (n=6) wetlands was 73.1 cm^2 $\pm$ 39.6 cm^2 and 109.5 cm^2 $\pm$ 98.5 cm^2. The average among-months variance for wetlands with no turtle encounters (n=4) was 149.3 cm^2 $\pm$ 98.5 cm^2. The average among-months variance for transiently used wetlands was 29.7 cm^2 $\pm$ 16.3 cm^2. A statistical test that the variance differed on *a priori* unused and used wetlands was not supported using MRPP ($\delta_{observed}$=82.5, $\delta_{expected}$=85.0, *P*=0.248). I applied the MRPP on among-months variances measured on *post hoc* wetlands with no turtle encounters (n=4) and breeding wetlands (n=6). This test showed a difference between variances ($\delta_{observed}$=77.0, $\delta_{expected}$=88.4, *P*=0.083).

Vertical Flow Measured Using Piezometer Nests

During the 14 months of record, the average monthly VG measured by piezometers and adjacent groundwater monitoring wells ranged between 0.42 and -0.20 cm/cm and the VG varied over time. Vertical gradients did not show the same pattern among the piezometer nest locations (Figure 1.4). Two of the piezometer nests indicated that the vicinity of the wetland where the measurements were taken showed consistent vertical flow over the entire study. Breeding wetland 1, piezometer nest 1, showed consistent discharge (upward) flow, while breeding wetland 4, piezometer nest 2 showed consistent recharge (downward) flow. The other two piezometer nests were located in dynamic areas of the wetlands where periods of both losing and gaining conditions were measured. Periods of groundwater discharge or recharge did not have a strong pattern with rainfall or wet and dry periods, although breeding wetland 4, piezometer nest 3 showed losing conditions during late summer dry periods and gaining conditions during the winter.

Surface Saturation

The area of surface saturation within 5 m of wells was inversely proportional to the depth to the water table recorded in the monitoring wells (Figure 1.5). Regression analysis indicated that surface saturation followed an exponentially decreasing relationship with linearly increasing depth to groundwater. Coefficients of determination (r^2) for breeding wetlands and wetlands with no turtle encounters were 0.93 and 0.86, respectively. The first of six saturation measurement events took place on 22 August, 2008. At this time all wetlands were at the driest recorded during the entire study. Rain events soon followed. One breeding wetland and two wetlands with no turtle encounters contained no saturation near the wells on 22 August, 2008. One of these wetlands with no turtle encounters contained no saturation near the wells during two other measurement events.

Average percent saturation near the wells over the six measurement events (± SD) was 34% ± 16, 45% ± 9, and 20% ± 17 for breeding wetlands, transiently used wetlands, and wetlands with no turtle encounters, respectively. Using mixed model analysis with wetland bog turtle use status as the main effect over the six discrete saturation measurement events, I did not detect a difference between surface saturation on *a priori* used and unused wetlands ($F_{1,10}$=0.83, P=0.3848) (Table 1.3). A significant difference was detected when *post hoc* breeding wetlands and wetlands with no turtle encounters were compared ($F_{1,8}$=3.70, P=0.091). A significant difference among the six repeated event measurements was found for both *a priori* and *post hoc* comparisons (P<0.001). The pattern of percent saturation over the measurement events was different for breeding wetlands relative to wetlands with no turtle encounters (Figure 1.6). The interaction between bog turtle use status and repeated events was also significant for both *a priori* and *post hoc* comparisons ($P \leq 0.018$). During the first and last measurement events the percent saturation was nearly equal between breeding wetlands and wetlands with no turtle encounters, but a discrepancy was apparent during the other four measurement events, particularly during the fall of 2008 and spring of 2009. This interaction was attributed to the more pronounced drop in the water table (leading to less saturation) during the drought on wetlands with no turtle encounters relative to breeding wetlands.

DISCUSSION

Differences in Average Depth to Water Table

The severe drought in 2007 and 2008, followed by average rainfall in 2009, offered a hydrologic perturbation that allowed me to test for any potential differences in hydrology on wetlands used and unused by bog turtles. I found evidence in the *a priori* analysis that used wetlands had a higher mean depth to the water table than unused wetlands. The two transiently used wetlands, where an observation of a single bog turtle occurred after the study began, also had high and stable water tables throughout the study. A strong difference in water table depth between breeding wetlands and wetlands with no turtle encounters was evident when transiently used wetlands were removed in the *post hoc* analysis. Over the entire study, the average difference in water table depth between breeding wetlands and wetlands with no turtle encounters was approximately 6 cm. The difference between water table heights on these same wetland groups during June through September 2008 was 13 cm, and in September 2008, the difference reached its maximum of 17 cm (Figure 1.2C).

There is evidence that the depth discrepancy between breeding wetlands and wetlands with no turtle encounters changed over the course of the study. Further, this discrepancy appeared to be related to different hydrologic responses to the drought conditions that began in 2007 and persisted through the spring of 2009. The discrepancy between wetlands with different bog turtle use status was in response to, but lagged behind, the months experiencing the most severe drought conditions according to the PHDI (Figure 1.2). Despite drought conditions in 2007, it was not until 2008 that the largest water table effects were measured in the study wetlands. A two sample t-test comparing breeding wetlands and wetlands with no turtle encounters between August and November 2008 showed that the depth to the water was greater on wetlands with no turtle encounters (df=3, t=1.92, P=0.03). The discrepancy between groups with different bog turtle use status was still evident at the end of the study despite the resumption of normal rainfall. This hydrologic response was likely related to the reduced groundwater discharge to wetlands with no turtle encounters. Water table drops in groundwater-driven wetlands would be expected to be more severe in wetlands that are recharged by local, rather than more widespread or regional groundwater flow systems (Bedford and Godwin 2003). Perhaps recharge areas are smaller in many wetlands unused by bog turtles relative to used wetlands. Inconveniently, recharge areas are not easy to identify for fen wetlands (Bedford and Godwin 2003).

In contrast to monthly water table characteristics, event-based water table levels fluctuated rapidly during the peak of the drought in 2008, revealing differential responses to drought in the study wetlands (Figure 1.7). Water table fluctuations revealed the importance of groundwater inflow to the water budget in the study wetlands. Minor rain events during the summer of 2008 were not sufficient to maintain high water tables. Water inputs must first saturate the soil, exceed the evapotranspiration potential of wetland plants, and recharge groundwater flow systems before sustained water table increases can occur (Moorhead 2003). Drought conditions in the study wetlands finally began to alleviate in the fall of 2008. Water tables on all wetlands were elevated to within 15 cm of the surface following a 10 cm rain event at the end of August 2008. Breeding wetlands sustained these water table levels throughout the following months. In contrast, water tables on wetlands with no turtle encounters were elevated for only a short time before dropping at a steeper rate than breeding wetlands. The immediate response of breeding wetlands to rainfall may appear contrary to expectations of a groundwater-driven wetland; after all, the observed water table drop in response to the drought occurred slowly over the two-year drought. In a Southern Blue Ridge fen in North Carolina, Moorhead (2001) also observed rapid water table response to rainfall following a drought. In that study, well transects parallel to the slopes surrounding the wetland showed that rainfall increased shallow groundwater flow to the wetland. This groundwater inflow was considered a greater factor in water table rise than direct input by the rainfall.

Comparison of Among-Months Variance of Depth to Water Table

Comparisons of among-months (n=28) variances using permutation tests showed that wetlands with no turtle encounters had a higher variance than breeding wetlands, with the variance twice as high on wetlands with no turtle encounters. These variance results reinforce those found using depth to the water table, and attest to the reduced groundwater inflow and different response to drought on wetlands with no turtle encounters. The rapid, yet brief, rebound in the elevation of the water table on wetlands with no turtle encounters may also indicate that these wetlands are more reliant on surface water and rainfall inputs than breeding wetlands.

High water events such as floods are typically brief in wetlands and are therefore difficult to detect with manual groundwater well measurements (Morgan and Stolt 2004). Although not well-illustrated by our hand-measured groundwater data, there was no qualitative evidence that indicated that high water events occurred more frequently on unused than on bog turtle used wetlands. I observed the wetlands during and within several hours of intense rain events in the spring and summer of 2009. Before this time, normal rainfall patterns had brought water tables near the surface, and moisture levels in non-wetland soils in the vicinity of the study wetlands were at field capacity. These conditions should have increased the likelihood of a flood event, yet I did not observe deep inundation on the order of greater than 20 cm on any of our study wetlands. Surface runoff from the wetlands was observed primarily as sheet flow that converged into stream channels. I did not observe overbank flooding that extended into the wetlands where groundwater wells were installed, nor did I see rack-lines of debris or flattened vegetation that would have indicated unobserved flood pulses passing through the area. Although original formation of soils in most fens is associated with alluvium transported through flood deposition, the fen wetlands of the region do not currently exhibit frequent flooding (Weakley and Shafale 1994). I suggest that the absence of frequent overbank flooding is an important feature of bog turtle habitat. High surface water velocity associated with flooding could facilitate erosion of the loose, mucky-silt sediments typical of bog turtle habitat, and may also result in direct mortality of nests and even turtles.

Surface Saturation - the Link between Hydrology and Bog Turtle Use?

A potential biological link between water table hydrology and wetland use by bog turtles is surface saturation. Surface saturation near wells on breeding wetlands changed from approximately 50% to 25% when water tables dropped from the surface to -15 cm. Surface saturation could diminish to less than 10% when water tables were at -50 cm. I found evidence that the proportion of area near wells saturated to the surface was greater on breeding wetlands than on wetlands with no turtle encounters, and that wetlands were responding differently over measurement events (Figure 1.6). Breeding wetlands rarely exhibited conditions where surface soil saturation was not permanent within some portion of the wetland. Only one breeding wetland showed complete surface drying during the peak of the drought in August 2008. In response, radioed bog turtles monitored at this site found refuge in a stream or within a saturated, meter-wide gravel roadside ditch. In contrast, surface saturation measurements showed that two wetlands with no turtle encounters were completely dry during the summer of 2008, and only one of these wetlands contained a nearby stream that did not also dry up. Even after normal rainfall resumed in 2009, one wetland with no turtle encounters remained completely devoid of surface saturation. This wetland had extensive surface saturation at this site at the beginning of the study.

Bog turtles use saturated areas even when their availability is limited, suggesting that wetlands lacking consistent saturation may preclude use by bog turtles. In the summer of 2008 when conditions were the driest, I observed that bog turtles were found in saturated areas during 65% out of 1,251 total turtle observations (Chapter 4). Summer observations of bog turtles using six different wetlands indicated that turtles used depths less than 15 cm on 99% of 1284 events (Chapter 4). Visual observations and hand captures during winter hibernating showed that turtles used depths ranging from -5 cm and -45 cm deep, but turtle carapace temperatures showed that most turtles were hibernating between -15 cm and surface (Chapter 3). These depth-related behaviors may indicate that nearly continuous surface saturation is critical for bog turtle survival and fitness. Examples of the biological mechanisms by which dry conditions can limit bog turtles are not clear; however, saturated soil enables turtles to submerge themselves in mud, which in turn is related to avoiding predators, thermoregulating in the summer, and preventing freeze damage during winter hibernation.

Changes to water table hydrology and surface saturation may be related to land use and human disturbance as well as natural disturbances such as beaver dam construction. As fen hydrology is dependent on the entire drainage area, activities outside of the wetland can even induce changes to hydrology (Richardson and Gibbons 1993). Such changes could reduce bog turtle use of wetlands or even render wetland uninhabitable. Ditching and other methods of draining are direct wetland activities that are effective at lowering the water table and reducing surface saturation. New ditching on farmland without previous draining management as well as ditch maintenance on farmland with ongoing draining management are still common activities in the study area of Virginia.

Large areas of standing water or inundation were not characteristics associated with bog turtle habitat. Pond construction can transform wetland areas with minimal standing water to open water areas with too much inundation to be used by bog turtles. Beaver dam construction would have a similar outcome by elevating water tables far above the level of the soil surface. Construction activities and development in the drainage area of wetlands results in impervious or easily eroded surfaces. These changes can lead to short periods of inundation from extremely high surface flows and sediment import to wetlands during storm events. Storm water diversions into a New Jersey wetland resulted in a transition from sheet flow and surface inundation to high velocity, channelized flow. These hydrology changes were considered the primary reason for extirpation of bog turtles from the wetland (Torok 1994).

A hydrologic analysis in Maryland found that highway construction and other development activities within the recharge area of a bog turtle wetland had a high likelihood of causing detrimental impacts to the existing wetland hydrology (Brennan et al. 2001). The study found that reduced recharge in the drainage area of the wetland would not have a great effect on water table levels, but that reduced head pressure in the crystalline metamorphic rock aquifer would reduce groundwater discharge to the wetland. Although not modeled by Brennan et al. (2001), reduced discharge coupled with evapotranspiration would reduce surface saturation and maybe result in indirect water table reductions in the long-term. As evapotranspiration rates in the wetland would remain relatively constant regardless of reduced discharge, greater losses to the atmosphere relative to inflow by groundwater would modify the water balance from its pre-construction condition. Regional drawdown of groundwater tables would have similar impacts on wetland water budgets as the reductions in recharge area described by Brennan et al. (2001).

A Broader View of the Study Wetlands

Despite apparent differences in depth to water table on breeding wetlands and wetlands with no encounters in the *post hoc* analysis, the biological relevance of the original *a priori* bog turtle use assignments is important to reiterate. Only the *a priori* used wetlands had potentially viable bog turtle populations where nesting and recruitment occurred. Wetlands infrequently visited by bog turtles (this study's transiently used wetlands) did not support recruitment, yet may have an important function for bog turtles. The mosaic of wetlands within the range of the bog turtle are part of a dynamic landscape where vegetative succession, land use, and hydrology change over time (Buhlmann et al. 1997). The transiently used wetlands in this study supported hydrology that was more similar to breeding wetlands than wetlands with no turtle encounters. In the future, current transiently used wetlands may transition to breeding wetlands where turtle recruitment can occur. Further, non-breeding transiently used wetlands may provide temporary habitats between high quality breeding wetlands (Gahl et al. 2009).

By design, the *a priori* unused wetlands selected for this study were similar to bog turtle used wetlands based on vegetation and other visually observable attributes. The primary purpose of the study was to test if subtle hydrologic differences could be detected between wetlands with different bog turtle use status. The biological relevance of the study would not have been as focused if wetlands were chosen with no regard to wetland type. However, a high likelihood exists for wetlands to occur in the Southern Blue Ridge that would have a distinctly different hydroperiod than the wetlands included in this study. These wetlands would almost certainly have less probability of bog turtle use. The hydrogeomorphic (HGM) approach is a classification system that uses landscape position, source water, and hydrodynamics to compare wetlands within a region (Cole et al. 2008). Although HGM is region specific and HGM development has not occurred in the Blue Ridge of Virginia, there is value in generalizing HGM results between regions when done with care (Cole et al. 2002). The HGM approach was used to describe and compare wetlands in four different mountain regions in the Appalachian Mountains of New York, Pennsylvania, and Virginia (Cole et al. 2008). The reference wetlands used in the HGM classification were located in Pennsylvania, but the authors found acceptable comparability to the Virginia wetlands. Using the classification described by Cole et al. (2008), the wetlands used in this study would best qualify as riparian depression wetlands on 1^{st} through 3^{rd} order streams. These wetlands were described as being linear features adjacent to streams, with hydrologic gradients perpendicular to the stream. These wetlands were gently sloped, located in a slight topographic depression with an outlet channel, and fed primarily by ground water. Some of these study wetlands may also classify as headwater floodplain or toe of slope wetlands. The water table measurements presented by Cole et al. (2008) from Virginia riparian depression wetlands were similar to the observations in this study, with a small range of water table fluctuation, water levels near the surface, and consistent root zone saturation. This study did not include wetlands classified in Cole et al. (2008) as stratigraphic slope wetlands, in-stream floodplain wetlands, or fringing wetlands, all of which occur in this study region. In addition to the wetlands used in this detailed hydrologic study, I have also determined stream order (USGS 7.5 minute quadrangle) in the vicinity of 44 other wetlands used by bog turtles (Chapter 5). None of these 44 wetlands were associated with 4^{th} order streams or greater.

Conclusions

Differences in water table hydrology and surface saturation were observed between wetlands that were used and unused by bog turtles. Hydrology differences between wetland groups with different bog turtle use status were not apparent at the onset of the study before the drought, suggesting that differences in surface hydrology between bog turtle used and unused wetlands may be a difficult feature to distinguish during normal rainfall conditions. High quality wetlands with bog turtle breeding would be expected to be hydrologically buffered from drought conditions and also to rebound quickly once normal weather patterns are resumed. I suggest that water table hydrology and related surface saturation may present a limiting factor for bog turtles at the wetland scale within the range of the bog turtle. On a larger scale, the types of wetlands that provide current or potential habitat for bog turtles display a different pattern of hydrology relative to other types of regional wetlands located in different landscape positions.

This study provides a baseline hydrology reference for hydroperiod in wetlands used by bog turtles in the southern Blue Ridge. These reference data are important for any future mitigation projects that may occur on or near bog turtle used wetlands. Such projects should recognize that mitigation design criteria related to bog turtles are more limiting than those required to simply achieve minimum wetland criteria. This study also provides a reference as to the degree of short-term (on the order of one or two years) water table reductions and related saturation reductions that can be experienced by wetlands supporting breeding bog turtles. According to

PHDI data, the level of drought experienced during this study only occurs about three or four times each century. I suggest that activities that have the potential to dry bog turtle wetlands to degrees beyond those observed in this study, in magnitude or duration, would drastically alter the wetland habitat and have unknown negative effects on bog turtles.

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Table 1.1. Rainfall and drought characteristics for the two years before and during the three-year study. Rainfall data originated from local weather stations. Monthly Palmer Hydrologic Drought Index (PHDI) values were averaged to calculate presented yearly data. Sustained moderate drought conditions occurred in 2007 and 2008, and few years have been drier based on the 114 year PHDI record available in the study area.

Year	Rainfall (cm)	% of long-term average	Yearly average PHDI	Probability of a drier year
2005	113.6	93	0.64	0.69
2006	125.3	102	-0.70	0.34
2007	105.6	86	-2.17	0.08
2008	87.6	72	-2.84	0.03
2009	118.6	97	0.97	0.76

Table 1.2. Number of groundwater monitoring wells installed on each study wetland, length of data record, and depth to water table statistics. Bog turtle use status groups were "breeding wetlands", "transiently used wetlands", or "wetlands with no turtle encounters." Among-months variance was calculated for each individual wetland from the set of 28 monthly mean depth to water table values. Statistics for overall groups calculated by averaging the individual wetland data over each of the 28 months and then tabulating statistics among months. Different overall group results would be obtained by taking the simple average of individual wetland values as displayed on the table, particularly for variance, min, and max statistics.

Bog turtle use status of wetland	Wells installed	Months sampled	Mean (cm)	Among-months variance (cm^2)	Median (cm)	Min (cm)	Max (cm)	% Months ≥ -30.5 cm	% Months ≥ -15 cm
			------------------Depth to water table------------------						
Breeding 1	6	28	-3.8	8.8	-3.3	-13.3	0.4	100	100
Breeding 2	3	28	-9.3	129.2	-4.3	-45.8	0.4	93	82
Breeding 3	7	28	-11.1	83.2	-7.0	-35.9	-0.6	96	71
Breeding 4	6	27	-7.7	58.5	-5.4	-31.5	0.8	96	82
Breeding 5	8	28	-8.1	67.1	-5.6	-41.7	1.4	96	93
Breeding 6	3	28	-8.2	89.8	-5.5	-32.4	0.9	96	75
Breeding Overall	33	28	-8.0	54.1	-5.1	-32.7	-0.3	96	86
Transiently Used 1	3	28	-5.9	18.2	-5.8	-14.6	0.1	100	100
Transiently Used 2	3	28	-7.8	41.2	-5.4	-28.1	-1.9	100	86
Transient Used Overall	6	28	-6.8	24.6	-5.3	-21.3	-1.0	100	96
No Turtle Encounters 1	3	28	-15.4	173.5	-13.8	-50.2	0.7	89	54
No Turtle Encounters 2	3	28	-10.7	15.8	-9.5	-22.9	-4.7	100	93
No Turtle Encounters 3	3	28	-14.0	155.5	-9.7	-45.7	1.3	86	61
No Turtle Encounters 4	3	28	-14.7	252.6	-7.7	-62.9	-0.2	86	71
No Turtle Encounters Overall	12	28	-13.7	114.6	-9.4	-45.4	-1.7	90	68

Table 1.3. Results of linear mixed modeling used to test for significant differences of depth to water table and surface saturation on used and unused wetlands. All tests were run on *a priori* and *post hoc* wetland groups with an autoregressive covariance structure used over the recurring months of water table measurements or recurring saturation measurements.

Variable	Wetland groups	Source	*df*	*F*	*P-value*
Depth to water table	*a priori*	Use status	1, 10	3.56	0.088
		Month	27, 269	23.86	<0.001
		Use status x Month	27, 269	0.97	0.510
	post hoc	Use status	1, 8	11.88	0.009
		Month	27, 216	20.20	<0.001
		Use status x Month	27, 216	1.32	0.145
Surface saturation	*a priori*	Use status	1, 10	0.83	0.355
		Event	5, 50	8.77	<0.001
		Use status x Event	5, 50	3.05	0.018
	post hoc	Use status	1, 8	3.70	0.091
		Event	5, 40	9.48	<0.001
		Use status x Event	5, 40	3.43	0.011

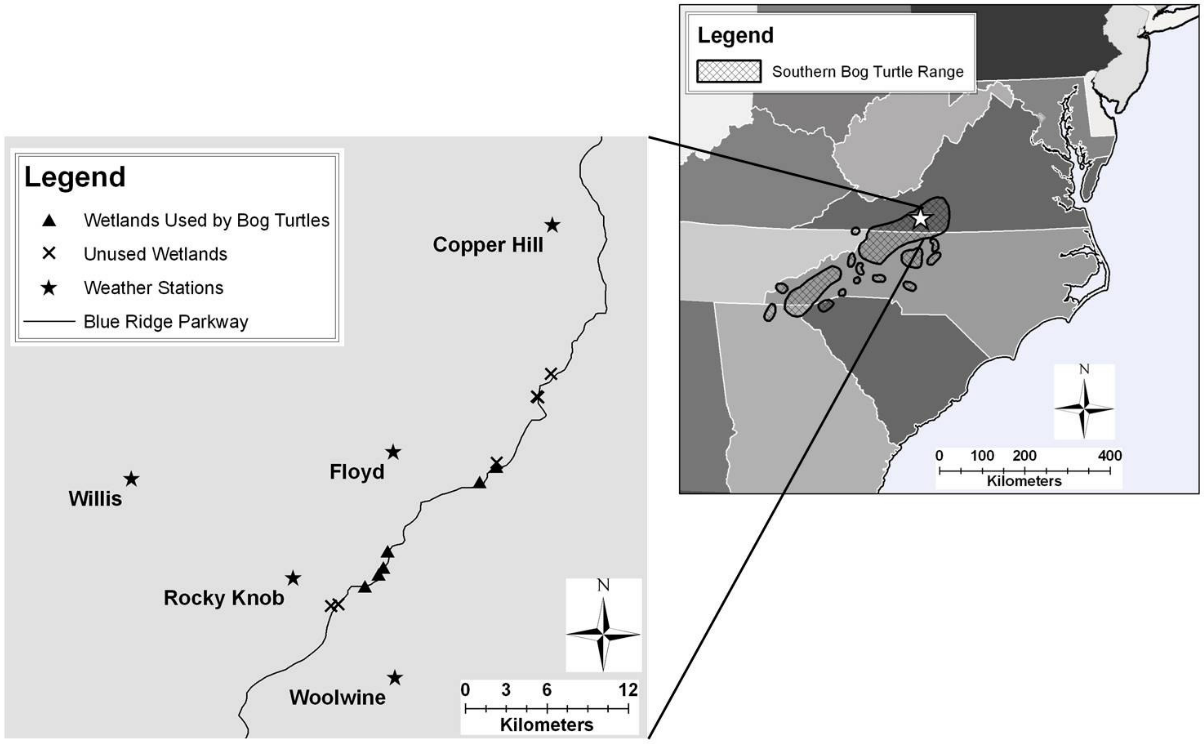

Figure 1.1. Study location in the Blue Ridge Physiographic Province of Southwestern Virginia. Shown on the map at right is the southern range of the bog turtle (Natureserve 2009). Shown on the map at left are the locations of *a priori* bog turtle used and unused wetlands and weather stations where rainfall statistics were recorded. Note: symbols for two unused wetlands in close proximity to each other are indistinguishable.

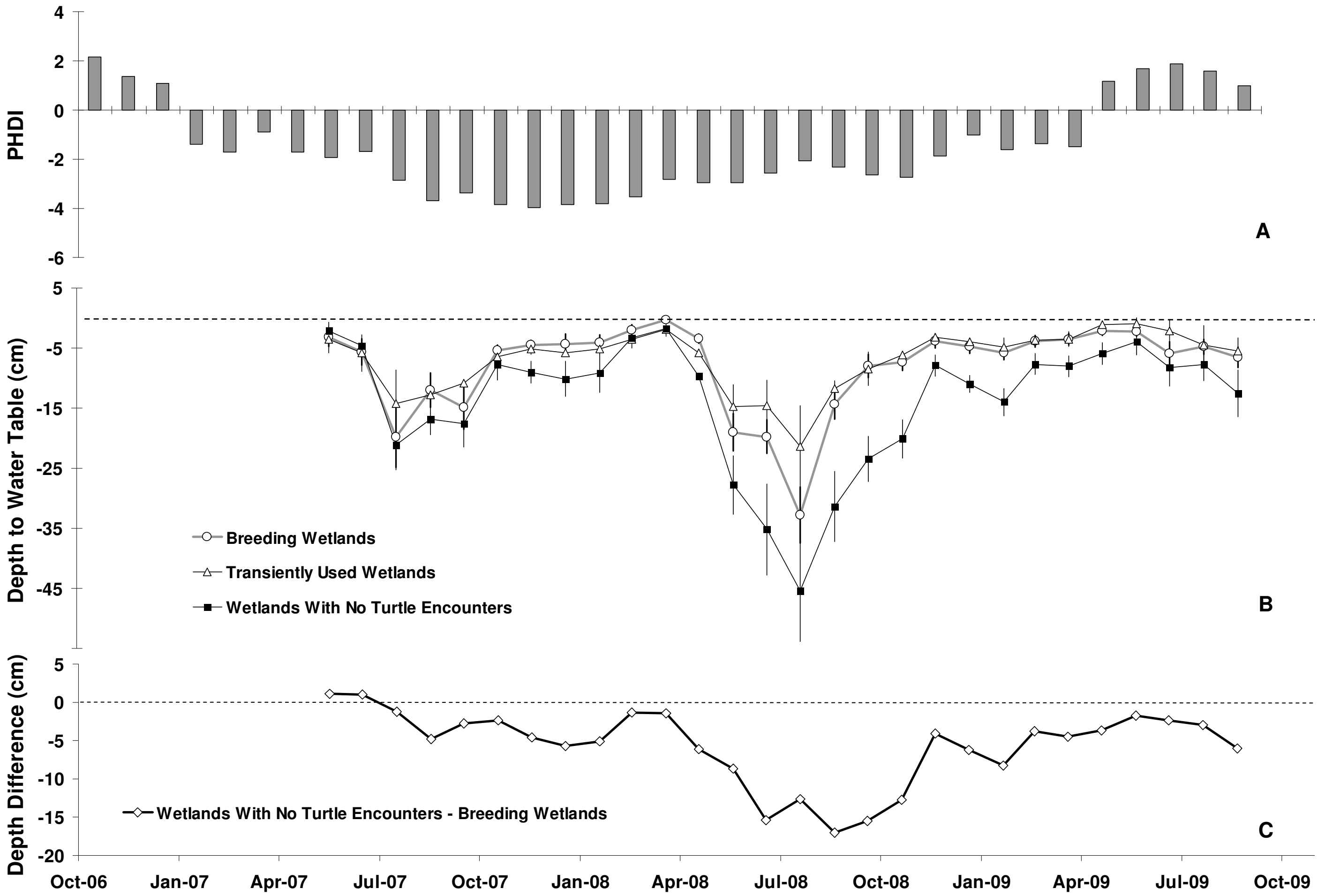

Figure 1.2. (A) Monthly Palmer Hydrological Drought Index (PHDI) values before and during the study. Moderate (-2.0 to -3.0) to severe (-3.0 to -4.0) drought conditions were present during the summer of 2007 and 2008. (B) Monthly average depth to water table on "breeding wetlands" (n=6), "transiently used wetlands" (n=2), and "wetlands with no turtle encounters" (n=4) as measured by shallow groundwater wells over the 28-month study period. Error bars (± SE) are calculated from wetlands with the same bog turtle use status. (C) Mean difference in depth to water table between "wetlands with no turtle encounters" and "breeding wetlands."

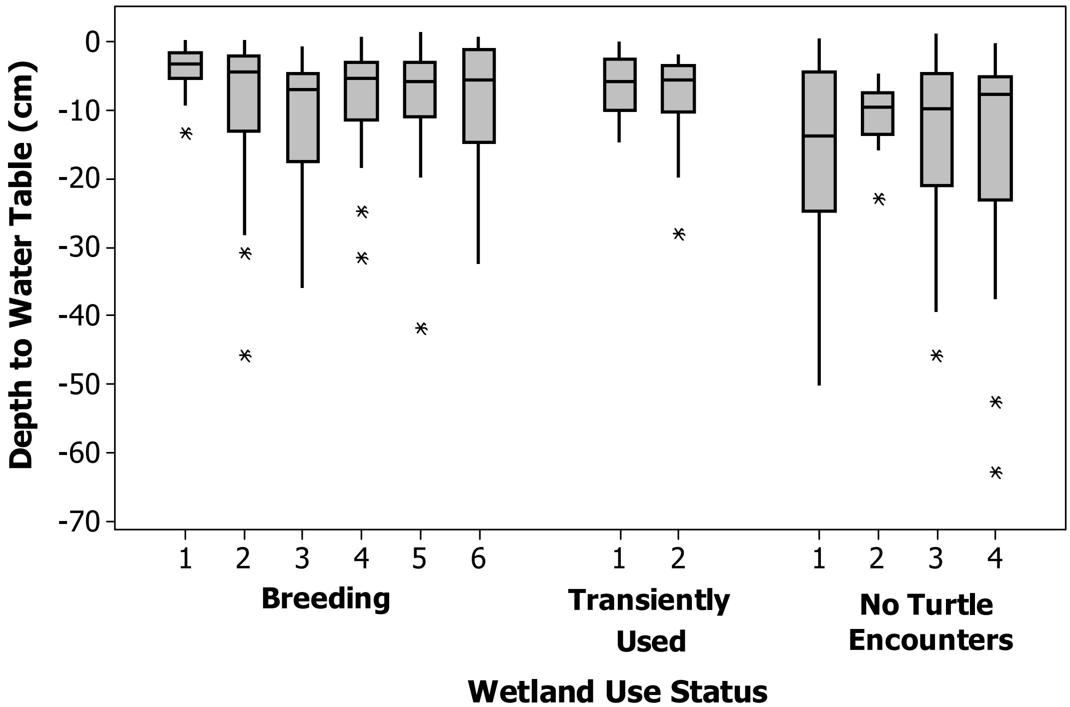

Figure 1.3. Box and whisker plots of monthly depth to water table values measured over the 28-month study period. The average variance (± SE) among "breeding wetlands" (n=6) and "wetlands with no turtle encounters" (n=4) was 73 cm^2 ± 16.2 and 149 cm^2 ± 49.3, respectively.

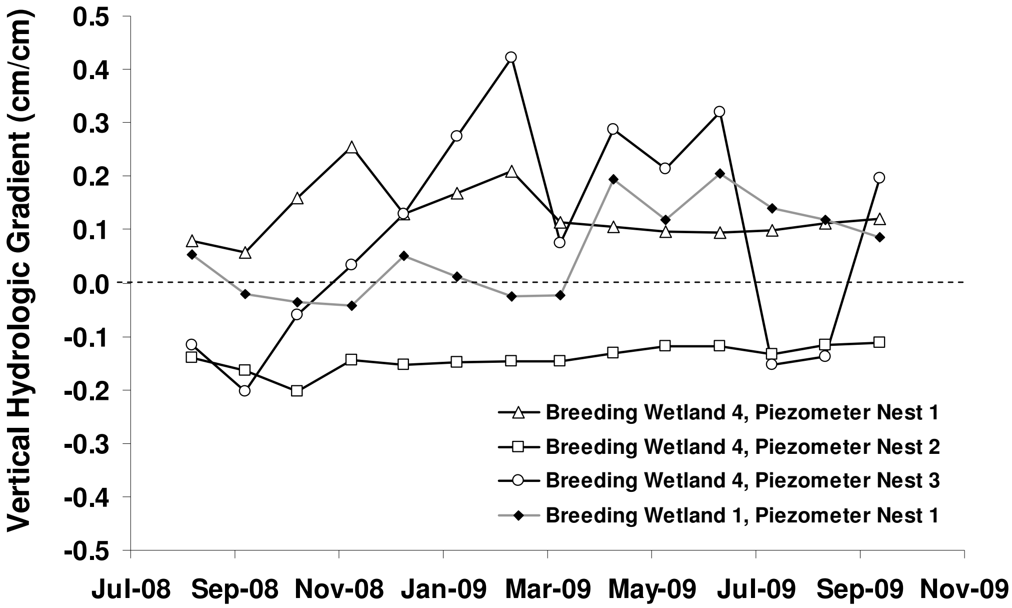

Figure 1.4. Vertical hydrologic gradient (VG) at four piezometer nests on two wetlands with breeding bog turtles. Values < 0 indicate downward movement of water while values > 0 indicate upward movement of water. Upward water movement is a characteristic of seepage areas.

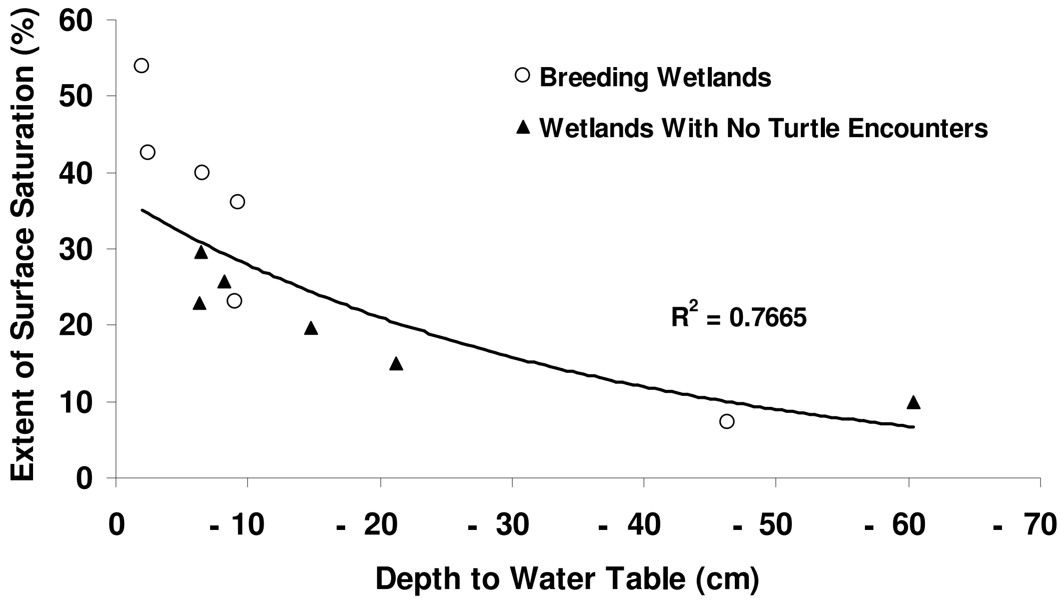

Figure 1.5. The decreasing and exponential relationship between depth to water table and the proportion of saturated surface area near groundwater wells. Data measured on "breeding wetlands" (n=6) and "wetlands with no turtle encounters" (n=4). Soil surface is at a depth of zero and lower water tables are more negative. Percent saturation was measured on six different events spanning August 2008 and August 2009 using point intercept transects radiating from the center point of each well.

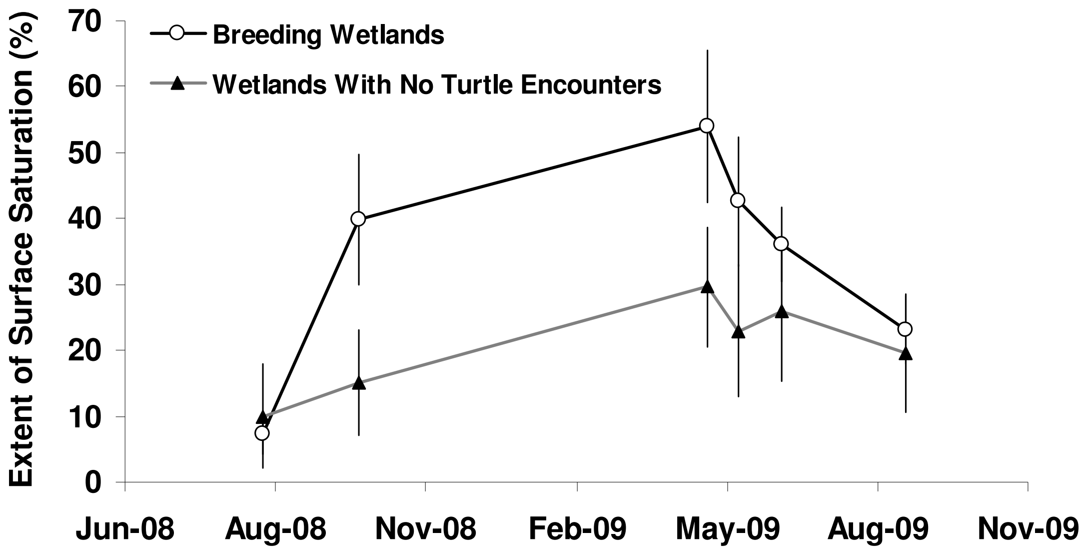

Figure 1.6. Percent saturated area near groundwater wells during six different events spanning August 2008 and August 2009. Repeated measures ANOVA provided evidence that "breeding wetlands" (n=6) had more saturated area than "wetlands with no turtle encounters" (n=4) ($F_{1,8}$=3.70, P=0.091). August 2008 was the month with the lowest saturated area and coincided with the period of the deepest water table.

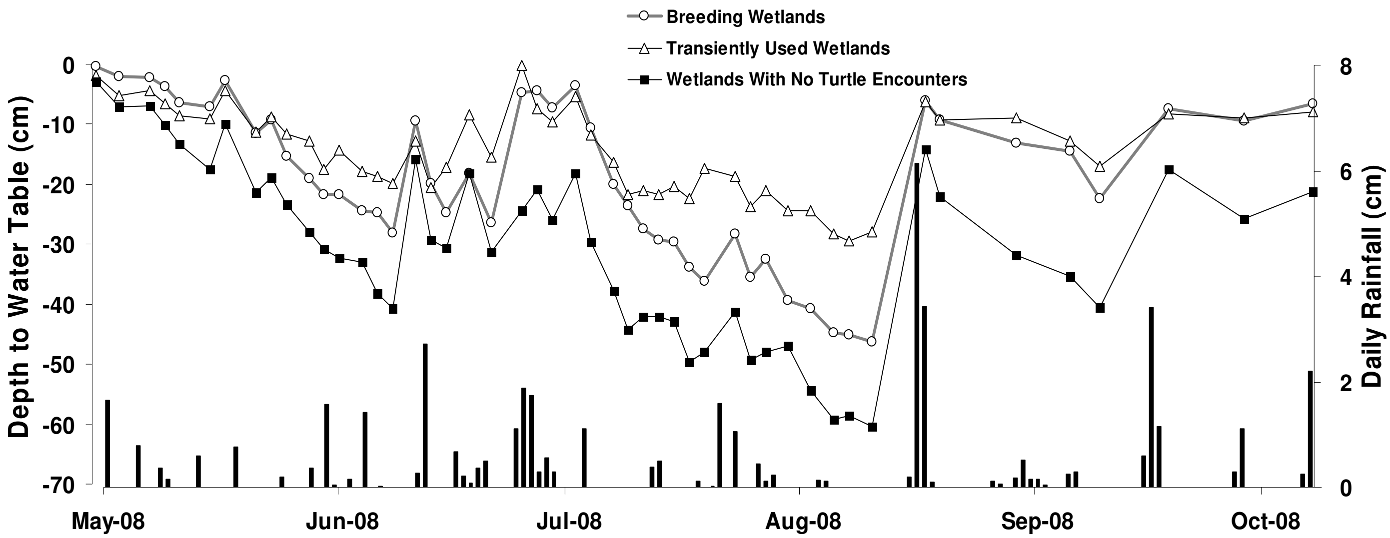

Figure 1.7. Depth to the water table on 49 individual sampling events spanning May through October, 2008. Each data point represents the mean depth in either "breeding wetlands" (n=6), "transiently used wetlands" (n=2), or "wetlands with no turtle encounters" (n=4). Daily rainfall totals are shown on the alternative y-axis. Rain events (shown as bars along x-axis) from May through August temporarily raised water tables, but were insufficient to maintain levels. A 10 cm rain event at the end of August brought all wetland groups to within 15 cm of the surface. "Breeding wetlands" and "transiently used wetlands" retained the high water tables, while water tables immediately dropped on "wetlands with no turtle encounters." The discrepancy among wetland groups with different use status was sustained until the spring of 2009.

Chapter 2: Soil organic carbon, particle size, and grazing effects on soil strength in bog turtle (*Glyptemys muhlenbergii*) wetlands

ABSTRACT

Bog turtles (*Glyptemys muhlenbergii*) access saturated wetland soils and move through them to thermoregulate, find cover, and hibernate. Variability in soil physical properties that may affect suitability for turtle use is little understood. Most wetlands used by bog turtles are also grazed by livestock that can compact and modify soil strength, resulting in unknown impacts to the species' habitat. I identified dominant soil series and sampled the top 18 cm of surface soils from wetlands used by bog turtles and similar, but apparently unused wetlands, in Southwestern Virginia. Samples were analyzed for organic carbon content and particle size distribution. Soil series present in the study wetlands were poorly developed alluvial soils with aquic soil regimes due to high water tables. Organic carbon content was greater in locations with more continuous surface saturation and averaged 10% overall in the wettest locations, indicating the presence of mucky modified mineral textures. Proportions of sand, silt, and clay were consistent with sandy loam and silt loam textures. Somewhat higher organic carbon content was present in wetlands that were used by bog turtles, while particle size was not different on wetlands that were used or unused by bog turtles. A static cone penetrometer was used to evaluate soil strength in specific locations where bog turtles were found and adjacent random areas. Bog turtle use was centered on low strength soils. Soil strength was evaluated in 5 m x 5 m plots where livestock grazing had been excluded for five years and on grazed control plots, with the expectation that grazing would modify mean soil strength and increase the variability of soil strength. The mean and variability of soil strength was not different between grazing treatments. The physical qualities of surface soils in bog turtle wetlands result from the depositional environment and hydrology.

***Key Words*:** hydric soil, penetrometer, saturation, fen, drought, Virginia, soil surface

INTRODUCTION

The southern range of the bog turtle (*Glyptemys muhlenbergii*) extends from approximately Roanoke, Virginia to Northern Georgia, primarily along the Blue Ridge Physiographic Province. Throughout this range, the proportion of available wetlands used by bog turtles is low despite the fact that many wetlands in the physiographic region appear similar upon a visual inspection. If wildlife managers could recognize how the occurrence of bog turtles is related to habitat differences among available wetlands, they could more efficiently identify occupied habitats and enact conservation measures for them. Soils are an integral part of bog turtle habitat that has not been described adequately in the literature.

The wetland fens used by bog turtles are characterized by groundwater supplied hydrology that results in saturation of surface soils, without deep inundation (Pitts 1978, Bury 1979, Chase et al. 1989, Buhlmann et al. 1997, Carter et al. 1999, Ernst and Lovich 2009, Chapter 1). The bog turtle spends much of its time submerged in saturated wetland soils that provide a medium for temperature regulation, shelter from predators, and hibernation (Chapter 3). Soil conditions in bog turtle wetlands are summarized in the biological literature as being deep, soft, and silty mud that is saturated and contains black organic material (Chase et al. 1989, Buhlmann et al. 1997, Ernst and Lovich 2009). More detailed, quantifiable, field characterization of soil properties in bog turtle wetlands may be more practical for identification and management of bog turtle habitats. Compiling soil information is particularly important in Virginia, where official United States Department of Agriculture general purpose soil surveys have been only recently published for counties in core parts of the bog turtle range.

General studies in mountain fens or bog type wetlands from within the narrow southern range of the bog turtle indicate the presence of soils formed from alluvium with moderate accumulations of organic matter and sphagnum moss at the surface (Weakley and Shafale 1994, Stolt and Baker 1995, Moorhead et al. 2000). Some of the wetland soils may qualify as organic soils. According to Stolt and Baker (1995), the most prevalent hydric soil present in the Blue Ridge Highlands of Floyd County had a fine loamy surface transitioning to sandy and rocky subsoil. Seepage areas were found to have a thicker and darker surface layer than adjacent floodplain soils.

The surface texture and organic carbon content of soils are characteristics that may be related to bog turtle use and selection of wetland habitats. Texture and carbon content are physical characteristics that can alter soil bulk density, how soil behaves when it is wet, and soil strength. Soil strength is defined as the property of the soil that causes it to resist deformation, and is increased by compaction (Brady and Weil 2008). Even at low proportions relative to other soil components, organic matter has a significant effect on soil structure, making it less dense and less easily compacted (Blanco-Canqui et al. 2009, Daum 1996). Clay is generally associated with stronger soils that are more easily compacted, while sandy soils tend to resist compaction (To and Kay 2005). Less dense organically rich saturated soils mixed with less cohesive granular sand and silt may provide a low strength substrate for bog turtles to move through. In Virginia, bog turtles used areas of a wetland that were closer to pockets of water and that contained deeper mud than paired random wetland areas (Carter et al. 1999). A standardized and repeatable in situ method such as a static cone penetrometer may be able to characterize saturated soil strength in bog turtle wetlands by measuring the penetration resistance of the soil.

Throughout the bog turtle’s range, the dominant current or former land use on many wetlands used by bog turtles was livestock grazing, and some wildlife managers assume that livestock are an important component for maintaining the open habitats preferred by bog turtles (Herman and Tryon 1997, Morrow et al. 2001). Bog turtles are also known to use the soil voids created by livestock hooves to access deeper soil, find cover from predators, and hibernate (Tesauro and Ehrenfeld 2007, Chapter 3). Little is known about how livestock activity affects soil strength in excessively saturated wetland soils. In some wetlands, livestock activity may be a factor in strengthening soils through compaction (Bhadha and Jawitz 2010). Alternatively, livestock activity may displace soils and destroy the soil structure that is held together by cohesion and roots. Other causes of soil disturbance (machinery) have been found to have unpredictable effects on the spatial variability of soil properties in wetlands (Bruland and Richardson 2005). It is uncertain whether the hoof prints left behind by livestock will have an overall effect on soil strength, or whether the spatial arrangement of the prints will result in an increase in the spatial variability of soil strength in grazed areas.

The overall purpose of this investigation was to describe the soils present in wetlands used by bog turtles relative to wetlands not used by bog turtles. Of primary interest were soil conditions in the upper part where bog turtles are found. I had several objectives that were investigated in the field and the laboratory: 1) Use the Soil Survey Geographic Database (SSURGO) to identify the soil series present in wetlands in the study area and to briefly interpret the taxonomic descriptions of these soil series; 2) Evaluate how the level of saturation is related to the particle size distribution and organic carbon content in the upper 18 cm of wetlands used by bog turtles and unused wetlands; 3) Investigate surface soil strength in specific locations where bog turtles are found; and 4) Use livestock exclosure fencing in bog turtle wetlands where livestock are present to test how livestock affect average surface soil strength and variability.

My general hypotheses were that surface soil conditions in wetlands used by bog turtles will differ from available but unused wetlands, and that livestock grazing activity can modify surface soil strength, leading to soil conditions that have impacts on bog turtle wetland use.

METHODS

Study Area

I conducted this investigation on 24 wetlands located in Floyd, Patrick, and Carroll counties within the Southern Blue Ridge sub-province of Virginia (Figure 2.1). The 24 study wetlands formed an elongated area stretching approximately 31 km. Precise wetland locations are not reported because of the federal and state protected status of the bog turtle and the risk of collection and trading. A wetland was considered a discrete study site when it was bounded by greater than 100 m of non-wetland, was bounded by the convergence of hydrology into a stream, or was separated from another site by a road. Wetlands were irregularly shaped with multiple projections and core areas of saturation due to irregularities in surface elevation and also the spatially irregular pattern of groundwater seepage areas. Groundwater was the primary hydrologic source for the study wetlands (Chapter 1). Wetland sites contained flora typically associated with bog turtles (Ernst et al. 1994, Morrow et al. 2001). Floral descriptions of bog turtle wetlands within the study area are available (Carter et al. 1999). Valley slopes where wetlands occurred were between 0 and 3%. The longitudinal axes of the study wetlands were not always oriented in the same direction as the valley slope, and wetland slopes along these axes were between 3 and 5%. Topography outside of the stream valleys was variable and ranged from gently rolling pastures to ridges and hills with steep slopes. Geology in the study region is characterized by coarse grained igneous and metamorphic rocks that create topology consisting of a broad upland plateau with moderate slopes. Average elevations in the area are 725 – 910 m with higher peaks rising above the uplands.

The 24 wetlands used in this study were divided into two groups of 12. The first 12, subsequently referred to as wetland Group A, were more intensively studied than the second group of equal size (Group B). Most of the activities described in this investigation occurred in wetland Group A, unless otherwise noted. Prior to beginning this study, I differentiated wetlands in both Group A and Group B based upon whether the wetland was known to be used or unused by bog turtles (bog turtle use status). Six used and six unused wetlands were initially identified in both wetland Groups A and B.

Ecological surveys designed to determine whether a species is occupying a defined habitat area have inherent error associated with non-detection of the species when the species is truly present. This error is related to the rarity of the species, how the species uses its habitat, how conspicuous the species is, and the density of the species on the survey site (Gu and Swihart 2004). The bog turtle is a species that is difficult to detect in surveys because the animals are small and inconspicuous in their coloration and behavior (Somers and Mansfield-Jones 2008).

I assigned seven wetlands as used based on multiple organized bog turtle surveys since 1987 that were completed and documented by biologists associated with the Virginia Department of Game and Inland Fisheries (VDGIF), the National Park Service (NPS), and collaborators. An additional five used wetlands were assigned based on turtle surveys that were completed in 2007 through 2009. All 12 used wetlands contained multiple adult bog turtles and nests have been observed on all of the wetlands in Group A. The 12 wetlands that were unused by bog turtles were assigned based upon VDGIF and NPS information and personal familiarity with wetlands in the area. The 12 unused wetlands were similar in position and slope to the used wetlands and were also dominated by emergent hydrophytic vegetation, contained hydric soils, and contained areas where surface saturation was evident during the growing season. I refer to the initial assignments of used and unused wetlands as the *a priori* wetland grouping.

In Group A wetlands, I completed additional bog turtle surveys in unused wetlands to reduce the inherent error associated with non-detection and also surveyed in wetlands used by bog turtles to establish realistic expectations of turtle captures given my survey effort. During the summer of 2007, I employed hand surveys (peering through vegetation and probing with a wooden stick) for 32 person hours and 106 person hours on *a priori* unused and used wetlands, respectively. No turtles were captured on unused wetlands, while hand surveys on used wetlands resulted in a capture rate of 2.6 turtles per 10 person-hours searched (expected captures on unused wetlands = 8.3 turtles). More survey hours were applied on used than on unused wetlands because of the need to capture turtle subjects for other research objectives.

I also used traps to survey for bog turtles (Chapter 1). During the summers of 2007 and 2008, I trapped for 10,536 trap hours and 16,296 trap hours on unused and used wetlands, respectively. No turtles were captured on unused wetlands, while trap surveys on used wetlands resulted in a capture rate of 2.3 turtles per 1,000 trap hours (expected captures on unused wetlands = 24.3 turtles). Because all of the study wetlands (with exception to one forested wetland) were dominated by herbaceous vegetation, there is no reason to assume differences in detection probability between these two groups of wetlands. Regardless of whether bog turtles may sometimes occur on the "unused" wetlands, there were lower densities of turtles there than on the "used" wetlands.

At the end of the study, the bog turtle use status of the *a priori* wetlands in Group A was modified to incorporate new information observed throughout the study period. During the course of concurrent radiotelemetry and hydrology characterizations on Group A wetlands, one bog turtle was found on each of two *a priori* unused wetlands. Unused wetlands in Group B were never changed from their *a priori* assignments because additional bog turtle surveys were not completed. For the remainder of this analysis, I refer to the two *a priori* "unused" wetlands where singular occurrences of bog turtles were recorded as "transiently used wetlands." Together, the 10 unused wetlands (four in Group A, six in Group B) where bog turtle encounters were never observed, along with the 12 used wetlands with multiple turtle encounters, comprise the *post hoc* experimental wetland grouping (see Appendices A.1 and B.1 for corresponding VDGIF site numbers of study wetlands). I justify using *post hoc* wetland groupings and the term "transiently used wetlands" because they imply that although bog turtles may occasionally use a wetland, the density of turtles cannot be great enough to support a viable turtle population.

All of the wetlands used by bog turtles were grazed by livestock within the last 15 years, and livestock presence or signs of livestock grazing were observed on 11 of the 12 wetland used by bog turtles. According to National Park Service, many of the wetlands not used by turtles were also grazed by livestock and used for agriculture in the past, but livestock presence or signs of grazing were evident on only three of the Group A wetlands and two of the Group B wetlands.

Identifying Soil Series on Group A Wetlands Using SSURGO

I used SSURGO data from Floyd and Patrick counties to determine the dominant soil series present within and in the vicinity of Group A wetlands (Soil Survey Staff 2009). To digitally sample the soils at the 12 wetland locations, I used the Soil Data Viewer extension created for ArcMap 9.2 (ESRI Redlands, CA, USA). I recorded the center point of all of the study wetlands using a GPS unit with approximately 4-m accuracy. I then created 1-ha circular polygons with the center point of the plot placed in the center of each study wetland. Finally, I used Soil Data Viewer to generate a report that provided the unique soil series present, the taxonomic description of the series, and the proportions of each series in each plot. Dominant soil types (by proportion) were examined for any obvious differences between wetlands used and unused by bog turtles, but statistics were not completed as the data were categorical and sample size was small. The dominant soil type and other site characteristics are provided in Appendix A (Table A.1).

Soil Sampling and Laboratory Analysis on Group A wetlands

Surface soil was sampled from Group A wetlands to evaluate organic carbon content and dominant particle sizes. To organize the sampling effort, I stratified sampling by the degree of wetness exhibited by each wetland. Degree of wetness could fall into five possible categorical strata (Table 2.1). I applied strata based on qualitative observations made during the yearlong period prior to sampling, which occurred in July 2008 (Figure 2.2). Severe drought conditions occurred in 2007 and 2008 (Chapter 1), and surface saturation in the study wetlands in July 2008 was reduced to only small areas that were topographically low or where groundwater seepage occurred.

I used an 8.9-cm diameter, 18-cm long bucket auger to collect at least 10 subsamples of the top 18 cm of soil from within each categorical wetness strata available in each study wetland. I did not sample deeper than the upper 18 cm of soil because concurrent studies established that hibernating and active bog turtles are almost always found at relatively shallow depths (Chapters 3 and 4). Subsamples were thoroughly mixed in a bucket on site and a composite sample was taken. Not all categorical wetness strata were available in each wetland. The active ditch stratum was only present on three wetlands (all wetlands used by bog turtles), and the always wet stratum was present on eight wetlands. The temporarily wet stratum was absent on one wetland unused by bog turtles. In total, I collected 45 composite samples from the 12 Group A wetlands.

I air-dried composite samples, ground them, and passed them through a 2-mm sieve to remove large plant material and gravel. Before particle size distribution analysis, I treated a 50-g portion of the composite sample with 30% hydrogen peroxide to remove organic matter. I added 5% sodium metaphosphate to the organic matter free soil and used the hydrometer method to determine particle size (Gee and Bauder 1979). I determined the percent content of organic carbon using combustion of an approximate 1-mg allotment of composite sample with a carbon nitrogen analyzer (Elementar VarioMax CNS, Hanau, Germany). I analyzed two replicate samples for organic carbon content per composite sample, and replicate samples were averaged prior to statistical analysis to reduce variability.

I tested the hypotheses that surface organic carbon content would be greater in wetlands used by turtles than in unused wetlands. I also tested if particle size was different between used and unused wetlands. An additional hypothesis was that organic carbon content would be higher in the wetter portions of the study sites. Response variables of percent organic carbon and percent silt were evaluated for the assumption of normality of residuals and analyzed using a general linear model with fixed effects (PROC GLM, SAS institute, Cary, NC). Fixed effects were wetland use status (used or unused), wetness stratum, and their interaction. Statistics were evaluated for both the *a priori* and *post hoc* wetland groupings. I determined where significant differences occurred between strata using Tukey's test for multiple comparisons. Significance was assumed at α=0.10. Only percent silt was tested statistically as the proportions of silt, sand, and clay in a soil sample are not independent. I chose to statistically test silt because basic summary statistics following particle size analysis indicated that this particle size class was both abundant in each of the samples and had the largest apparent discrepancies among wetness stratum and between bog turtle used and unused wetlands.

Soil Sampling and Laboratory Analysis on Group A and B Wetlands

In June 2009, I collected composite samples from Group B wetlands as well as new composite samples from the previously sampled Group A wetlands. Sampling differed from the method used to sample only Group A wetlands in that subsamples were collected from the wettest areas of each wetland, and sampling was not stratified by multiple wetness strata. Weather conditions in June 2009 were average to wet. As a result, subsamples were collected from any areas of the wetland qualifying as “always wet”, “usually wet”, or “temporarily wet” (Table 2.1). Only one composite sample was removed from each of the 24 wetlands. At the time of sampling, I recorded the pH at each wetland by taking the average from three subsamples. All collected samples were air-dried and analyzed for organic carbon and particle size distribution. As with samples from only Group A wetlands, I statistically tested the hypotheses that surface organic carbon content and the proportion of soil classified as silt would be greater in wetlands used by bog turtles than in unused wetlands. Soil percent carbon and percent silt were evaluated for the assumption of normality of residuals and analyzed using a two-sample t-test. Statistics were evaluated for both the *a priori* and *post hoc* wetland groupings.

Evaluating Soil Penetration Resistance at Points of Turtle Use

In June 2008, I used a digital logging static cone penetrometer (Field Scout SC900 Soil Compaction Meter, Spectrum Technologies, Inc., Plainfield Illinois) to investigate the selection of soil compaction by bog turtles within a wetland area. The SC900 is capable of logging the compaction of soils from 0 to 45 cm at 2.5-cm increments. To accommodate the relatively low strength of saturated soils inherent to the study wetlands, I used a 20.27-mm diameter cone rather than the 12.83-mm diameter cone provided with the penetrometer (American Society of Agricultural and Biological Engineers 2004). I multiplied all cone index readings (kPa) by the scalar 0.40 to compensate for the larger cone. I compared the soil strength by measuring the penetration resistance at locations used by turtles and random locations within the wetlands that were available to the turtle. All data pairs were recorded by the same operator to reduce observer variance (Herrick and Jones 2002). Turtle-centered (used) locations were any location where a bog turtle was found, as long as the turtle was not walking at the time of capture. Random locations were generated using a random compass bearing and distance between one and five meters of the turtle-centered locations. Random locations were also constrained to areas meeting wetland criteria (Wetland Training Institute, Inc. 1995). At each turtle-centered and random position, I made nine subsample penetration profiles. Subsamples were taken at the center point and at 50 and 100 cm from the center in each of the cardinal directions. For analysis, all subsamples were averaged by depth to provide two profiles (used and random) for each turtle. Twelve individual turtles were used for this analysis, providing 12 pairs of profiles for comparison. I compared soil strength at depth using graphical methods and paired t-tests to test the hypothesis that soil strength was lower in turtle-centered areas than in random areas. I also used simple linear regression to test for an interaction (difference in slope) or a difference in the intercepts in the relationships of soil strength with depth at turtle-centered and random locations. Soil strength was natural log transformed before regression and interaction modeling to improve the assumption of normality of residuals.

Livestock Exclosure Experiment Design and Soil Measurements

In 2001 and 2002, Virginia Tech Department of Fisheries and Wildlife Sciences and the Blue Ridge Parkway constructed 10 fenced livestock exclosure plots within random locations of six wetlands used by bog turtles in Floyd and Carroll counties. Each 5 x 5 m ungrazed exclosure plot was paired with a nearby grazed control plot to allow for habitat measurements that could be analyzed using statistically-paired comparisons. By June of 2008, grazing livestock were present in only five of the original 10 pairs of plots. The five active plot pairs occurred on three different wetlands, and are subsequently referred to as OG-1, OG-2, ST-1, ST-2, and CW-1. Communication with local ranchers and Blue Ridge Parkway managers indicated that livestock grazing occurred continuously at the active plots since the construction of the exclosures. Although the stocking density of livestock was variable during this period, grazing activity was substantial enough to maintain visually obvious removal of the upper parts of wetland plants, as well as numerous holes from the hoof action of the livestock.

To determine if differences in the mean or spatial variability of penetration resistance could be attributed to grazing activity, I made 32 separate penetration profiles from a systematic grid placed within each of the active exclosures and control plots where grazing activities were confirmed. Plots were designed to constrain access while making measurements to the outside perimeter of the plot. Therefore, the grid was established in the center of the plot and consisted of outside dimensions of 4 x 4 m and contained 16 nodes. At each node, I recorded two penetration profiles. Profiles at the same node were spaced approximately 20 centimeters apart. Following the penetrometer measurements, I collected composite samples of the surface soil from each plot. These composite samples were analyzed for organic carbon content using the aforementioned methods.

Using plot as an experimental unit, I averaged all 32 penetration profiles by depth to calculate one penetration profile for each exclosure and control. This sub-sampling technique resulted in a sample size of five pairs. I then used a paired t-test to determine whether the mean soil strength from the surface to 18 cm was different on exclosure and control plots. I used the modified Levene test to test the hypothesis that variability on control plots was greater than on exclosure plots. The Levene test does not need to have normally distributed data, which is an assumption for the F-test (Neter et al. 1996). I also used each of 32 individual penetration measurements as an experimental unit to compare the variability in each exclosure and control pair. For each plot, I created a frequency histogram showing the occurrence of penetration resistances from the surface to 18 cm that spanned between 0 and 420 kPa. I graphically placed the histograms of exclosure pairs side by side to detect if the distribution of resistances were visually different. Again, I used the modified Levene test to test for evidence that soil strength was more variable in control plots than in exclosure plots.

RESULTS

Identifying Soil Series on Group A Wetlands Using SSURGO

The report from SSURGO indicated that three different hydric soils were present in the 12 Group A wetlands. No apparent differences in the frequency of soil series were detected between wetlands with different turtle use status. The most common soil series present was the hydric Hatboro sandy loam (fine-loamy, mixed, active, nonacid, mesic Fluvaquentic Endoaquepts), comprising approximately 50% of the soil coverage in the study wetlands. The other hydric series present included the Kinkora series (fine, mixed, semiactive, mesic Typic Endoaquults) and the Nikwasi series (coarse-loamy over sandy or sandy-skeletal, mixed, superactive, nonacid, mesic Cumulic Humaquepts). The most common non-hydric soil series present in the vicinity of the wetland sites were the Ashe (coarse-loamy, mixed, active, mesic Typic Dystrudepts), Delanco (fine-loamy, mixed, semiactive, mesic Aquic Hapludults), Edneyville (coarse-loamy, mixed, active, mesic Typic Dystrudepts), and Myersville (fine-loamy, mixed, active, mesic Ultic Hapludalfs).

Soil Conditions in Group A Wetlands

Statistical results comparing organic carbon content were consistent for both *a priori* and *post hoc* wetland groupings. Organic carbon content in wetland soils was significantly dependent on wetness strata, but was not different between wetlands with different bog turtle use status. There was not a significant interaction between turtle use status and wetness strata (Table 2.2). Organic carbon content increased as the degree of saturation in strata increased (Figure 2.3). Average organic carbon content (± SE) in the "always wet" and "usually wet" strata that are frequently used by bog turtles were 10.9% ± 0.9% and 8.2% ± 0.7%. Organic carbon content of the "temporarily wet" and non-wetland strata were 4.7% ± 0.8% and 4.0% ± 0.7%. The organic carbon content from the top 18 cm of the active ditch stratum was 3.3% ± 0.5%. This stratum was only present on three bog turtle used wetlands and therefore was not a part of the general linear model. Tukey's multiple comparisons among strata indicated that the "always wet" and "usually wet" strata were not different from each other, but were both different than the "temporarily wet" and non-wetland strata. The "temporarily wet" stratum and the non-wetland stratum were not significantly different. Comparisons of organic carbon content indicated that "always wet" strata were different from non-wetland strata in *a priori* wetlands used by bog turtles and unused wetlands (Table 2.3).

Statistical results comparing percent silt content were also consistent for both *a priori* and *post hoc* wetland groupings. The amount of silt was not different among wetland strata, nor was it different between wetlands grouped by bog turtle use status (Table 2.2 and 2.3). Overall Group A averages of percent sand, silt, and clay were 47%, 47%, and 6%, respectively. The particle size distribution of the mineral component of surface soils within and in the non-wetland vicinity of Group A wetlands qualifies as a sandy loam texture.

Soil Conditions and pH in Group A and B Wetlands

Potential differences in organic carbon content were detected between wetlands with different bog turtle use status when I added the 12 Group B wetlands to the data set. These results were consistent for both *a priori* and *post hoc* wetland groupings (Table 2.4). Organic carbon content (± SE) of surface soil was approximately 2.1% ± 1.2% higher in *a priori* bog turtle used wetlands than in unused wetlands (df=22, t=1.74, P=0.048). Differences (3.1% ± 2.2%) were stronger using *post hoc* wetland groupings (df=20, t=3.31, P=0.002). Results of particle size analyses were not markedly different than those found on only Group A wetlands, and the proportion of silt was not different between wetlands with different turtle use status. The average content of sand, silt, and clay in all 24 wetlands was 41%, 51%, and 8%, respectively, giving an overall silt loam texture class. The pH on bog turtle used and unused wetlands (± SE) was 6.3 ± 0.12 and 6.3 ± 0.11, respectively. A two-sample t-test did not show a difference in pH values of wetlands grouped by turtle use status (df=21, t=0.12, P=0.91).

Soil Penetration Resistance at Points of Turtle Use

The penetration resistance profiles at turtle-centered locations were visually and statistically different than profiles at random wetland locations (Figure 2.4). For depth between

0 and 18 cm, the average penetration resistance (± SE) at 12 turtle locations was 127 kPa ± 39 kPa compared to 250 kPa ± 54 kPa for random locations. This difference in soil strength was significant according to a one-tailed paired t-test (df=11, t=2.00, P=0.035). Linear regression and interaction analysis (Figure 2.5) of the relationship of soil strength to depth at turtle-centered and random locations revealed that soil strength increased with depths between 0-20 cm for both locations (df=1,209, t=2.68, P=0.008). A significant interaction (slope difference) was present between depth and turtle-centered or random location (df=1,209, t=2.02, P=0.048). Soil strength was relatively high on the surface at random locations and increased moderately with depth, while soil strength was low at the surface and increased more rapidly at turtle-centered locations. Soil strength at the surface (the intercept) was lower at turtle-centered locations than at random locations (df=1,209, t=-4.60, P<0.001).

Soil Response to Livestock Grazing

When the entire plot was considered to be the replicated experimental unit, no differences in soil strength were detected between exclosure and control plots. Mean soil strength as measured by the penetrometer cone index from 0 to 18 cm (± SE) was 159 kPa ± 37 kPa in control plots and 145 kPa ± 15 kPa in exclosure plots, indicating no statistical difference according to a paired t-test (df=4, t=0.51, P=0.64). A Levene's test of variability did not detect a significantly different variability on control plots than on exclosure plots (df=1,3, W=2.20, P=0.176), although the standard error was slightly higher on control plots. Mean organic carbon content (± SE) was 10.3% ± 1.0% in control plots and 10.4% ± 0.7% in exclosure plots, and was not statistically different between treatments according to a paired t-test (df=4, t=0.12, P=0.91).

Information about the variance of soil strength within plot pairs was revealed when the replicated experimental unit was the 32 penetrometer profiles taken in each control and exclosure plot (Table 2.5). Paired plots tended to have a similar frequency distribution of soil strength between 0 and 18 cm, although differences in the distribution among wetlands were evident (Figure 2.6). Plot pairs within the same wetland, i.e. OG-1 and OG-2, appeared to have similar resistance distributions. Control plots had a higher penetrometer cone index range on the ST-1, ST-2, and CW-1 pairs, yet only the ST-1 control plot had a significantly higher variability according to a Levene test (df=1,62, W=8.54, P=0.005). The two OG plot pairs had higher variability in exclosure plots, with a significant difference on the OG-2 exclosure plots (df=1,62,

W=3.90, P=0.053). When I compiled all penetrometer measurements together, there appeared to be an overall trend of higher variability on control plots than on exclosure plots (df=1,158, W=24.24, P=<0.001).

DISCUSSION

Soil Series and Taxonomy

Soil series and taxonomic classifications reported from SSURGO provided a way to standardize soil information from bog turtle wetlands and allow for widespread comparisons to other soil series described by soil scientists. As soil series names are derived from the family level (5th level) of taxonomy names, the full taxonomic classification of the study soils were useful because they identified more basic formative soil characteristics (Soil Survey Staff 2006). Hydric soils in Group A wetlands were primarily of the order Inceptisol, attesting to the lack of structure and clay development in the subsoil. The most abundant soil in the study area, the hydric Hatboro series (fine-loamy, mixed, active, nonacid, mesic Fluvaquentic Endoaquepts), is saturated throughout the profile from water originating in the ground (Endo), as opposed to a perched water table originating from surface runoff. The Hatboro soil is formed under conditions of flooding, and has very little development with exception to organic matter accumulation at the surface (dark epipedon). The floodplain position of the Hatboro soil is consistent with the sandy loam surface material characterizing most of the study wetlands. Further, an increase in gravel and cobble material with depth indicates that fluvial deposition is a factor in the Hatboro series. In Chapter 1, I provided soil profile descriptions as part of the installation of groundwater wells on Group A wetlands. Findings indicated that a gravel and cobble layer commonly occurred at approximately 55 to 65 cm, and auger refusal on large alluvium occurred at a mean depth of 63 cm. There was a gradual boundary between dark-colored organically enriched soil at the surface and organically deficient subsoil that lacked structure. The process of soil formation by flooding does not imply that flooding is frequent on bog turtle wetlands. Other studies of wetlands in the Blue Ridge of North Carolina, many of which contained bog turtles, noted that the wetlands were "non-alluvial" in terms of their hydrology source, but that the soils consisted of coarse alluvial materials (Weakley and Schafale 1994).

Another hydric soil present in the study wetlands was the Nikwasi series (coarse-loamy over sandy or sandy-skeletal, mixed, superactive, nonacid, mesic Cumulic Humaquepts). This soil differed from the Hatboro because it had an over thickened dark epipedon, indicating that organic matter was accumulating on the surface. From soil profile descriptions during well installation (Chapter 1), I found that some study soils contained a very dark layer to approximately 11 cm. The most common non-wetland soils in the vicinity of the study wetlands were loamy soils with developed clay layers below the surface. These soils had variable base saturation and formed from residuum and colluvium.

Organic Carbon and Mineral Soil Texture in Bog Turtle Wetlands

The organic carbon content of surface soils was significantly greater in the more saturated areas (always wet and usually wet strata) of the Group A study wetlands. There was not statistical evidence that surface organic carbon varied between wetlands with different bog turtle use status in Group A wetlands, regardless of whether *a priori* or *post hoc* groupings were compared. However, when I considered soil information from both Group B and Group A wetlands, surface organic carbon content was significantly different between bog turtle used and unused wetlands. Based on particle size distribution analysis, soils were primarily sandy loam or silt loam textures. These mineral textures did not differ significantly among wetness strata, although the wetter strata appeared to contain a greater proportion of silt and less sand than the drier and non-wetland strata. This pattern is common in alluvial soils (Stolt et al. 2001). The sand and silt may have originated as sediment that was imported from non-wetland areas.

Laboratory analyses indicated that organic carbon content of surface soils was generally below the threshold to qualify the surface soil as organic material, even in many wetland areas that were saturated enough to be considered always wet. Soil qualifies as organic material when substantial organic carbon is present, and is also dependent on the clay content of the soil. When no clay is present, the threshold for organic material is 12% organic carbon. I found average clay contents between 5 and 10%, resulting in an approximate 13% organic carbon threshold for organic material (Soil Survey Staff 2006). Most of the surface soils sampled in this study were below this threshold, with a mean organic carbon (± SE) of 9.9% ± 1.5%. One transiently used wetland contained organic carbon levels of 21% in the always wet strata. This was the only wetland in the study covered by a closed canopy of trees, and had a large quantity of leaf litter inputs, continuous saturation, and abundant sphagnum moss. Elevated organic carbon levels have also been observed in similar closed canopied wetlands in the Blue Ridge Mountains of North Carolina (Reynolds et al. 2007).

With the quantity of organic carbon (5 to 12%) found in the always wet and usually wet strata, surface soils in these areas classified as mucky modified mineral soils. Mucky modified material must exceed 5% organic carbon when no clay is present. Only the surface soils of the wetland with the forest canopy were thick enough and contained enough organic material to qualify as a histic epipedon. Within study wetlands, organic carbon content was somewhat variable, even within the same wetness strata. There are several factors that can cause organic carbon content to vary within a wetland. It is possible that the large range of organic carbon content was due to non-uniform coverage of sphagnum moss. Areas containing abundant sphagnum moss are known to greatly increase the organic carbon content of soil (Thompson et al. 2007). Sphagnum moss decomposes slowly relative to other types of wetland plants, resulting in organic carbon accumulation (Moore et al. 2007). Vertical hydrologic gradients can be variable within a wetland, causing local seepage areas that are more consistently saturated than other portions of the wetland (Chapter 1). Seepage areas have been found to increase organic accumulation in the Blue Ridge of Virginia (Stolt and Baker 1995). Finally, livestock activity may also facilitate the accumulation of organic matter by pushing living plant parts deeper into the soil where decomposition rates are slower (Moore et al. 2007). Highly variable organic carbon contents between 2 and 21% were found in the surface horizons of four different fens in the Blue Ridge province of North Carolina (Moorhead et al. 2000). The high variability in carbon content in that study was attributed to geomorphic setting, with sloped areas having less organic carbon than flat areas. Another factor in the variability seen in North Carolina fens was the long-term human activities and grazing that occurred in the study area. These land use patterns also applied in this study.

Linking Soil Conditions with Bog Turtle Use

According to measurements of penetration resistance recorded by a data-recording penetrometer, turtles were found in locations with significantly lower strength soils than nearby random wetland areas. Further, interaction analysis using simple linear regression found that the relationship of soil strength with depth differed on turtle-centered and random locations. Random locations had higher strength soils at the top 15 cm, where bog turtles are frequently found, while turtle-centered locations had low strength soils at the surface and a steady increase in soil strength down to 20 cm. The higher strength soils at the top of the soil profile in random locations would make it difficult for turtles to submerge themselves. Soil strength remained lower at bog turtle-centered areas until approximately 40 cm, when random locations began to have lower strength soils. This outcome was likely due to the presence of deeper soils at random locations compared to coarse alluvial materials at turtle-centered locations. Coarse materials are difficult to penetrate and can represent discontinuities in soil deposition sequences (Shanley et al. 2003). In these study wetlands, the low soil strength areas used by turtles may coincide with topographic low spots where fine sediments have accumulated over large alluvium, such as in a former stream bed. Stolt et al. (2001) also found that fine particles settled out in topographic low spots. Very wet areas would also be expected to record lower penetration resistances because soils can behave more as a liquid at high water contents (Brady and Weil 2008).

A notable exception of bog turtles selecting for lower strength soils occurred during the most severe portion of the drought occurring in 2007 and 2008. At this time, the proportion of area covered by surface saturation became limited in the study wetlands (Chapter 1). The only areas in the wetland where turtles could access saturated soil were in the deepest livestock hoof prints, but water was also available in the coarser textured shallow sediment at the bottom of active ditches and small streams, which constituted the active ditch stratum. During this time, many bog turtles used the organically deficient active ditch stratum (Chapter 4). Ditch use was not common during the non-drought portions of the study when the usually wet strata and temporarily wet strata were saturated. Research has documentd bog turtle use of streams and ditches during dry periods (Pittman and Dorcas 2009).

Was bog turtle use of areas with lower strength soils related to the organic carbon content in the surface? Even small amounts of organic carbon can lower soil strength by reducing the susceptibility of soil to compaction (resulting in stronger soils) by creating stable structural aggregates, and lowering the bulk density of soil (Daum 1996, Blanco-Canqui et al. 2009). It was not practical to measure the average organic carbon content of turtle-centered areas relative to the remainder of the wetland. Therefore, I cannot conclude that bog turtle access to low strength soil is related to organic matter content. Nonetheless, analysis of soils from the larger dataset of 24 wetlands found significantly higher surface organic carbon on wetlands used by bog turtles than on unused wetlands. These results may be interpreted that bog turtles are more successful in wetlands with more organic carbon because carbon content reduces the density of soils and lowers soil strength.

Bog turtle use and occupancy of wetland habitats may be a combination of the presence of abundant saturation and subsequent accumulation of organic matter. Organic carbon tends to accumulate where saturation is persistent (Bruland and Richardson 2006, Moore et al. 2007). The presence of sphagnum moss, a major factor in organic matter accumulation, is associated with good turtle nesting habitats (Mitchell 1994). Therefore, hydrology may be the primary factor in bog turtle use of wetlands, with organic carbon and soft sediment deposition a secondary factor. As evidence for this claim, one of the wetlands with the highest density included in the study actually had soils with relatively little organic carbon. In this wetland, the "always wet" and "usually wet" strata had organic carbon contents of 5.3% and 4.4%, respectively. This wetland was ditched in the past, but remained saturated in the majority of the ditches. Water velocity in the ditches was minimal, and ditch flow did not respond dramatically during storm events, allowing silt and clay sediments to settle in the ditches. The soft sediments allowed turtles to cover themselves in mud and move through in the same manner as observed on more organically-rich wetlands where bog turtles are present. The influence of hydrology on bog turtles was also observed on two bog turtle used wetlands where the always wet stratum was absent. These same two wetlands contained active ditches that were used by bog turtles when the wetlands were driest. In some wetlands, the presence of inundated ditches may provide an alternative saturated habitat to organically rich soil areas (always wet strata) as long as the usually wet strata remain saturated during all but the worst droughts.

Potential Changes to Soil Properties by Grazing Activity

Using plot pairs as experimental replicates, livestock grazing did not result in any statistically detectable trends in mean organic carbon content, mean soil strength, or variability in resistance. Soil compaction by means of livestock has been reported in grazed wetlands (Bhadha and Jawitz 2010). Mechanical destruction of soil structure was qualitatively visible in grazed areas of the study wetlands, as any formation of soil aggregates were destroyed through mixing by livestock hooves.

Human activities associated with farming and heavy land use are often expected to homogenize soils and reduce the variability of organic matter and particle size over the surface and vertically through the profile (e.g. Stolt et al. 2000, Bruland and Richardson 2005). However, I hypothesized higher surface variability of penetration resistance in grazed (disturbed) control plots than exclosure plots. I expected that livestock activity in saturated soils would result in a soil system with alternating areas of low resistance hoof prints consisting of water and mud filled voids and relatively compacted mounds of displaced soil and root masses. Looking at the distribution of soil strength measurements within plots provided some evidence that livestock activity can affect the variability of soil in a small space, but livestock activity did not appear to only increase variability as hypothesized. Variability was higher in three out of five control plots, but only one of these differences was statistically significant. Similar to the soil system described in Bruland and Richardson (2005), the results of this study appear to indicate that it is difficult to predict whether variability will increase or decrease following disturbance. It is important to note that grazing had occurred for decades prior to the onset of this cattle exclosure study. The cattle exclosures had only been active for six years at the time of soil strength measurements, thus soil conditions may not have had sufficient time to respond to changes in grazing management.

Management implications

Bog turtles were found to use wetland areas that had low strength soils, potentially enabling them to submerge themselves below the soil surface. Being able to access soils is important to bog turtles because soil access has biological links to turtle thermoregulation and predator avoidance. Organic carbon accumulation at the surface, an outcome of nearly continuous saturated conditions, was found to occur in bog turtle wetlands and may be an important component in maintaining the low strength soils facilitating bog turtle use. Considering the prevalent use of low strength soils by bog turtles, it follows that maintaining the presence of low strength soils and monitoring the availability of this resource in bog turtle habitats is important to the species.

Wetland activities that lower the water table or concentrate flow through channels have been shown to reduce organic carbon contents of wetland soils through increased decomposition of organic matter and dissolved organic carbon losses (Strack et al. 2008). Wetland activities involving machinery, ditching, and pond building continue to occur in the Virginia Blue Ridge. These activities threaten to change the mucky-modified sandy loams and silt loams currently present in Virginia bog turtle wetlands. Besides being diligent about enforcing existing wetland law, managers should pursue activities that maintain high water tables without creating excess inundation. Limiting or prohibiting construction of open water habitats (farm ponds) can prevent inundation of the wetland fens used by bog turtles. Erosion control of stream banks in some heavily grazed wetlands is one way to maintain high water tables. Reducing grazing pressure is an effective way to decrease bank erosion (Zeckoski et al. 2007). The effect of total livestock exclusion in bog turtle wetlands remains a debatable issue; however, as grazing livestock are implicated in the maintenance of wetlands with open canopies. The United State's Department of Agriculture's Natural Resources Conservation Service manages the cost sharing Conservation Reserve Enhancement Program (CREP) designed to protect environmentally sensitive areas and restore wetlands on lands used for agriculture. Although CREP has the potential to be incorporated into the management of bog turtle wetlands, grazing activities are completely excluded from CREP lands (United States Department of Agriculture 2007), which may be undesirable in or near bog turtle habitats. It has been suggested that microtopography is an important trait of biologically diverse wetlands, particularly in the Blue Ridge province (Rossell et al. 2008). Research should continue evaluating the importance of spatially-variable soil conditions in bog turtle habitats, as these conditions may be dependent on livestock grazing, microtopography, and organic matter accumulation at the soil surface.

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Table 2.1. Criteria used to stratify area of wetland before soil sampling and analysis. Strata were identified using qualitative observations of soil surface saturation recorded from June 2007 through July 2008. Hydrologic conditions in late July and August 2008 were the driest recorded during the study. Moderate to severe drought conditions occurred in 2007 and 2008 (Chapter 1).

Wetness Strata	Definition
Always wet	Remained saturated to the soil surface throughout the study, including the summer of 2008 when water tables dropped following two years of drought. Occurred in seepage areas or topographic low spots. Bog turtles frequently used this stratum.
Usually wet	Vegetation and water table hydrology were indistinguishable from the always wet stratum during the majority of the study. On normal years this stratum remained saturated throughout the summer. This stratum dried during the summer of 2008. Bog turtles frequently used this stratum.
Temporarily wet	Met wetland criteria (Wetland Training Institute, Inc. 1995), but only had surface saturation or water pockets during early spring or after rain events. Occurred at the edge of the wetter strata or on topographic high spots within an otherwise saturated area. Bog turtles crossed this stratum frequently. May be important to bog turtles during wetter than average years.
Non-wetland	Did not meet wetland criteria (Wetland Training Institute, Inc. 1995). Occurred between wetland areas or between seepage areas separated by topographic high spots. Turtles were observed crossing this stratum to access saturation, but did not remain in stratum (Chapter 4).
Active Ditch	Human-created wetland feature. Remained saturated throughout entire study, but occurred in wetlands or small streams that had been channelized. Hydrology differed from other strata because of the higher velocity associated with concentrated flow. Turtles used the ditch stratum, particularly when no other wet areas were present. Not present in most wetlands.

Table 2.2. Results of analysis of variance (Type III SS) testing for dependence of organic carbon content and percent silt on wetland bog turtle use status, wetness stratum, and the interaction of these factors. The *a priori* wetland groupings were based on bog turtle wetland use status at the beginning of the study (n=6 used; n=6 unused), while the *post hoc* groupings had two transiently used wetlands removed from the *a priori* unused group where a single bog turtle was found during the study.

Property	Source of variation	*df* *	*F*	*P-value*	*F*	*P-value*
			a priori		*post hoc*	
%O.C.	Bog turtle use status	1	0.15	0.702	0.64	0.430
	Wetness stratum	3	15.24	< 0.001	13.39	< 0.001
	Use status*Stratum	3	0.60	0.618	0.57	0.637
%Silt	Bog turtle use status	1	2.45	0.127	0.00	0.976
	Wetness stratum	3	1.39	0.263	1.78	0.174
	Use status*Stratum	3	0.88	0.461	1.30	0.295

*** Error degrees of freedom in all models=35.**

Table 2.3. Mean soil properties in variably wet strata of 12 wetlands (Group A) grouped by bog turtle use status. The *a priori* wetland groupings were based on bog turtle use status at the beginning of the study (n=6 used; n=6 unused), while the *post hoc* groupings had two transiently used wetlands removed from the *a priori* unused group where a single bog turtle was found during the study.

Bog turtle use status	Wetness stratum	N	Organic carbon	Sand	Silt	Clay
			---------------- % (SE) from 0 – 18 cm -----------			
Used	Always wet	4	9.9 (1.5)	39.2 (7.5)	54.1 (6.4)	6.7 (1.6)
a priori	Usually wet	6	8.6 (1.1)	39.7 (1.8)	52.3 (2.1)	8.0 (0.6)
	Temporarily wet	6	5.0 (0.5)	49.8 (4.1)	44.0 (3.8)	6.1 (1.5)
	Non-wetland	6	3.6 (0.8) [ab†]	46.2 (2.8)	47.3 (2.9)	6.5 (1.5)
	Active ditch*	3	3.5 (0.33)	61.3 (4.2)	32.0 (5.5)	6.8 (1.7)
Unused	Always wet	4	11.9 (3.1)	49.6 (3.9)	42.4 (3.3)	8.0 (1.7)
a priori	Usually wet	6	7.9 (0.7)	42.6 (5.9)	50.2 (6.3)	7.2 (0.7)
	Temporarily wet	5	4.4 (0.3) [a]	49.9 (4.8)	46.1 (4.6)	4.0 (1.7)
	Non-wetland	6	4.4 (0.6) [a]	56.0 (5.3)	39.0 (5.0)	5.1 (1.6)
Unused	Always wet	2	9.1 (0.5)	49.5 (8.4)	43.6 (7.7)	6.9 (0.6)
post hoc	Usually wet	4	7.2 (0.7)	35.8 (6.1)	57.4 (6.5)	6.9 (1.1)
	Temporarily wet	4	4.3 (0.3)	45.7 (3.0)	50.4 (2.2)	3.9 (2.1)
	Non-wetland	4	4.5 (0.9)	49.4 (5.2)	46.0 (3.4)	4.5 (2.4)

† Significant differences (*P* <0.05) within wetlands with the same bog turtle use status in the "always wet" stratum is indicated by an "a." Differences from the "usually wet" stratum are indicated by a "b."
*** The wetness stratum "active ditch" was not compared among other strata in the mixed model because it was not represented in the group of wetlands that were unused by bog turtles.**

Table 2.4. Mean pH and soil properties in 24 wetlands (Group A and Group B) that were used and unused by bog turtles. Unlike the stratified sampling technique used in the other portion of this study, these values originate from one composite sample that was drawn from each wetland. The *a priori* wetland groupings were based on each wetland's bog turtle use status (n=12 used and n=12 unused), while the *post hoc* groupings had two transiently used wetlands removed from the *a priori* unused group where a single bog turtle was found during the study.

Bog turtle use status	N	pH (SE)	Organic Carbon	Sand	Silt	Clay
			-------------- % (SE) from 0 – 18 cm --------------			
Used *a priori*	12	6.3 (0.13)	8.8* (0.66)	38.8 (2.9)	52.2 (3.1)	9.0 (1.3)
Unused *a priori*	12	_	6.7 (1.0)	42.9 (3.2)	51.0 (3.2)	6.1 (0.62)
Unused *post hoc*	10	6.4 (0.13)	5.7 (0.68)	40.9 (3.4)	53.5 (3.3)	5.6 (0.59)

*** A two-sample t-test with the hypothesis that mean % organic carbon was greater on *a priori* bog turtle used wetlands than unused wetlands was significant (*df*=22, *t*=1.74, *P*=0.048). The same comparison with *post hoc* wetland groupings showed stronger differences (*df*=20, *t*=3.31, *P*=0.0018).**

Table 2.5. Results of soil strength measurements taken between 0 – 18 cm depth in 5 m x 5 m livestock grazed control plots and ungrazed exclosure plots. Strength was determined using 32 static cone penetrometer repetitions in each plot. Mean soil strength did not differ between control and exclosure plots (see text). To test for differences in variability of penetration resistances in paired control and exclosure plots on the same site, the modified Levene statistic was used.

			Penetration Resistance (kPa)			
Site	Treatment	n	Mean	Standard Error	Levene test (*W*)	*P* > *W*
CW	Control	32	127.1	12.0	1.28	0.262
	Exclosure	32	120.3	8.6		
ST-1	Control	32	247.8	16.1	8.54	0.005
	Exclosure	32	169.5	9.0		
ST-2	Control	32	247.7	14.1	0.83	0.367
	Exclosure	32	178.1	10.8		
OG-1	Control	32	78.8	8.9	0.54	0.466
	Exclosure	32	100.0	10.4		
OG-2	Control	32	94.1	8.0	3.90	0.053
	Exclosure	32	158.7	14.6		
Overall*	Control	160	159.1	8.0	24.24	<0.001
	Exclosure	160	145.3	5.4		

*** A paired t-test used to compare the mean soil strength of the 5 plot pairs on the different sites did not show a significant difference (*df*=4, *t*=0.51, *P*=0.638). A Levene test of the same pairs did not show a difference in variability (*df*=4, *W*=2.20, *P*=0.176).**

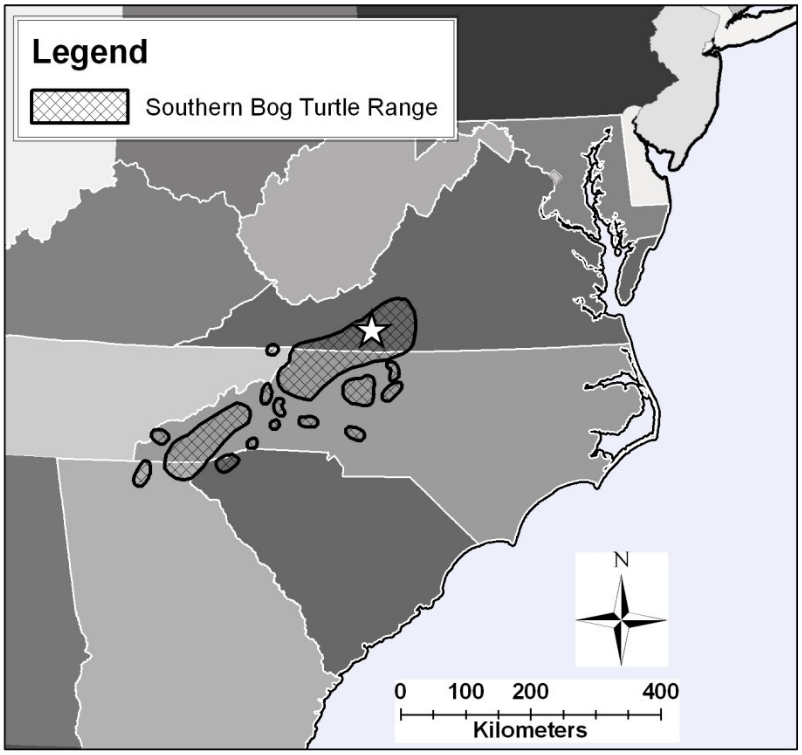

Figure 2.1. Study location (star) in the Blue Ridge Physiographic Province of Southwestern Virginia. Shown is the southern range of the bog turtle (Natureserve 2009).

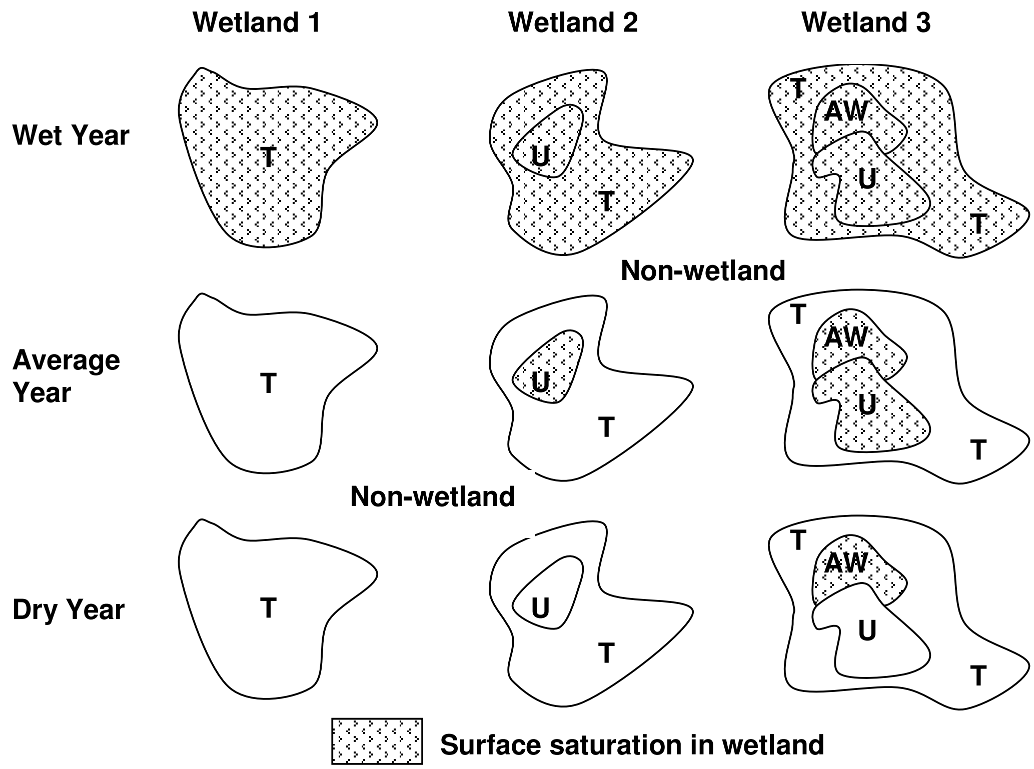

Figure 2.2. Theoretical schematic showing how surface saturation can vary among and within wetlands depending on yearly weather conditions. This study took advantage of dry conditions in 2008 to establish wetness strata for sampling surface soil in bog turtle wetlands. Areas with an AW, U, and T, correspond to the "always wet", "usually wet", and "temporarily wet" strata, respectively. Not all wetness strata were present in every wetland, even when official wetland criteria were met (Wetland Training Institute, Inc. 1995). The non-wetland strata did not meet wetland criteria.

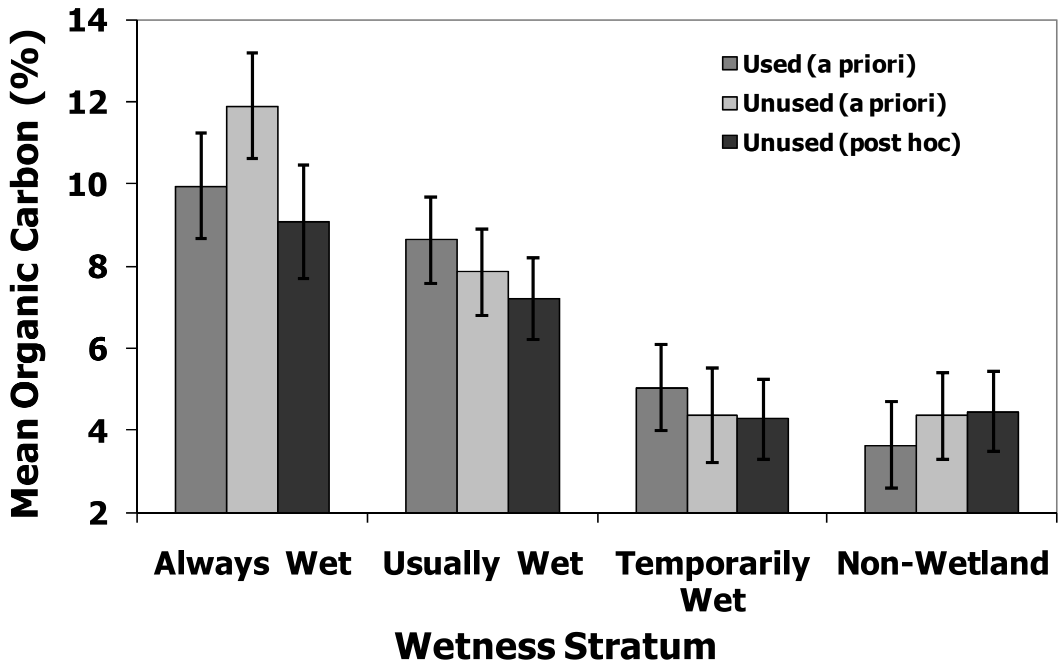

Figure 2.3. Mean organic carbon content (%) in wetlands grouped by bog turtle use status. Wetlands were stratified according to their degree of saturation at the time of sampling. The *a priori* wetland groupings were based on bog turtle use status at the beginning of the study (n=6 used; n=6 unused), while the *post hoc* groupings had two transiently used wetlands removed from the *a priori* unused group where a single bog turtle was found during the study.

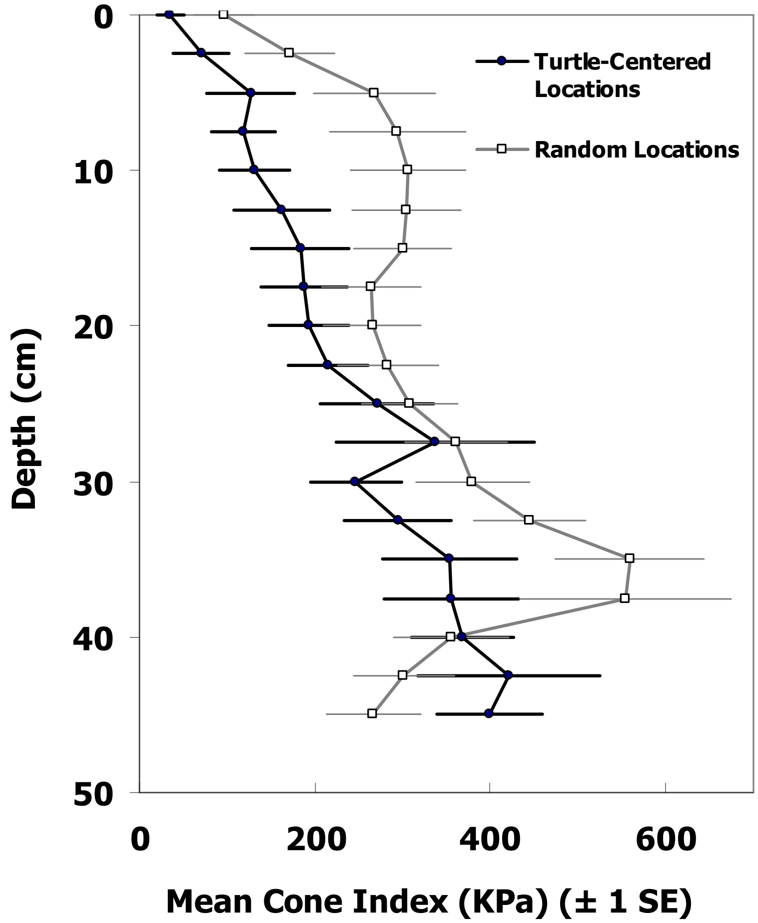

Figure 2.4. Mean penetrometer cone index values (kPa) over depth for bog turtle-centered (n=12) and paired random locations. Random locations were anywhere within a 1 to 5 m radius of the turtle-centered locations. Random locations met wetland criteria (Wetland Training Institute, Inc. 1995). A paired t-test of the average difference in penetration resistance from 0 – 18 cm depth between turtle-centered and paired random locations indicated that turtles used wetland areas with lower strength soils (difference=-124 kPa, *df*=11, *t*=2.00, *P*=0.035).

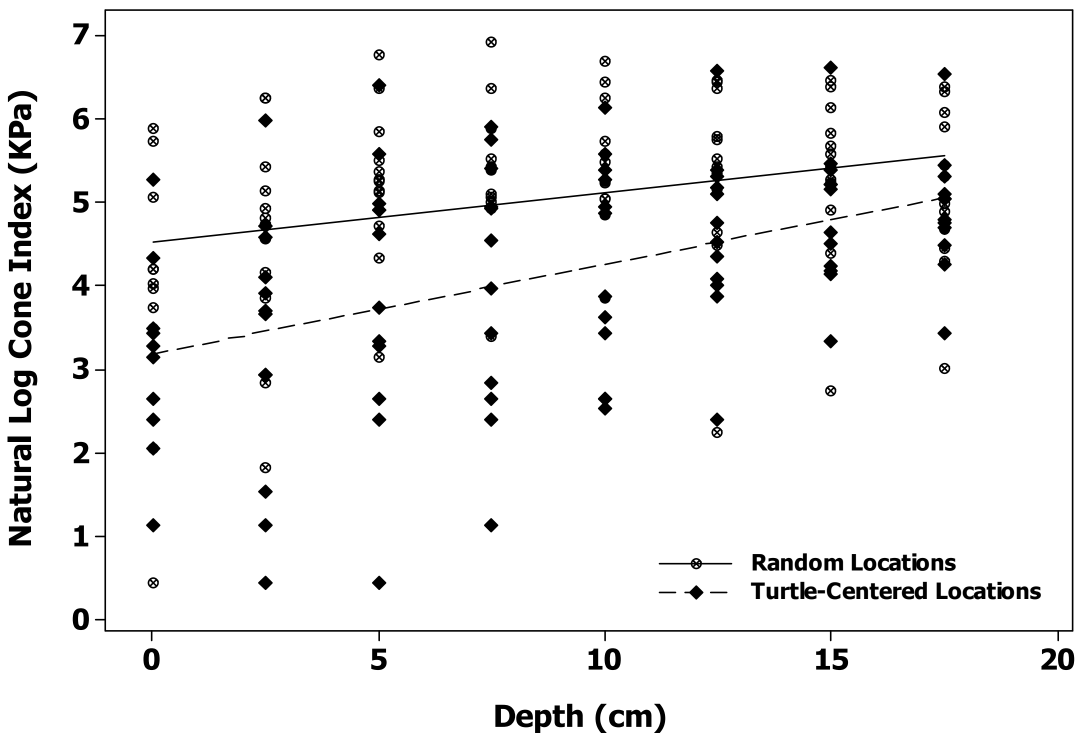

Figure 2.5. Linear relationship of natural log transformed (to improve assumption of normality of residuals for statistical tests) soil strength (kPa) to depth between 0-20 cm depth for bog turtle-centered (n=12) and paired random locations. Random locations were anywhere within a 1 to 5 m radius of the turtle-centered locations. Random locations met wetland criteria (Wetland Training Institute, Inc. 1995). Soil strength was recorded at 2.5 cm increments using a penetrometer. I used simple linear regression to test for an interaction or a difference in intercepts between the linear relationships of log transformed soil strength and depth at turtle-centered and random locations. Soil strength increased with depth for both locations (df=1,209, t=2.68, P=0.008). A significant interaction (slope difference) was present between depth and location (df=1,209, t=2.02, P=0.048). Soil strength at the surface (the intercept) was lower at turtle-centered locations (df=1,209, t=-4.60, P<0.001).

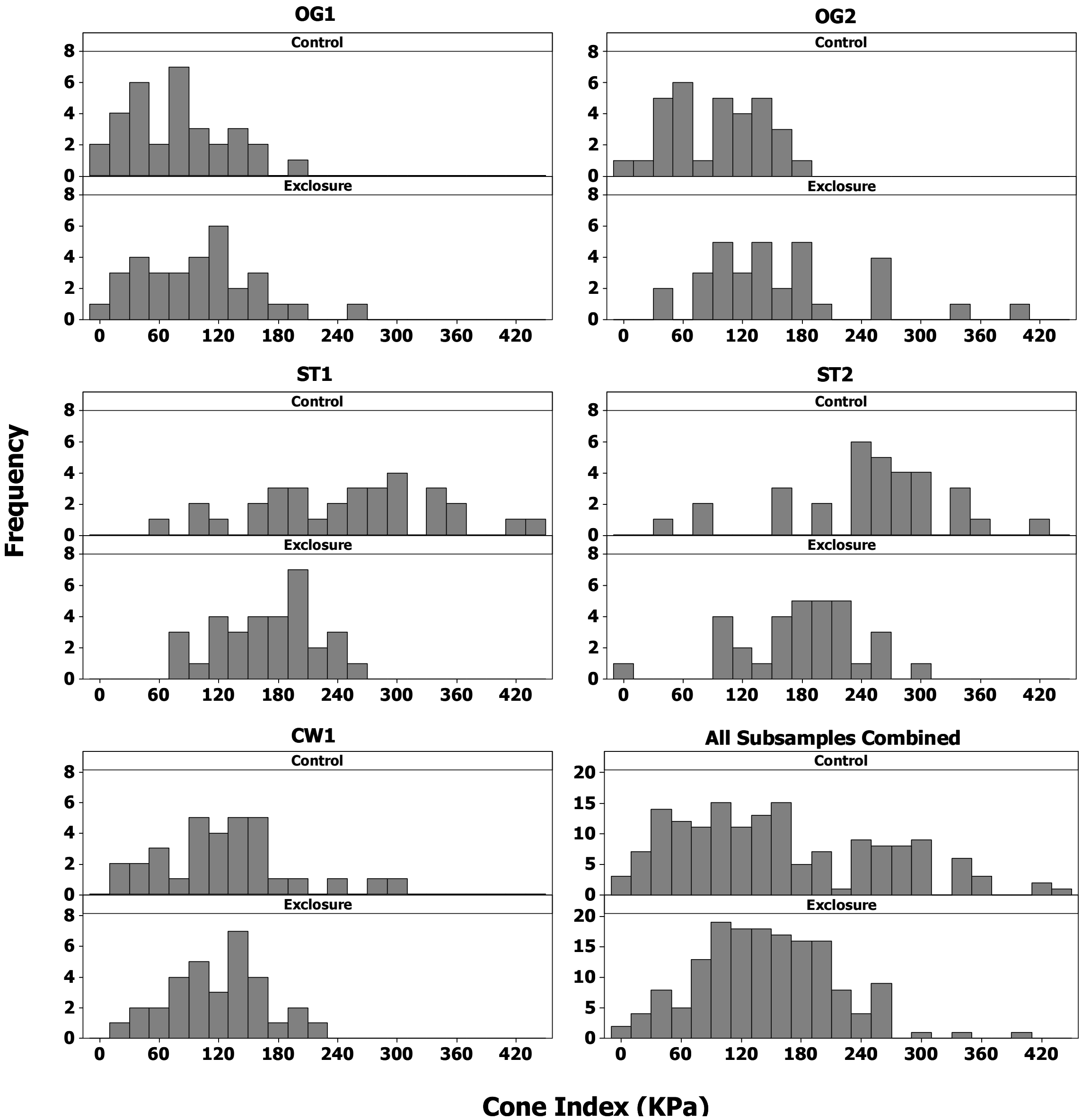

Figure 2.6. Frequency distributions of mean penetrometer cone index values (kPa) recorded between 0-18 cm depth on livestock grazed control plots and paired ungrazed exclosure plots. Each 5 m x 5 m plot had 32 penetrometer measurements that were spaced systematically along a grid.

Chapter 3: Seasonal thermal ecology of bog turtles (*Glyptemys muhlenbergii*) in Southwestern Virginia

ABSTRACT

Temperatures of ectotherms are dependent on the temperatures available throughout their habitats and on behaviors and movements related to thermoregulation. For aquatic and semi-aquatic turtle species such as the bog turtle (*Glyptemys muhlenbergii*), thermoregulation is dependent on the availability of thermally buffered saturated areas that enable turtles to modify temperatures during periods of activity and sustain temperatures above freezing during aquatic winter hibernation. I deployed recording data loggers during summertime and wintertime in bog turtle occupied wetlands in Southwestern Virginia to contrast the temperatures of ambient air and wetland surface soils to turtle carapace temperatures. Temperature signatures were used to evaluate the timing of spring emergence and its cues. I measured soil temperature profiles during winter in saturated hibernacula and similar but unsaturated structures to evaluate the dependence of temperature on water table depth. Mean daily turtle temperatures (n=16 turtles) during the coldest portion of two winters ranged between 1.3°C and 6.1°C, with one turtle experiencing 14 continuous days at temperatures between -1°C and 0°C when ambient temperatures dipped below -10°C. Water tables remained within 10 cm below the soil surface throughout the winter, preventing freezing temperatures for shallow hibernating turtles. The date of first turtle emergence differed by 15 days between the two study years, with soil temperatures at 10 cm apparently serving as a primary cue. The relation of summertime turtle temperatures to soil surface temperatures showed periods when turtles thermoregulated and thermoconformed to soil temperatures, suggesting that turtles alternated between basking and accessing deep, thermally buffered saturated soil. Daily mean summer turtle temperature (±SE; n=8) was 20.8°C ± 0.15°C, while the mean maximum temperature (short duration) was 36.3°C ± 0.63°C. The highest 24-hour long temperature for an individual turtle was 25.1°C. Individual turtle temperature profiles show that availability of shade and saturated soil are important determinants of thermoregulatory behavior during the summer.

***Key Words*:** hibernation, emergence, basking, activity, groundwater, drought, thermal stability, fen, thermoregulation, Virginia

INTRODUCTION

As ectotherms, turtles thermoregulate behaviorally, so the thermal environment affects how they use their habitat. Digestion, growth, and activity are all influenced by body temperatures (Huey 1982). Aquatic and semi-aquatic turtles are able to thermoregulate in their environments through the processes of basking and conforming to water and mud temperatures (Grayson and Dorcas 2004, Rowe and Dalgarn 2009). The relatively high specific heat of water helps it to resist rapid temperature changes relative to air and mineral substrates. As a result, the properties of water make it an effective thermoregulation medium for aquatic turtles.

Bog turtles (*Glyptemys muhlenbergii*), in the southern portion of their range, live in wetland ecosystems that have a long hydroperiod and nearly constant saturation at the soil surface (Chapter 1). Abundant groundwater inflow through multiple seeps results in heterogeneous areas of saturation (Arndt 1977, Bury 1979, Chase et al. 1989, Carter et al. 1999, Ernst and Lovich 2009). Soils in bog turtle wetlands contain mucky organic material and abundant silt and sand in the upper part (Pitts 1978). The composition of these soils and the presence of saturation reduce the soils' strength, creating a soft mud that bog turtles can easily move through (Chapter 2). The conditions resulting from the hydrology and soils of bog turtle wetlands allow the species to spend much of their lives below the soil surface. It follows that we must understand the thermal environment of saturated soils in bog turtle wetlands to understand how bog turtles thermoregulate. Further, changes to the hydrology of bog turtle wetlands are considered a major factor in the degradation of bog turtle habitat and one of the causes of the species' apparent decline (Bury 1977, Mitchell 1994, Buhlmann et al. 1997, Copeyon 1997, United States Department of Agriculture 2006). Studying the thermal regimes of bog turtles in wetlands known to support reproducing bog turtles is important if we desire to make thermal comparisons to regimes in hydrologically impacted wetlands or recognize temporal changes to thermal regimes.

During hibernation, aquatic turtles avoid freezing and desiccation by remaining dormant underwater in substrates that vary in material and oxygen availability (Ultsch 2006). Oxygen availability in the hibernation microenvironment is important for turtle survival; oxygen requirements vary among turtles species, with several species capable of enduring anoxic conditions for extended periods (Ultsch 2006). Several authors have noted the thermal stability and selection of near zero temperatures associated with hibernating aquatic turtles (Litzgus et al.

1999, Greaves and Litzgus 2007, Rollinson et al. 2008, Edge et al. 2009). This strategy may be particularly important for turtles living in northern climates, where turtles hibernate for up to six months. Water table fluctuation has the potential to affect the thermoregulation of turtles, and may be associated with winter mortality (Brooks et al. 1991, Bodie and Semlitsch 2000, Ultsch 2006). In Virginia, hibernation of bog turtles begins in October or November (Ernst et al. 1989, Carter et al. 2000). Bog turtles hibernate, often communally, at depths of 5 to 55 cm from the soil surface in soft mud, hoof prints of livestock, or in small burrows created by small mammals or crayfish (Bloomer 2004, Ernst et al. 1989, Carter et al. 2000, Pittman and Dorcas 2009). Bog turtles can hibernate in a shallow condition, but may adjust their depth to regulate temperature (Chase et al. 1989, Ernst et al. 1989). Wintertime cloacal temperatures from bog turtles in Pennsylvania and New Jersey ranged between 2.6 and 16.0 C (Ernst et al. 1989). Although average winter temperatures in the bog turtle's southern range are not as cold as those experienced in the northern range, extreme and rapid temperature cycles are common.

Bog turtle emergence, estimated from the first observations of surface activity, generally occurs in Virginia in March or April (Ernst et al. 1989, Mitchell 1994). The cues for spring emergence of bog turtles and other aquatic or semi-aquatic turtles are poorly understood. The emergence of Blanding's turtles (*Emydoidea blandingii*) and spotted turtles (*Clemmys guttata*), species that live at northern latitudes, have been associated with the physical break up of ice (Litzgus et al. 1999, Newton and Herman 2009). In more southern climates where continuous ice cover is uncommon, turtle emergence is not physically limited and other cues must be involved such as air temperature, substrate temperature, or both. Bog turtles in Maryland and North Carolina have been observed making short moves between hibernation areas between November and March (Chase et al 1989, Lovich et al. 1992). That bog turtles are capable of winter activity suggests that ambient air temperature may be an important cue for emergence and hibernation. Zappalorti (1976) associated the first bog turtle activity of the season (approximating time of emergence) with ambient temperatures above 21 °C. For terrestrial *Terrapene ornata* and *T. carolina* hibernating in Missouri in non-wetland soils containing abundant leaf litter, emergence was associated with subsurface (10 – 20 cm) temperatures of 7°C that lasted five days (Grobman 1990). However, Bernstein and Black (2005) studied *T. ornata* in Iowa and did not find a rigid temperature requirement for emergence. Instead, they found that turtles emerged after experiencing a range of soil temperatures and suggested that an interaction of substrate moisture and temperature could be a factor in emergence.

Bog turtle activity during the summer may be dependent on the availability of saturated mud and the abundance of shade provided by vegetation. During normal conditions from late spring to early fall, bog turtles move into and out of small pockets of open water or liquefied mud, presumably for feeding, cover, and thermoregulation (Carter et al. 1999). Pittman and Dorcas (2009) found that bog turtles in North Carolina basked frequently between 10:00 and 15:00, with peak basking between 12:00 and 14:00. Further, these authors found that bog turtle basking events were more frequent in June and July than they were in August, which could have been due to late summer drought conditions. Some bog turtles have been found aestivating, possibly in response to thermal stress or drying (Ernst and Lovich 2009). Observations of aestivation and reduced basking during drought suggest that bog turtles may avoid high temperatures when available thermal inputs exceed the turtles' requirements. During periods of warm weather activity, heat avoidance by turtles may be a normal thermoregulation strategy (Plummer 2003). Aquatic and semi-aquatic turtles may respond to excessively hot and associated drying conditions by moving away from drying habitats to wetter ones (Gibbons et al. 1983, Roe and Georges 2008).

The purpose of this study was to evaluate the thermal ecology of Virginia bog turtles during the periods of winter hibernation, springtime emergence, and summer activity. I evaluated bog turtle thermal ecology by measuring carapace temperatures of individual turtles and measuring available temperatures in the air and substrate of bog turtle wetlands. An underlying goal of the study was to assess how saturated conditions are related to temperatures in bog turtle wetlands. Thermal relationships were measured using three different observational field studies, each varying in the type or depths of substrate where temperatures were recorded or the season of measurement. Study 1 used daily wintertime air, soil, and turtle temperatures to test the hypothesis that bog turtle temperatures would be thermally stable and remain above the freezing point, and that soil substrate temperature will be a cue for turtle emergence. Study 2 used temperature measurements in saturated hibernation areas and similar but unsaturated substrates to evaluate the role of saturation in regulating the temperature of hibernacula. Here, I tested the hypothesis that high water tables maintain thermal stability and prevent freezing conditions. Study 3 used daily summer air, soil, and turtle temperatures to evaluate daily turtle temperature regimes and test the hypothesis that turtle thermal signatures will reveal periods of basking and sun avoidance, particularly when shade availability and saturation are limited.

METHODS

Study Area

I conducted this investigation on four individual wetlands in Floyd County within the southern part of the Blue Ridge physiographic province of Virginia (Figure 3.1). Precise wetland locations and local wetland names are withheld to reduce human disturbance on bog turtle wetlands and prevent collection of turtles. For this document, wetlands will be referred to as DA, GDM, GDF, and SK. These four wetlands correspond to the VDGIF database site numbers 1, 2, 18, and 19. Wetlands were situated linearly along the landscape with the DA wetland approximately 3.0 km southwest of the GDM and GDF wetlands. The GDM and GDF wetlands were separated by approximately 140 m that consisted of non-wetland pasture. The SK site was approximately 8.5 km northeast of the GDM and GDF wetlands. Each of the wetlands was between 0.25 and 0.5 ha in size, irregularly shaped with multiple projections, and with core areas that were more saturated than nearby wetlands. Two out of the four study wetlands were identified on the U.S. Fish and Wildlife Service's National Wetland Inventory mapping series and are described as palustrine emergent (Cowardin et al. 1979). Valley slopes where the study wetlands occurred were between 0 and 3%. All wetlands were used for livestock grazing before the study and three of the wetlands were actively grazed throughout the duration of this study.

Wetland sites contained flora typically associated with bog turtles (Ernst et al. 1994). Floral descriptions of bog turtle wetlands within the study area are available (Carter et al. 1999). Herbaceous vegetation covered the ground surface under all but the thickest alder (*Alnus serrulata*) areas. The GDM wetland consisted entirely of low, herbaceous vegetation, while the nearby GDF wetland contained more than 50% coverage of shade-bearing shrubs or trees as estimated using ArcMap 9.2 (ESRI Redlands, CA, USA) and aerial photographs. A severe drought in the summer of 2007 through early 2009 affected hydrology on all sites (Chapter 1). Areas of surface saturation were present on at least a portion of the GDF, DA, and SK wetland during the dry summer of 2008. The GDM wetland was drier on the surface than the other wetlands, and only contained water at the bottom of hoof prints. Heavy livestock grazing on

GDM resulted in vegetation that was only approximately 20 cm high, increasing the chance for sun exposure to any turtles using the wetland.

Thermal characterization - General

All measurements for the three field studies were made using DS1921G thermochron iButton dataloggers (resolution 0.5°C, reported accuracy ± 1°C Dallas Semiconductor Corp, Dallas, Texas), capable of measuring and storing 2048 temperature values over user-programmed time intervals. I prepared the thermochrons for underwater use by coating each unit with hardening liquid plastic (Grayson and Dorcas 2004, Pittman and Dorcas 2009). Plastic coating was achieved using a light gauge wire that was wrapped around the thermochron and held by the wire's tag end. The tag end of the wire was useful for attaching the thermochrons to other objects. Each thermochron weighed approximately 4.5 grams after being coated in plastic.

I captured study turtles by hand or trap and marked them for future identification. I attached plastic coated thermochrons to 3.8-g radiotransmitters (Holohil Systems Ltd. Carp, Ontario) and then bonded both devices simultaneously to the posterior plural scutes of the bog turtle using Devcon Plastic Welder™. Radiotelemetry was primarily used for concurrent movement studies, but also served to recover the thermochrons. Total weight of equipment attached to the carapace never exceeded more than 10% of the turtle's total body weight, and typically was in the range of 7 to 8%. Previous studies using carapace-attached thermochrons have shown a strong correlation of turtle shell temperature to turtle cloacal temperature (Grayson and Dorcas 2004). Nonetheless, the potential exists for maximum turtle shell temperatures to exceed internal body temperatures, particularly when turtles are basking (Edwards and Blouin-Demers 2007).

Thermochrons used to measure ambient air temperatures were hung in the open air on light-gauge wire and kept away from heat-emitting surfaces. Ambient thermochrons were exposed to full sun. A test of full sun temperatures measured by plastic coated and uncoated thermochrons revealed no difference in response due to the plastic. Thermochrons buried in the soil were attached by wire to a non-conductive PVC stake to facilitate finding and recovering the units. Thermochrons used to characterize temperatures on vertical surfaces were attached by wrapping the light-gauge wire around galvanized nails pressed into the soil at the desired depth. For each mensurative experiment, I programmed the thermochrons to initiate temperature measurements at the same time and recorded temperatures using identical time intervals (Table 3.1). This design resulted in each thermochron recording the same total number of measurements over specified time periods, and facilitated calculation of descriptive statistics and data interpretability.

Field Study 1 – Wintertime Temperature Regime and Spring Emergence

The first field study used daily wintertime air, soil, and turtle temperatures to evaluate the thermal regime during hibernation and determine the cues for spring emergence. This study took place on all four study wetlands in the winter from 2007-2008 and on GDM, GDF, and SK wetlands from 2008-2009. The temperature record for the first winter was measured at 160 minute intervals, beginning on 21 December 2007 and concluding on 4 April 2008. The temperature record for the second winter was measured at 180-minute intervals, beginning on 20 October 2008 and concluding on 13 April 2009. For both winters, thermochrons were deployed on turtle carapaces, in ambient air, on the soil surface, and at 10 cm soil depth. Soil temperatures were also recorded at 25 cm soil depth during the second winter. Measurements were replicated at multiple locations in each wetland and in multiple wetlands (Table 3.1). I selected random locations to deploy thermochrons in the soil environment with the constraint that pockets of surface saturation were present within 5 m of each thermochron's location. I applied this constraint because observations of bog turtle hibernation are limited to saturated areas (Ernst et al. 1989). In the second winter, thermochron deployments at the SK wetland were constrained to within 5 m of hibernacula known to be used the previous winter. The 32-day time period from 15 January through 15 February was selected to statistically describe the thermal environment during both 2008 and 2009, as this time period was, and typically is, the coldest part of the year in the study area.

Carapace temperatures were compared to substrate and ambient air temperatures from mid-February through March for evidence of turtle emergence (first basking). I plotted daily maximum temperature for each turtle to determine the exact day when solar heating resulted in a temperature spike that was much greater than concurrent soil substrate temperature and turtle temperatures recorded on previous days. The date of emergence was recorded as the first day a temperature spike was recorded. I only recorded one emergence event for each turtle each year, although cold temperatures may have caused the turtle to move back into the hibernaculum, resulting in a second temperature spike when warm weather and basking resumed. Radiotelemetry of turtles in the temperature study confirmed that turtles were indeed emerging and concentrating their activity near hibernacula during the weeks when temperature spikes indicative of emergence were occurring.

I investigated whether ambient air temperature, soil temperature at 10 cm, or both were cues for emergence. The data source included soil temperatures from the wetland where each individual turtle resided, and ambient air temperatures that were averaged across all wetlands. First, I recorded daily average soil and ambient temperatures at time of first emergence. Second, I recorded the daily maximum soil and ambient air temperatures at the time of emergence. To evaluate the hypothesis that a one-day occurrence of a particular maximum temperature can be a cue for turtle emergence, I investigated daily maximum temperatures both before and during the date of emergence. To do this for each turtle, I counted the number of days that occurred before the day of emergence when maximum temperature was greater than or equal to the maximum temperatures during emergence (Bernstein and Black 2005). To be counted, days did not need to occur in consecutive order, i.e., any day prior to emergence could be counted, even if temperatures the day before emergence was much colder than those recorded at the day of emergence.

Field Study 2 – Role of Saturation in Regulating Temperature of Hibernacula

The second field study attempted to identify the importance of saturation during hibernation by comparing the temperatures in saturated hibernacula that were used by turtles (true hibernacula) to the temperatures in unsaturated, hand excavated, soil voids (simulated hibernacula). This study took place during the winter of 2008 and 2009 on the SK wetland. To develop the model for simulated hibernacula, I made some basic observations and measurements of true hibernacula during the previous winter of 2007 and 2008. In this pilot study, I found that turtles at the SK wetland frequently hibernated in hollow voids with narrow openings that were bounded by clayey material. The voids may have been burrowed by muskrats, meadow voles, or other rodents and expanded by the bog turtles (Ernst et al. 1989). Depths of these hibernacula ranged between 10 cm to 45 cm. The upper portions of the hibernacula were approximately 15 cm in diameter, with the dimensions narrowing at the bottom. Several of the hibernacula had a mixture of soil, roots, and leaf litter that covered the upper part of the void, somewhat hiding the entrance. Hibernacula frequently had standing water within them, but the walls of the void contained sufficient clay to maintain form and prevent sloughing of soil. Consistent with other biologists' observations on other bog turtle wetlands (Ernst et al. 1989, Bloomer 2004), some of the hibernacula were occupied by multiple turtles, and one hibernaculum was used by at least eight overwintering bog turtles.

I excavated four simulated hibernacula to compare to four true hibernacula similar to those described above. Areas used for simulated hibernacula were randomly located in unsaturated areas on local micro-topographical high spots bounded by saturated areas or immediately adjacent to the wetland. The furthest simulated hibernaculum was approximately 50 m from a true hibernaculum. These areas had similar slopes, were at approximately the same elevation, and contained vegetation with similar height and structure as the emergent vegetation surrounding the true hibernacula. I created the simulated hibernacula by using an 8.9-cm diameter mud auger to excavate down to 30 cm. I used a spade to widen the upper diameter to 15 cm and shaped the excavation similar to a trapezoid with a bottom width of 8.9 cm. I used a 1.27-cm thick, unfinished plywood board to partially cover the opening of the excavation. This board was an attempt to mimic the soil, roots, and leaf litter that covered the true hibernacula. The final entrance orifices to simulated hibernacula were approximately 10 cm x 6 cm.

For each true or simulated hibernaculum, I deployed thermochrons from the surface to 30 cm at 10 cm depth increments, with exception to two true hibernacula where available depth was limited to only 20 cm. I also deployed thermochrons in ambient air (Table 3.1). Temperature readings were recorded at 180-minute increments, beginning on 20 October 2008 and concluding on 13 April 2009. As I was interested in how bog turtles cope with the coldest winter temperatures, I concentrated this statistical analysis on the consistently cold eight-day period spanning between 15 January 2009 and 22 January 2009. I evaluated the hypothesis that drier simulated hibernacula would experience colder temperatures and that soil temperature would increase with depth. Heating and cooling events over the entire winter period are frequent for ambient temperature and therefore cause numerous temperature inversions between surface soil and shallow soil temperatures. Choosing a consistently cold period provided a better chance of avoiding this type of temperature response during the evaluation period.

Water Table Measurements in Hibernacula Area

I measured the depth to the water table during the winter hibernation period to investigate the relationship between wetland saturation and temperature. In October 2007, I installed a shallow groundwater monitoring well in the SK wetland that was located within two meters of two of the true hibernacula used to compare to simulated hibernacula. The 70 cm deep well was constructed of 3.8-cm outside diameter PVC pipe with factory-cut 0.025-cm horizontal slots spaced at 0.5 cm over the entire length from the bottom end cap to the top of the riser. The borehole used for the well installation was dug using an 8.9-cm diameter mud auger. The annular space between the pipe and borehole was filled with medium-grade sand. I referenced depth to the water table as the distance from the mineral soil surface to the measured water surface in the well. Depth from the surface datum was negative. Water depth was recorded using a Hobo U20 Water Level Logger (Onset Computer Corporation, Bourne, Massachusetts, USA). Measurements were made at 120 minute increments and later averaged to build a continuous record of weekly water table height from November 2007 through July 2009. Groundwater wells were not placed near simulated hibernacula, but visual observations confirmed that groundwater (the water table) was not present in the well-drained soils over the winter.

Field Study 3 - Summertime Temperature Regime and Heat Avoidance

The third field study used daily summer air, soil, and turtle temperatures to evaluate daily turtle temperature regimes. This study was completed in the summer of 2008 on all four study wetlands. The 47-day temperature record was measured at 90-minute intervals, beginning on 15 June 2008 and concluded on 31 July 2008. Thermochrons were deployed on turtle carapaces, in ambient air, on the soil surface, and at 10 and 25 cm soil depths. Measurements were replicated at multiple locations in each wetland and in multiple wetlands (Table 3.1). I randomly selected locations to deploy thermochrons in the soil environment with the constraint that abundant surface saturation was available within the 5 m radius around the thermochron's location. I applied this constraint because bog turtles use areas of wetlands that are close to pockets of standing water (Carter et al. 1999). I calculated average temperatures measured in each stratum and on turtles from 0:00 hours and 22:50 hours based on the 90-minute thermochron sampling interval.

I used the relationship between concurrently measured turtle temperatures and soil surface temperatures to make inference on the thermoregulatory activity of bog turtles during the summer activity period. I determined whether a turtle was actively thermoregulating by finding when carapace temperature was greater than, less than, or conformed to soil surface temperatures. The 90-minute temperature intervals over the 47-day period provided 752 unique data pairs of surface soil and turtle temperature for each turtle.

I compared the average daily mean and maximum temperatures of turtles residing in the GDM wetland to turtles residing in the other three wetlands to explore how temperature signatures differ in turtles residing in wetlands with little to no available shade as opposed to wetlands with abundant shade. Shade availability on the GDM wetland was virtually nonexistent, with exception to the shade provided by 20 cm high grazed vegetation and the micro-relief provided by livestock hoof prints. Each of the other wetlands had shade in the form of scrub shrub vegetation that was located adjacent to the emergent wetland, contained saturated pockets, and had abundant herbaceous vegetation that was tall and thick enough to provide ground level shade.

Statistical Analyses

I used graphical methods and descriptive statistics to summarize temperature data collected by thermochrons. Descriptive statistics were calculated using Microsoft Excel and SAS (SAS Institute, Cary, NC). For mean values, thermochron deployments at multiple locations within a wetland were treated as subsamples to provide one average value for the entire wetland. Mean temperature values are given ± standard deviation (SD), unless otherwise indicated. I used SD as a measure of variation when calculating a mean based on numerous temperature readings that were not independent, i.e. when calculating the temperature of an individual turtle over a set of days. I also used SD when I desired a larger (and thus more sensitive) measure of variability, as in the case with detecting emergence of bog turtle in spring. The standard error (SE) was used to express variation around a mean calculated from independent measurements, i.e. when calculating the temperature of multiple turtles over a season. Correlation coefficients and t-tests were calculated using MINITAB Student Release Version 14.11.1 (State College, PA). I used a linear mixed model (PROC MIXED, SAS Institute) in field study 2 to test for statistical differences among depths and among groups of true hibernacula and simulated hibernacula, which consisted of four repetitions in each group over the eight repeated days of temperature measurements.

RESULTS

Thermal Characterization – General

In total, data from 149 successful multi-month thermochron deployments and approximately 165,000 individual temperature records were used. Failures of thermochrons occurred during each experiment, particularly for units deployed on the turtles, in ambient air, and on the ground surface (Table 3.1). Failure rates on turtles were approximately 33%. Failures were higher in these locations because of the increased likelihood of damage to the plastic coating around the thermochrons from friction and tampering by animals. Despite thermochron failures, thermal observations were successful for eight turtles during each experiment. Multiple thermochron subsamples of environmental strata were available to calculate stratum averages for each wetland, with the exception of the winter of 2008 to 2009 when wetland averages had to be calculated from only one successful thermochron deployment at the 25 cm soil strata on wetland GDF and at the soil surface strata at the GDM wetland.

Field Study 1 – Wintertime Temperature Regime and Spring Emergence

Turtles selected three different types of areas in which to hibernate: 1) Burrow hibernacula were the deepest, and consisted of hollow voids that appeared to be dug by rodents. The deepest example of this type of hibernaculum was approximately 45 cm. These hibernacula were most likely to contain multiple bog turtles and were abundant on the SK wetland; 2) Turtles on wetlands with abundant alders tended to hibernate along root systems, often in mucky substrate formed from the inputs of alder leaves and leaves of other deciduous trees in the area; 3) Where little or no woody vegetation was present, or where burrow hibernacula were not present, bog turtles were found hibernating in small and shallow voids or depressions, most of which were created by livestock hooves.

Average turtle temperatures (± SE) (n=8) between 15 January and 15 February were 2.7 ± 0.5°C in 2008 and 2.3 ± 0.3°C in 2009. These values were on average greater than, but far less variable than the average temperatures measured in the ambient air and on the ground surface (Table 3.2). During these 32-day periods, the minimum and maximum whole day temperatures (mean temperature from 0:00 to 24:00) measured on a turtle carapace were 0°C and 9.5°C in 2008 and -0.7°C and 7.1°C in 2009. Turtle whole day temperatures during both years were frequently ≤ 1.0 °C during the coldest portion of the winter. The turtle subjected to the coldest body temperatures measured during the study, T252, never experienced freezing body temperature in 2008, yet sustained a body temperature of between -1.0°C and 0.0°C for 20 out of 32 days in 2009. Turtle 252 hibernated in a livestock hoof void during both winter seasons and it was often visible through shallow ice cover.

Temperature patterns in January and February 2009 show the thermal relation of air and soil strata to the carapace temperature of three bog turtle using root-associated hibernacula (Figure 3.2). Turtle temperatures were responsive to increased ambient air and soil temperatures. The variability of temperatures and the absolute value of extreme temperatures recorded on turtles were smaller than those measured in ambient air and on the ground surface (0 cm depth). The most stable thermal environment was recorded at 25 cm. For all 59 days between January 1 and February 28, 2009, the root mean squared errors (RMSE) between the set of daily temperature values measured on the turtle's carapace versus the ambient air, the ground surface, 10 cm soil depth, and 25 cm soil depth were 5.2°C, 3.9°C, 0.6°C, and 1.6°C. The correlation coefficients between turtle temperatures and ambient air, the ground surface, 10 cm soil depth, and 25 cm soil depth were 0.41, 0.53, 0.97, and 0.71, respectively. The fact that the tip of the approximate 15-cm radio antenna was often visibly protruding above the frozen soil and water was evidence that turtles were frequently hibernating at depths approximating 10 cm. Based on this method of estimating hibernation depth by observing the radio antennae, the shallowest hibernating turtles were at approximately 5 cm depth from the soil or water surface to the top of their carapaces.

Date of turtle emergence was variable among the turtles within the year and between years (Table 3.3). In 2008, emergence occurred between 22 March and 4 April. In 2009, six turtles emerged between 7 March and 9 March. The last two turtles emerged on 29 March and 5 April. On average, male bog turtles emerged earlier than female turtles during both years; however, variation was evident within both sexes. In 2008, the average daily maximum ambient air and 10 cm soil temperatures (±SE, n=8) on the date of first emergence were 22.7 ± 0.7°C and 10.7 ± 0.4°C, respectively. In 2009, the average daily maximum ambient air and 10 cm soil temperatures (±SE, n=8) on the date of first emergence were 28.0 ± 1.3°C and 9.8 ± 1.1°C, respectively. Daily maximum ambient temperatures before the date of first emergence were frequently greater than or equal to the measured maximum ambient temperature during the day of emergence. This condition occurred for seven out of eight turtles in 2008 and four out of eight turtles in 2009. Days where ambient temperatures exceeded ambient temperature at emergence often occurred a week or more before the emergence date (Figure 3.3). This condition occurred even in 2008, when emergence occurred approximately two weeks later than in 2009. For 10 cm soil depths, daily maximum temperatures before the date of first emergence were greater than or equal to the measured maximum soil temperature for only two turtles each of the study years. When this condition occurred, it was usually during the consecutive days preceding the day of emergence. These results suggest that turtle emergence responds more acutely to the temperature at 10 cm depth rather than the ambient temperature.

Field Study 2 – Role of Saturation in Regulating Temperature of Hibernacula

I measured an overall average ambient air temperature of -5.6 °C during the eight-day period used to observe the relation between saturation, depth, and temperature. Whole day average ambient air temperature ranged from -12.5°C to -0.7°C. The least squares mean of true and simulated hibernacula were 1.4°C and -0.02°C, respectively, with a difference in temperature of 1.4°C ($F_{1,18}$=13.99, P=0.002). Temperatures became greater with depth for both hibernacula groups ($F_{3,18}$=7.64, P=0.003) (Figure 3.4). Freezing temperatures were only measured on the surface of the true hibernacula group and were above freezing at 10 cm and deeper depths. Freezing temperatures were measured at the surface and down to 20 cm depth in the simulated hibernacula group. Fluctuation in ambient temperatures caused an interaction between depth and day ($F_{27,162}$=4.84, P<0.001). This interaction occurred because of relatively warm ambient temperature on January 18 and 19 that caused the soil surface to temporarily become warmer than soil at 10 cm depth.

Groundwater characterization in hibernacula area

The groundwater monitoring well installed in the vicinity of multiple hibernacula, including two of the hibernacula used for comparison to simulated hibernacula, provided a continuous measurement of depth to the water table from November 2007 through July 2009. Depth to water table measurements showed that bog turtles hibernated in a portion of the wetland where the elevation of the water table was consistently above the bottom of their hibernaculum, yet not inundated above the soil surface (Figure 3.5). These hydrology conditions persisted throughout both of the winter periods, even after the severe drought of 2007 and 2008. This drought caused the water table to drop to unusually low levels throughout the study area (Chapter 1).

Field Study 3 Summertime Temperature Regime and Heat Avoidance

Summertime thermal regimes between 15 June 2008 and 31 July 2008 were characterized by daily warming and cooling cycles that showed peak temperatures for ambient air, turtles, and the soil surface occurring between 13:30 and 15:00 (Figure 3.6). Ambient temperatures showed the earliest daily warming. Soil surface warming was a similar magnitude as ambient warming, yet was delayed by approximately 90 minutes. The timing of turtle heating and cooling cycles was similar to that of surface warming. The average daily turtle temperature range (16.0°C to 26.0°C) was smaller than that of the ground surface (15.3°C to 29.4°C). Deeper soil strata showed warming and cooling cycles that were delayed compared to other strata. Soil at 10 cm showed an approximate 2.3°C fluctuation, with the warmest temperatures occurring around 19:30. Temperature fluctuation at 25 cm was negligible. Turtle, 10 cm soil, and 25 cm soil temperatures between 21:00 and 7:30 were higher than those measured in ambient air and the soil surface. Turtles remained warmer at night than air or surface temperatures.

Eight successful thermochron downloads over the 47-day period provided 6016 data pairs of surface soil and turtle temperatures (Figure 3.7). These data pairs showed that turtle temperature did not follow a linear relationship with the soil surface temperature, i.e., turtles did not conform to surface temperatures, particularly when soil temperatures were colder or warmer than the average across the entire 47 day period. When surface soil was <15°C, turtle temperatures tended to be higher than 15°C, but when surface soil was >30°C, turtle temperatures were lower than those at the surface. Between 15°C and 30°C, turtle and surface soil temperatures tended to be positively and linearly correlated. Basking events when turtles experienced direct solar heating were frequent between 15°C and 30°C, as indicated by turtle temperatures exceeding this range.

Two out of the three turtles originally instrumented with thermochrons in the GDM wetland moved approximately 100 meters to the more shaded GDF wetland at the beginning of

June 2008. This occurrence left only one turtle (T252) in the sun-exposed GDM wetland to compare with the other turtles using shade. During the drought conditions of 2008 (Chapter 1), the surface of the GDM wetland dried out so that the only visibly available water was in the deepest livestock hoof prints. Hydrologic conditions in the other three wetlands also responded to the drought, but surface saturation was present and these areas were available to turtles.

Turtle T252's average temperature (21.1°C) over the 47-day period was not significantly different than the average temperature of the seven other turtles during the same period (20.7°C) (n=7, t=-2.25, P=0.065) (Table 3.4). Although average temperatures did not differ, T252's relation to soil surface temperatures showed evidence that T252 used its habitat differently than the seven turtles with available shade (Figure 3.7). First, some of the coolest surface temperatures measured occurred at GDM, likely because of the lack of water and vegetative cover to moderate temperatures. During these cold periods, T252's temperatures were lower than those measured on other turtles. A large proportion of the highest surface soil temperatures also occurred at GDM, which is supported by the higher average temperature measured on GDM relative to other sites. Despite high surface temperature available at GDM, T252 recorded a body temperature ≥ 27°C on only five occasions when soil temperatures were <30°C, while other turtles showed frequent events >30°C, suggesting that basking was occurring. Average daily maximum temperature of T252 (27.4°C) was lower than the daily maximum temperatures of the seven other turtles (29.7 ± 0.42) (n=7, t=12.0, P<0.001). The finding that T252 had a similar mean daily temperature compared to other turtles while also having a significantly lower daily maximum temperature compared to other turtles suggests that T252 did not need, or even avoided, basking.

DISCUSSION

Groundwater Saturation and Soil Depth Moderate Winter Temperatures

Bog turtle whole day average temperatures during the coldest parts of winter 2008 and 2009 ranged between -0.7°C and 9.5°C. The magnitude of wintertime temperature fluctuation measured for bog turtles contrasts with those of other turtle species. Ranges of wintertime temperatures reported for other semi-aquatic and aquatic turtle species were 0.3°C to 3.9°C for *Clemmys guttata* (Litzgus et al. 1999), -1°C to 1°C for *Glyptemys insculpta* (Greaves and Litzgus 2007), 0°C to 3°C for *Chrysemys picta* (Rollinson et al. 2008), 0°C to 6°C for *Emydoidea* *blandingii* (Edge et al. 2009) and 0°C to 4°C for *Chelydra serpentina* (Brown and Brooks 1994). All of these other studies took place in the northern portions of the species' respective ranges, and are derived from temperature readings covering four to five months of dormancy. My findings are derived from only two years of data collected during the 32-day period from 15 January through 15 February, and therefore encompass only a portion of the period between November and mid-March when bog turtles are inactive in Virginia. Had I used the entire period of bog turtle dormancy for my characterization, I would expect an increase in the range of temperature (and average temperature) because of higher ambient temperatures.

These findings suggest that other aquatic turtle species may be able to select more thermally stable environments than bog turtles, even when living in northern climates. All of the other turtle species discussed above were found to hibernate beneath a column of standing or moving water, often covered with insulating ice and snow. As a result, minimum temperatures in these other studies were similar to, and maximum temperatures were greater than, those recorded in this southern study. Illustrating the capacity for snow and ice to thermally buffer turtles from extreme temperatures, Litzgus et al. (1999) observed ambient temperatures at an Ontario swamp fluctuate between –35 and 2°C over a five-day period, while the carapace temperature of spotted turtle remained between 1 and 2°C. Thermal buffering by snow and ice would not be expected to be the normal condition in Southwestern Virginia, where ambient temperatures fluctuate around 0°C and little if any snowpack is present.

The measured correlation coefficients and RMSEs between average turtle temperature to soil temperature suggests that turtles on these wetlands frequently hibernate near 10 cm depth and shallower than 25 cm. I found that approximately half of the radioed bog turtles were visible hibernating just below the surface of frozen mud and ice between 5 and 15 cm from the water surface, supporting the observations of Chase et al. (1989) in Maryland. Hibernating bog turtles have been observed at deeper depths up to 55 cm in New Jersey (Bloomer 2004, Ernst et al. 1989). I observed bog turtles at the SK wetland hibernating deeper (down to 45 cm) than turtles in the other three wetlands. Deeper hibernation was possible because the burrow-type hibernacula were mostly filled with water rather than soil, enabling turtles to easily move to the bottom without resistance. These thermally buffered hibernation conditions explain the narrower range of extreme temperatures experienced by the SK turtles. My findings indicate that Virginia bog turtles generally hibernate in substrates deep enough to avoid freezing temperatures, but do not always access depths that prevent direct influence from the wide range of ambient air temperatures inherent to Virginia winters.

Based on thermal measurements in turtle true and simulated hibernacula, depth was a factor and presence of saturation may have been a factor controlling hibernation temperature. The presence of consistent saturation was confirmed by the groundwater monitoring well installed in the vicinity of the SK hibernacula. Average depth to water table remained approximately 15 cm during both winters of the study, even following a severe two-year drought (Chapter 1). During cold ambient temperatures, the average temperature difference was 2°C higher at 10 cm depth in saturated true hibernacula compared to simulated hibernacula where the water table was not present. Freezing temperatures were consistently recorded in the simulated hibernacula. Thermochrons inside the hibernacula were actually embedded approximately 1 cm into its vertical soil walls. Even colder temperatures could be expected in the center of the air-filled void in the simulated hibernacula, as apparently dry soil still contains water that could buffer temperature.

Should bog turtles be forced to choose areas with conditions similar to those measured in the simulated hibernacula, they may be more susceptible to freezing and desiccation. Not only would bog turtles lack the buffering capacity of the water, but drier soil, coarser soil, or soil with less organic matter could result in innoculative freezing (Costanzo et al. 1998). Innoculative freezing occurs when the formation of tissue-damaging crystallized ice is facilitated by contact with other ice or particulate impurities. Costanzo et al. (1998) showed that ice crystal formation and innoculative freezing occurred more readily in sandy soils with little organic matter. Exposure of damaged integument to freezing conditions may further increase the risk of ice crystals penetrating into the body. Willard et al. (2000) found that at temperatures between -0.9°C and -2.2°C 100% of *C. picta* and *Trachemys scripta* with damaged integument (n= 5) froze during exposure, compared to 27% of turtles (n=22) without prior damage. Bog turtles are frequently found with active or healed injuries that could reduce the effectiveness of the integument to resist freezing. It follows that the risk of damaging bog turtle tissues during cold snaps could be more severe if turtles are forced to hibernate in wetland soils that have become coarser or have lost organic matter.

Anthropogenic activities involving machinery tend to homogenize soil properties, often bringing coarser textured soils to the surface and decreasing organic matter (Paz-Gonzalez et al.

2000, Bruland and Richardson 2005). Alluvial systems are typically stratified with finer soils at the surface and coarser soils at depth (Stolt et al. 2001). Ditching activities that are commonly used to drain the small wetlands used by bog turtles can bring deeper, coarser soils to the surface (fill) or expose coarse soil at the bottom of the ditch. Erosion and deposition events in wetlands associated with agriculture or construction may result in unpredictable changes to particle size and organic carbon content. Increased aeration and associated increases in decomposition of organic matter have been associated with lowered water tables in wetlands that have been ditched (Strack et al. 2008). Restored wetlands have also been found to have coarser soils and reduced organic matter relative to natural wetlands (Stolt et al. 2000, Bruland and Richardson 2005). That restored wetland areas may differ in soil qualities from natural wetland areas may be an important consideration for future restoration efforts near known bog turtle habitats.

Turtle T252 carapace temperatures remained between -1°C and 0°C for 20 days during January to February 2008 when ambient temperatures were consistently below freezing and at times were < -10°C. These temperatures were apparently not cold enough to cause mortality or visible freezing damage in T252. Possibly, the coldest temperatures may have been localized to the portion of the carapace carrying the thermochron. If freezing of the turtle did occur, the initiation of freezing temperatures may have not been abrupt enough to result in the tissue-damaging ice crystal formation associated with rapid freezing (Packard and Packard 2004). Numerous non-lethal freezing events (≥ -1.4°C) of maximum durations of four hours were also recorded for one bog turtle in North Carolina that was hibernating in a shallow soil depression similar to the conditions used by T252 (Pittman and Dorcas 2009). Freeze survival of adult turtles has been documented by Bernstein and Black (2005) when they attached thermochrons to hibernating *T. ornata* and observed approximately 45 continuous sub-zero days (min of -8.0°C) for two turtles hibernating in sand at depths less than 75 cm.

The upward gradient of groundwater typical of the types of fens where bog turtles can be found in Virginia may import additional thermal energy that moderates bog turtle hibernation temperatures. Earlier ice thaw and moderation of surface soil temperatures have been associated with wetland fens where groundwater inflow was a dominant source of water (Hunt et al. 1999, Amon et al. 2002). Large groundwater withdrawals or loss of groundwater recharge areas through construction of impermeable surfaces have the potential to reduce groundwater flow in bog turtle wetlands (Brennan et al. 2001). In a large-scale hydrologic analysis, those authors found that groundwater withdrawals would reduce upland pressure heads related to seepage discharge in downstream bog turtle wetlands. Reduced flow and thermal energy imports may result in infrequent yet severe freeze events that could penetrate wetland substrates to depths greater than the hibernation depths of some bog turtles.

The potential exists that wintertime conditions in the range of the southern bog turtle may be more energetically costly than conditions in colder climates, as snow and ice cover over aquatic systems insulates turtle temperature. This could force turtles to expend metabolic energy that is vital for post-emergent activities such as mating and nesting. Metabolic rates in turtles are generally positively correlated to temperature (Litzgus and Hopkins 2003). Many types of turtles do not feed below 15°C (Ultsch 1989). I recorded daily temperatures in January and February as high as 9.5°C for shallow hibernating turtles, when activity and efficient basking are unlikely. These results indicated that bog turtle may endure long periods when metabolic expenditures are relatively high while there is little potential for feeding and efficient digestion.

Shallow hibernation may be the only option for bog turtles living in wetlands with shallow soils, lack of soil structure associated with large rooted woody vegetation, absence of burrowing rodents, or otherwise hard-to-penetrate subsoil. Shallow hibernation may increase exposure to predators at a time when cold conditions diminish the mobility needed to avoid predation (Ultch 2006, Greaves and Litzgus 2007). A potential benefit to shallow hibernation is that it would facilitate aerobic respiration (Litzgus et al. 1999, Edge et al. 2009, Newton and Herman 2009). Whether bog turtles more frequently use aerobic or anaerobic metabolism during hibernation is unclear, although the association of bog turtles with mud burial and hibernation under ice for months or more suggests that the species is anoxia-tolerant (Ultsch 2006).

Soil and Ambient Temperature as a Cue for Springtime Emergence

Emergence of turtles began 15 days earlier in 2009 than it did in 2008, but variability among turtles occurred in both years. In 2009, the last turtle did not emerge until 29 days after the first turtle emerged. Male turtles emerged several days earlier than females during both study years. Although emergence date was variable for both sexes, earlier emergence by males may be an expression of evolutionary adaptation for earlier springtime activity to maximize breeding opportunities (e.g. Gregory 1974). Several recently emerged turtles were observed near their hibernacula, apparently remaining near so that they could reenter when ambient temperatures dropped. Turtles could easily be captured by hand from hibernacula during the weeks following first emergence. Individuals did not appear to show fidelity to hibernacula during this post-emergence period, although turtles remained in the same general area.

Overall, the average ambient air daily maximum temperature at first emergence was 25.4 ± 1.0°C (±SE, n=16) and ranged between 19.5°C and 30.8°C (median =24.4°C). Despite later emergence in 2008 than in 2009, days in 2008 with ambient maximum temperatures ≥ the temperatures recorded during the day of emergence occurred for all but one turtle. Ambient maximum temperatures in 2009 at time of emergence were higher on average, particularly on March 7th when temperatures of 30.8°C resulted in four turtles emerging despite daily high temperatures near freezing within the week prior to emergence. Overall, the average 10 cm soil daily maximum temperature at emergence was 10.3 ± 0.6°C (±SE, n=16), and ranged between 6.8°C and 14°C (median =10.1°C). Only two turtles each year experienced prior days with maximum soil temperatures ≥ the temperatures recorded at time of emergence (Table 3.3). Grobman (1990) found an emergence response of terrestrial *T. ornata* to temperatures at 10 to 20 cm depth, but unlike his study, I did not find that there was a set temperature at which all turtles responded. These results appear more similar to those of Bernstein and Black (2005), who found that *T. ornata* emerged when soil temperatures were around 8.8°C, but soil temperatures at emergence ranged between 6.4°C and 13.1°C. These authors also found many days prior to emergence with temperatures greater than those recorded at time of emergence.

These results suggest that daily maximum soil temperatures measured at 10 cm depth was a primary cue for emergence, with maximum ambient air temperature as a secondary cue. Soil temperatures approximating 10°C may cue emergence following moderately high ambient temperatures that steadily warm the soil. This cue may occur because of net metabolic energy costs associated with remaining buried at relatively warm and stable temperatures. Alternatively, bog turtles may be stimulated to emerge during extremely high ambient air temperatures, even in the absence of warm soil temperatures. For this to occur, bog turtles must be able to detect the high ambient temperatures or a temperature gradient that extends from the surface to hibernation depth (Ultsch 2006). This is plausible, particularly at SK where bog turtles hibernated in the burrow-type hibernacula that contained open, air-filled channels leading directly to the surface. Within these hibernacula, warm surface temperatures could be detected, particularly if bog turtles move toward the soil surface in expectation of spring emergence, as observed in *T. ornata* and *T. Carolina* (Grobman 1990, Bernstein and Black 2005). Turtles at SK emerged in 2009 when daily max temperatures at 10 cm were only 6.2°C (lower than average), yet ambient temperatures were 30.8°C during that time. Chase et al. (1989) observed bog turtles moving out of hibernacula during winter warm spells, suggesting that high ambient temperature during winter may even stimulate early or temporary emergence.

Daily Temperature Patterns, Basking, and Avoidance of High Temperatures

Average turtle temperatures over the course of the day were cyclic and followed a similar pattern observed on active *C. picta* in Michigan (Rowe and Dalgarn 2009). Those authors recognized a warming phase between 8:00 and 12:00, a peak between 12:00 and 18:00, and a gradual cooling phase from 18:00 until thermal warming resumed the following day. Bog turtles in this study experienced their highest body temperatures during the midday period, when sustained average turtle temperatures were around 25°C for approximately 4.5 to 6 hours each day. Average daily maximum temperatures were 29.4 ± 0.3°C (± SE, n=8). Previous bog turtle studies have found average cloacal temperature of 25.3°C (range 22.0°C to 31.0°C) for basking turtles (Ernst and Lovich 2009). Cloacal temperatures of bog turtles captured while basking have been found to be lower than ambient air temperatures (Arndt 1977, Ernst et al. 1989). The relatively small body size of bog turtles should result in rapid equilibrium between shell and internal body temperatures.

Bog turtle temperature relative to the ambient and surface soil temperature suggested that bog turtles were thermoregulating by making vertical movements in the soil or possibly moving to shade in order to moderate their temperature throughout the daily temperature cycle. When the soil surface is <15°C, bog turtle carapace temperatures were lower, suggesting that bog turtles were accessing warmer soils. Turtle carapace temperatures either conformed to, or were higher than, available surface soil temperatures when they were between 15°C to 30°C. This suggests that turtles frequently bask at this temperature range. When the soil surface is between 30°C to 48°C, turtles avoided high surface temperatures either by accessing deeper soil depths or well-shaded areas. Turtle temperatures frequently remained between 15°C and 20°C during periods of high surface temperatures. Available soil temperatures at 10 cm and deeper were in this range (Figures 3.6 and 3.7). Temperature-derived vertical locations of bog turtles in the soil column follow daily patterns based on the frequency distribution of surface soil temperatures measured throughout the day during the summer (Figure 3.8). For example surface soil temperatures <15°C occurred primarily between 21:00 and 7:30, while temperatures > 30°C occurred primarily between 12:00 and 16:30. Bog turtle behavior at times of high surface temperature may indicate a daily activity that exists to deal with excess heat. This activity has been observed in turtles, particularly in desert biomes (Plummer 2003).

Although basking events are evident by spikes in turtle temperature relative to surface temperature, little can be inferred from this data set about the number of daily active basking events. Surface temperatures are highly variable and thus difficult to distinguish between active basking temperatures. Defining basking events as exceeding 10 cm soil temperature would have the effect of overestimating basking events because midday substrate temperatures apparently rise rapidly between 10 cm and the soil surface. Pittman and Dorcas (2009) used thermochrons buried at 5 cm and estimated that bog turtles were actively basking about 2.1 times each day in June and July. Those authors also found a strong correlation between turtle temperature and 5 cm depth, suggesting that turtles were frequently in a partially buried or submerged position. Temperatures at 5 cm soil depth were often > 25°C, a magnitude at least as high as average daily bog turtle temperatures measured in this study. Considering the findings from Pittman and Dorcas (2009) and this current study, the possibility exists that bog turtles could achieve warming through association with warmed soil substrate rather than active basking out of water. Warming through soil contact may explain the reduced number of active basking events observed in August by Pittman and Dorcas (2009). Whether mid and late summer basking out of mud and water is important to bog turtles for other physiological processes besides thermoregulation is unknown.

Only T252 remained in the GDM wetland during the summer 2008 study period, reducing the statistical comparisons that I could make in regard to the temperature response of turtles with or without available shade. Further, dryer conditions in GDM relative to the other three wetlands made it impossible to isolate the effect of shade on turtle temperature, as both shade and saturated conditions are factors in turtle thermoregulation. Nonetheless, I found some evidence of bog turtle behavioral changes in response to combined soil temperature and drying. In addition to the two turtles instrumented for this thermal study, at least three other adult bog turtles left the GDM wetland for the GDF wetland where shade and saturation were abundant. This movement may have occurred in response to the drying of the GDM wetland. Migration to other wetlands as a response to drying has been observed in other aquatic and semi-aquatic turtle species (Review in Gibbons et al. 1983, Roe and Georges 2008).

Data collected as part of a concurrent telemetry study indicated that T252 was located in surface saturation during 47% of 49 events in 2008, compared to 65% of 1198 events for turtles on other sites (df=1, n=1247, χ^2=6.64, P=0.012). Yet, T252 did not have a higher average temperature than the other seven turtles in the study and actually had a significantly lower daily maximum temperature. This is presumably because T252 did not frequently bask directly in the sun out of soil and water; instead receiving sufficient thermal inputs by its association with warmed soils in the GDM wetland. Compared to T54, which resided in the nearby GDF wetland with available shade, typical daily temperature signatures for T252 do not show a spike in body temperature consistent with basking. Instead, T252 shows a gradual temperature rise that occurs later in the day following peak soil surface temperatures (Figure 3.9).

Bog turtle selection for taller vegetation and greater canopy density was observed by Carter et al. (1999) on some of the same wetlands used in this analysis. This is potentially because of the ability for vegetation to moderate ground temperatures. Soil temperatures in the sun-exposed GDM wetland were higher than those measured in the other wetlands, and were more variable (Table 3.4). Weisrock and Jansen (1999) found that vegetation cover was a significant factor in temperature on the ground (in this case *C. picta* nests on the ground) with temperatures 4°C lower on areas surrounded by 100% cover versus 0% cover. Plummer (2003) found that *T. ornata* using bare soil had the hottest temperatures, followed by those using grass areas and shrub areas. Radiotelemetry and personal observation in summer 2008 indicated that T252 moved little and remained in close proximity to livestock footprints in the soil and the scattered vegetation tussocks that provided minimal cover and shade. On 7 August through 28 August 2008 when water table was deepest and the soil surface was hottest, T252 left the GDM wetland and remained underneath the cut bank of a USGS 7.5' quadrangle map-identified 3rd order stream. The turtle finally broke its inactivity following approximately 10 cm of rainfall associated with a tropical storm on 27 and 28 August. Turtle T252 moved briefly to the forested GDF wetland, but returned to GDM by 28 September 2008. Other turtles were found to use ditches and streams during the excessively dry summer of 2008 (Chapter 4). Use of stream habitats by bog turtles has been documented (Somers et al. 2007). Further, stream use in August and throughout the following hibernation season may have been associated with excessively dry conditions (Pittman and Dorcas 2009).

Conclusions

Whether during hibernation or periods of summer activity, Virginia bog turtles spend much of their time submerged at shallow depths in the soft soil or near the ground surface. For these turtles, thermoregulation entails active movements through soils where temperature is a function of ambient temperature, depth, degree of direct solar radiation, and degree of saturation. Although bog turtles can regulate their body temperature through their use of the wetland, they may also be passive subjects to the temperatures in their wetland habitat, particularly when they are inactive during the winter or when dry conditions prevent turtles from accessing deep soil or shade. In winter, bog turtle hibernacula remained consistently wet. Saturation of hibernacula during the winter was associated with temperatures that were highly variable at the surface, but more stable and above freezing at deeper areas.

Managers must understand how wetland hydrology, vegetation, and soils are related to turtle temperature. Drainage of wetlands by ditching, erosion and incision of stream channels, or reduction in recharge areas by creating impervious surface may cause wetland drying and associated changes in thermal environments at time scales too rapid to expect successful behavior changes in local bog turtle populations. Reductions in organic carbon content and increasing the proportion of coarse soils though mechanical mixing of horizons in wetlands used by bog turtles can potentially change how bog turtles cope with sub zero temperatures when hibernating in a shallow condition.

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Table 3.1. Number of thermochrons successfully deployed and downloaded during three field studies completed on four wetlands. The figures in parentheses indicate the number of thermochrons that were deployed but failed in a given wetland location.

Period	Logging rate (min)*	Wetland	Deployment locations of temperature loggers						
			Turtles	Ambient	Soil				
					0 cm	10 cm	20 cm	25 cm	30 cm
Field Study 1 winter 2007-2008	160	GDF	2 (0)	0 (3)	3 (0)	3 (0)	-	-	-
		GDM	2 (0)	0 (3)	2 (1)	3 (0)	-	-	-
		SK	2 (2)	0 (3)	2 (1)	3 (1)	-	-	-
		DA	2 (2)	3 (0)	6 (0)	4 (2)	-	-	-
Field Study 2 winter 2008-2009	180	GDF	3 (2)	3 (0)	3 (0)	3 (0)	-	1 (2)	-
		GDM	1 (0)	3 (0)	1 (2)	3 (0)	-	3 (0)	-
		SK hibernacula	4 (1)	3 (0)	3 (1)	4 (0)	4 (0)	-	2 (0)
		SK simulated hibernacula	-	-	4 (0)	4 (0)	3 (1)	-	2 (2)
Field Study 3 summer 2008	90	GDF	1 (2)	0 (3)	3 (0)	2 (1)	-	3 (0)	-
		GDM	1 (1)	0 (3)	2 (1)	3 (0)	-	3 (0)	-
		SK	4 (1)	3 (0)	4 (0)	4 (0)	-	4 (0)	-
		DA	2 (3)	3 (0)	3 (1)	4 (0)	-	4 (0)	-

*** All loggers started at 0:00.**

Table 3.2. Descriptive statistics for mean turtle carapace and environmental temperatures during the same 32-day period in winters 2008 and 2009. All mean temperatures calculated from the 32-day period include error estimates (± SD). Coldest day and warmest day are entire day averages of turtle carapace temperatures calculated from multiple logging events over one day. Maxima (max) and minima (min) consisted of the single most extreme logging event over the 32-day period.

Time period	Wetland	Turtle	Turtle carapace temperatures (°C)						Environmental temperatures (°C)			
			Daily mean	Coldest	Warmest	Days ≤ 1°C	Min	Max	Ambient air	Soil surface	Soil at 10 cm	Soil at 25 cm
Jan 15 – Feb 15 2008	GDF	54 M	1.8 ± 1.7	0.1	6.8	14	0.0	8.5	1.4 ± 5.6	0.4 ± 3.6	1.8 ± 1.9	Data not collected
		554 M	2.5 ± 2.1	0.5	8.6	8	0.5	10.0				
	GDM	233 F	2.7 ± 2.0	1.0	8.4	6	1.0	10.0		1.8 ± 2.9	2.9 ± 1.8	
		252 M	2.6 ± 2.0	0.8	9.5	2	0.5	10.5				
	SK	307 M	2.3 ± 1.5	0.8	6.7	2	0.5	7.5		1.6 ± 2.3	4.6 ± 1.3	
		3000 M	6.1 ± 0.7	4.7	7.4	0	4.5	7.5				
	DA	417 F	1.3 ± 1.2	0.0	4.7	19	0.0	7.5		0.4 ± 3.4	2.3 ± 1.3	
		3213 F	2.3 ± 0.9	1.4	5.3	0	1.0	6.0				
Jan 15 – Feb 15 2009	GDF	54 M	1.7 ± 1.2	1.0	4.8	10	1.0	5.5	0.7 ± 6.6	0.1 ± 4.6	1.2 ± 1.3	3.0 ± 0.5
		3216 F	1.7 ± 1.3	0.6	4.6	18	0.5	5.0				
		3227 F	1.6 ± 1.3	0.4	4.7	15	0.0	5.0				
	GDM	252 M	1.5 ± 2.3	-0.7	7.1	20*	-1.0	8.5		0.8 ± 3.9	2.4 ± 1.9	3.0 ± 1.4
	SK	544 M	4.0 ± 0.7	3.4	5.5	0	3.0	5.5		1.3 ± 2.6	2.3 ± 1.4	2.4 ± 0.9**
		546 F	3.1 ± 0.8	2.0	5.0	0	2.0	5.0				
		553 F	2.7 ± 1.4	1.1	5.9	0	0.5	6.5				
		3000 M	2.3 ± 1.3	0.4	5.3	4	0.0	5.5				

*** Recorded 15 days at temperatures -1 °C to 0 °C.**
**** 25-cm depth estimated for SK wetland winter 2008 – 2009 using average of 20 cm and 30 cm depth**

Table 3.3. Date of emergence (first basking) observed for turtles in the spring of 2008 and 2009. Ambient air and soil substrate temperatures at time of emergence are shown. Daily maximum temperature is the average of the maximum temperatures measured on all thermochron subsamples located at the specified strata. Soil temperatures are wetland specific, while ambient air temperatures are the same for all wetlands.

Time period	Wetland	Turtle	Date emerged (Male)	Date emerged (Female)	Temperatures on day of emergence (°C)				Ambient air max already achieved*	10 cm soil max already achieved*
					Ambient air max	Ambient air average	10 cm soil max	10 cm soil average		
Spring 2008	GDF	54 M	3/22	-	19.5	12.1	9.7	7.4	Yes (2)	Yes (2)
		554 M	4/1	-	24.0	15.7	12.3	9.8	Yes (1)	No
	GDM	233 F	-	4/1	24.0	15.7	12.0	9.6	Yes (1)	No
		252 M	3/27	-	24.7	15.2	11.3	8.4	No	No
	SK	307 M	4/4	-	21.5	11.6	9.8	8.3	Yes (4)	Yes (4)
		3000 M	3/28	-	19.8	15.2	10.4	9.4	Yes (4)	No
	DA	417 F	-	4/1	24.0	15.7	10.1	8.1	Yes (1)	No
		3213 F	-	4/1	24.0	15.7	10.1	8.1	Yes (1)	No
	Mean (SE)	-	3/28	4/1	22.7 (0.74)	14.6 (0.61)	10.7 (0.36)	8.6 (0.30)	-	-
Spring 2009	GDF	54 M	3/9	-	26.1	15.7	12.7	10.1	Yes (2)	Yes (2)
		3216 F	-	4/5	25.2	14.3	14.0	9.2	Yes (3)	No
		3227 F	-	3/8	28.4	17.9	12.7	9.7	Yes (1)	Yes (1)
	GDM	252 M	3/7	-	30.8	17.6	8.8	5.6	No	No
	SK	544 M	3/7	-	30.8	17.6	6.8	5.4	No	No
		546 F	-	3/29	21.3	11.7	9.9	8.6	Yes (10)	No
		553 F	-	3/7	30.8	17.6	6.8	5.4	No	No
		3000 M	3/7	-	30.8	17.6	6.8	5.4	No	No
	Mean (SE)	-	3/7	3/20	28.0 (1.25)	16.3 (0.79)	9.8 (1.06)	7.4 (0.76)	-	-

*** Figure in parentheses is the number of days before the day of emergence when the recorded maximum temperature was greater than or equal to the measured maximum temperature during the day of emergence. Days before emergence did not need to be consecutive with the emergence day.**

Table 3.4. Descriptive statistics for turtle carapace and environmental temperatures during a 47-day period in summer 2008. All mean temperatures calculated from the 47-day period include error estimates (± SD). Coldest and warmest day are entire day averages of turtle carapace temperatures calculated from multiple logging events over one day. Maxima (max) and minima (min) consisted of the single most extreme logging event over the 47-day period.

Time period	Wetland	Turtle	Turtle carapace temperatures (°C)						Environmental temperatures (°C)			
			Daily mean	Coldest	Warmest	Min	Max	Daily mean max	Ambient air	Soil surface	Soil at 10 cm	Soil at 25 cm
June 15 - July 31 2008	GDF	54 M	20.0 ± 1.9	16.1	23.0	11.5	36.5	28.9 ± 3.7	22.0 ± 2.2	17.8 ± 1.4	17.0 ± 1.2	17.2 ± 1.0
	GDM	252 M	21.1 ± 2.3	17.1	24.4	11.0	32.5	27.4 ± 2.5		23.3 ± 1.9	21.3 ± 1.4	20.5 ± 1.0
	SK	3000 M	20.7 ± 2.0	16.1	23.5	12.0	36.5	29.4 ± 4.1		22.3 ± 1.6	19.2 ± 0.9	18.2 ± 0.7
		307 M	21.0 ± 2.1	16.4	23.9	11.5	37.5	29.3 ± 4.6				
		3217 M	21.0 ± 1.8	17.4	23.4	11.5	35.0	30.4 ± 3.5				
		610 M	20.5 ± 1.7	15.7	23.7	12.5	37.5	29.9 ± 3.3				
	DA	410 M	21.3 ± 1.7	16.3	25.1	14.0	38.0	29.9 ± 4.4		20.4 ± 1.4	19.2 ± 1.0	18.4 ± 0.7
		1155 F	20.7 ± 1.7	16.0	24.4	10.5	37.0	29.9 ± 4.9				

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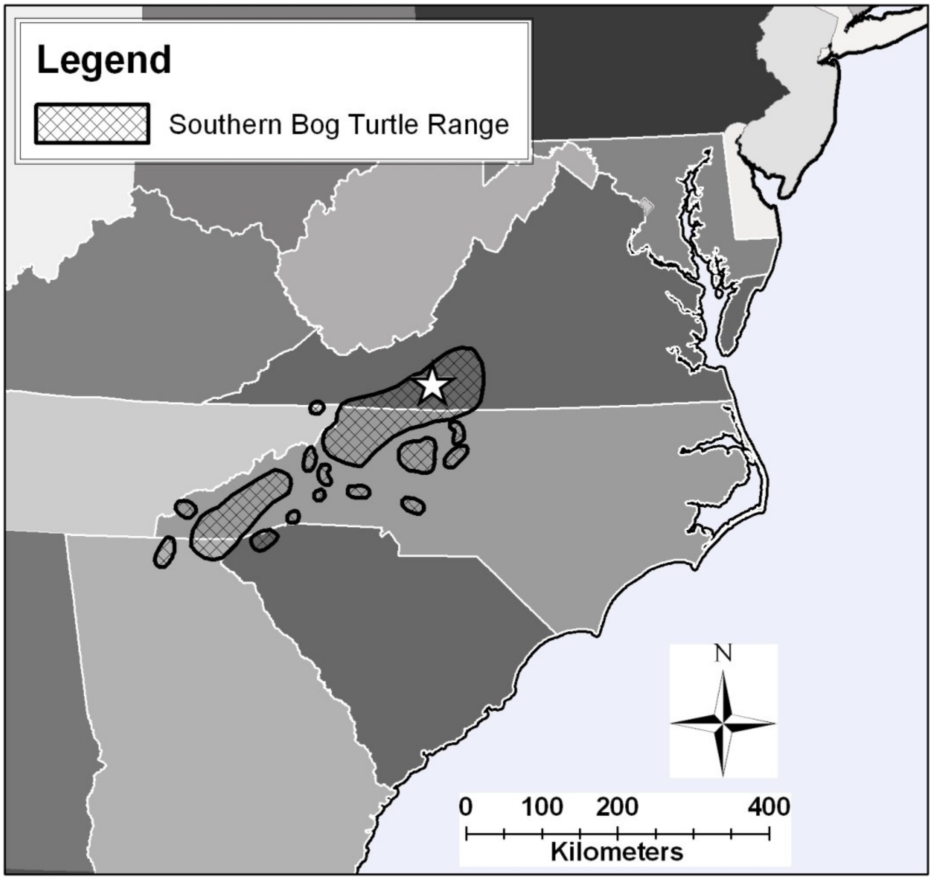

Figure 3.1. Study location in Blue Ridge Physiographic Province of Southwestern Virginia. Shown is the southern range of the bog turtle (Natureserve 2009).

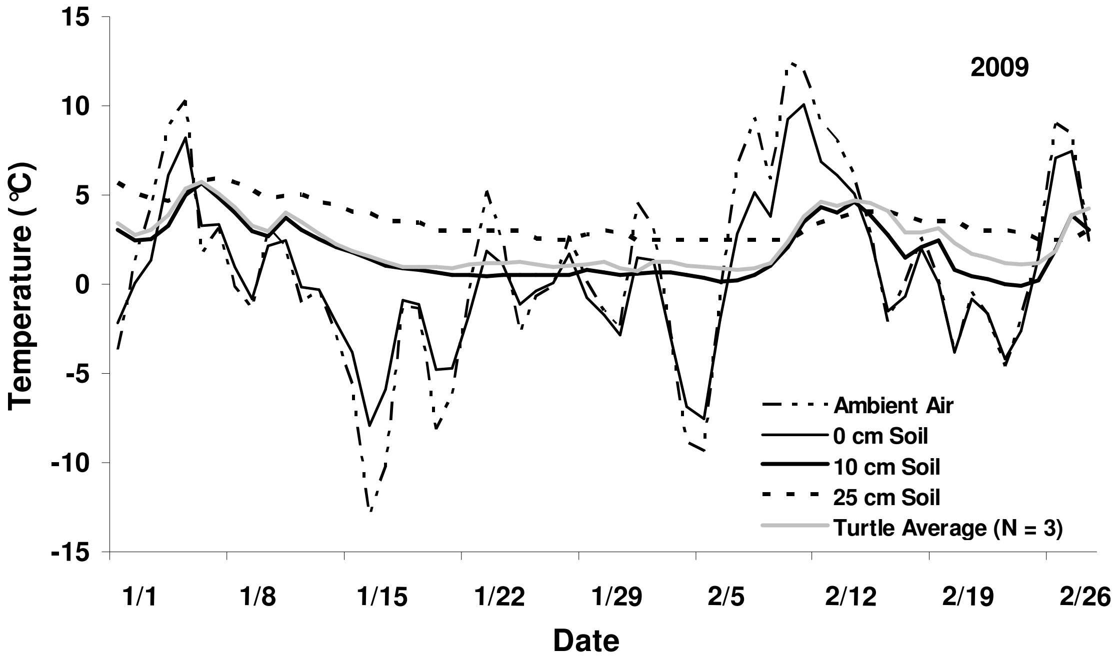

Figure 3.2. Typical wintertime average daily temperatures of bog turtles and surrounding environment measured at the GDF wetland in January and February, 2009. Data were measured using 13 thermochrons deployed on the carapaces of turtles and in ambient air and soil. Thermal regimes of the ambient air and the soil surface had temperatures that fluctuated around 0ºC. Temperature changes at 10 cm and 25 cm soil depth were dampened by residual ground heat and the high specific heat of soil water.

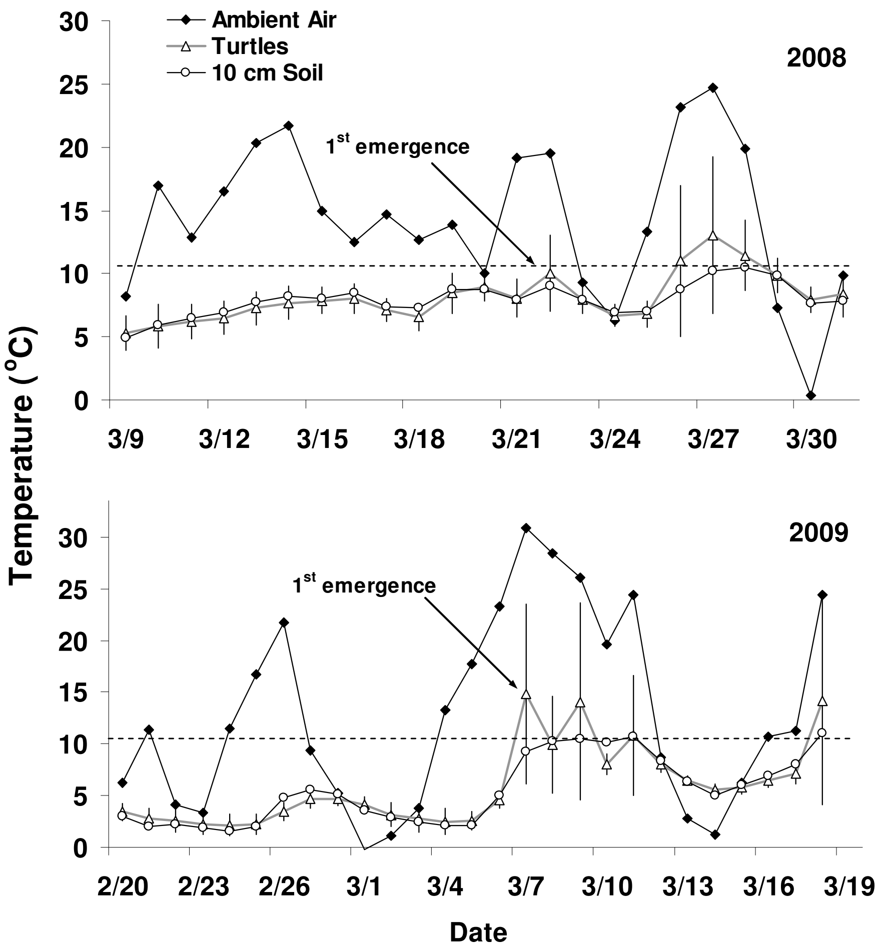

Figure 3.3. Average daily maximum temperatures of ambient air, soil at 10 cm depth, and carapaces of bog turtles (n=8) before and during the time of emergence from winter hibernacula in 2008 (top) and 2009 (bottom). Error bars on average turtle temperatures shows the standard deviation among the turtles. Standard deviation was large during days when one or more turtles basked. Dotted line is at 10.3°C, the average maximum 10 cm soil temperature at time of emergence. First turtle emergence in 2008 occurred 15 days later than emergence in 2009, despite higher average ambient temperatures prior to emergence in 2008. Soil temperatures at 10 cm were more likely a factor in triggering emergence in 2008 than ambient air temperatures.

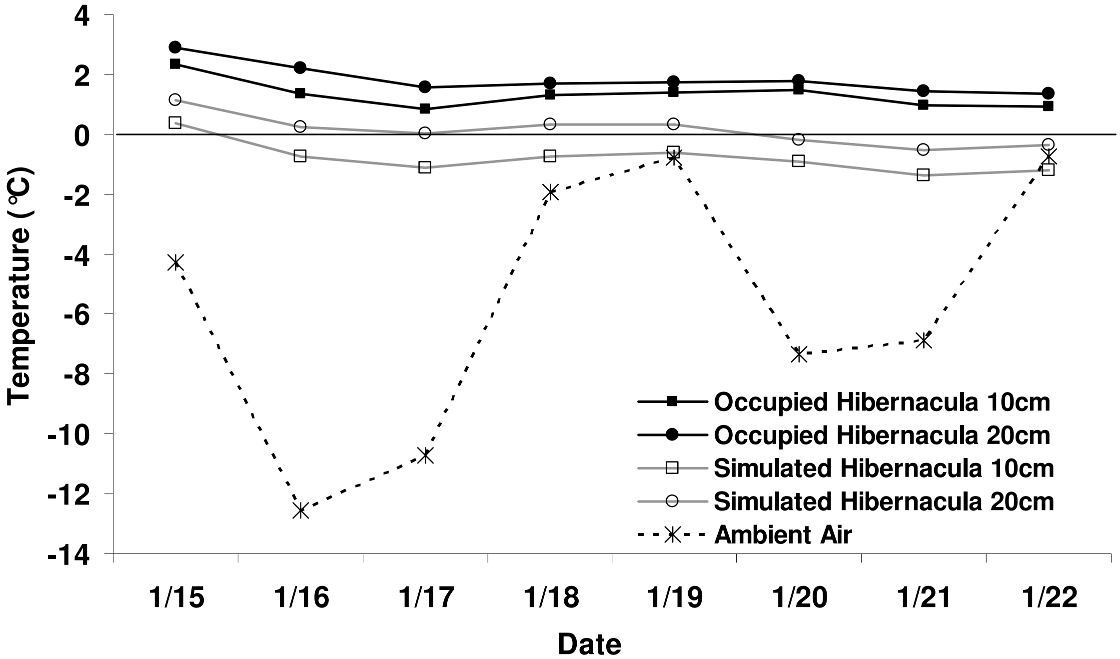

Figure 3.4. Average daily temperature of ambient air and the soil inside of true and simulated hibernacula during an eight-day consistently cold period in January 2009. Simulated hibernacula (n=4) were excavated in randomly selected areas of drier soil located within an approximate 50-m distance to the true hibernacula (n=4). Dimensions were similar for simulated and true hibernacula. Thermochrons were placed at the soil surface (data not shown), 10 cm, 20 cm, and 30 cm (not shown) in each replicate. Temperatures remained above freezing in true hibernacula, while sub-zero temperatures were measured in simulated hibernacula.

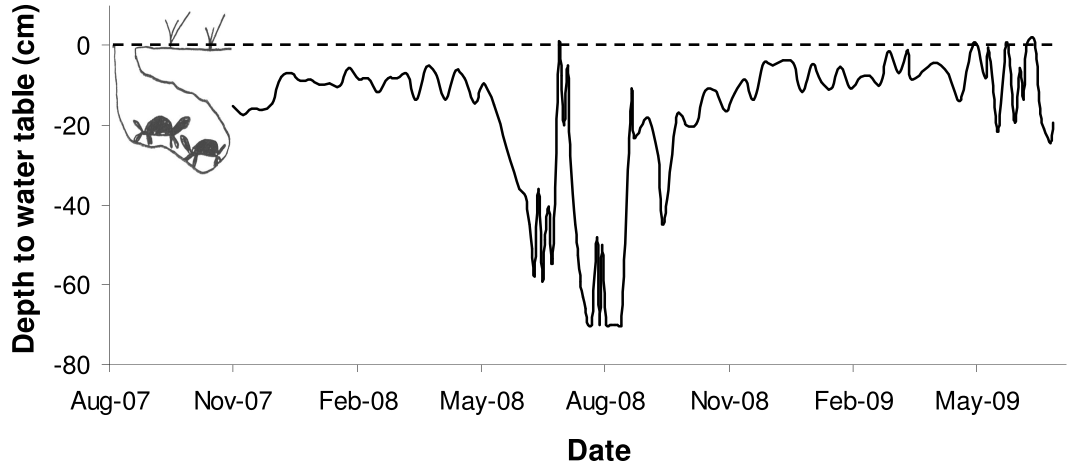

Figure 3.5. Depth to the water table at the location of multiple bog turtle hibernacula over two winters in Southwestern Virginia. Water table values were averaged over seven-day periods. The hibernacula were approximately 30 cm deep and the water table remained above this level during winters 2007-2008 and 2008-2009. The drawdown of the water table in the summer of 2008 corresponded with a two-year drought (Chapter 1).

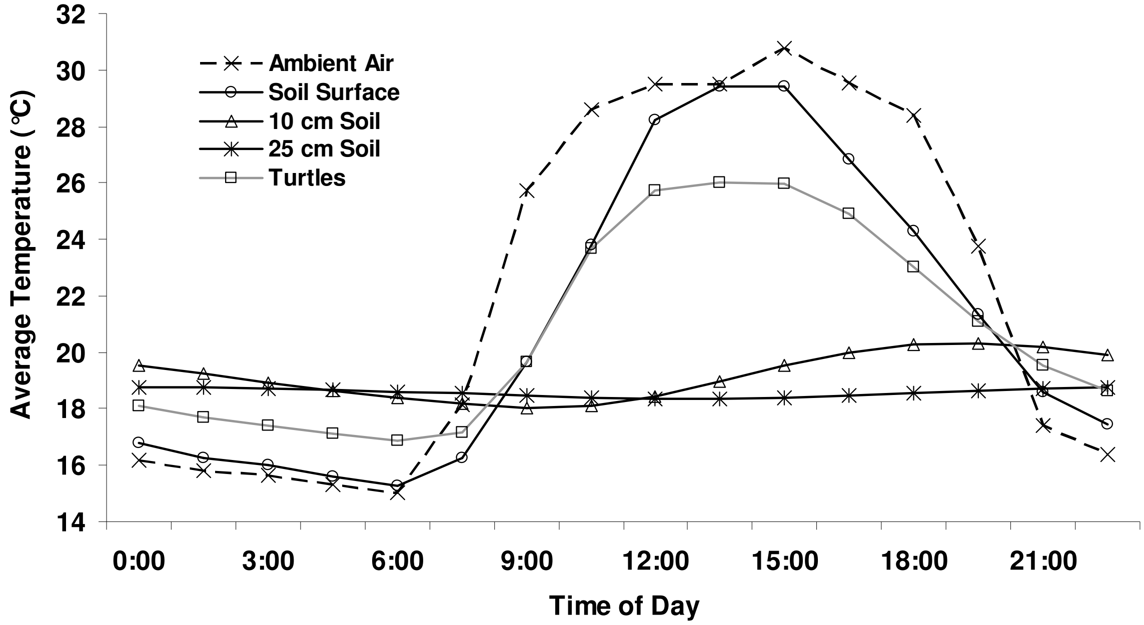

Figure 3.6. Average temperatures throughout the day between 15 June 2008 and 31 July 2008 in Southwestern Virginia for ambient air, soil at several depths, and bog turtle carapaces (n=8). Data were recorded with multiple thermochrons deployed at 90-minute intervals. Timing of thermal warming and cooling appeared similar for ambient air, the soil surface, and turtles. Soil at 10 and 25 cm depth were cooler than ambient air during the day and warmer than ambient air at night, potentially providing a thermal buffer available to moderate turtle temperature.

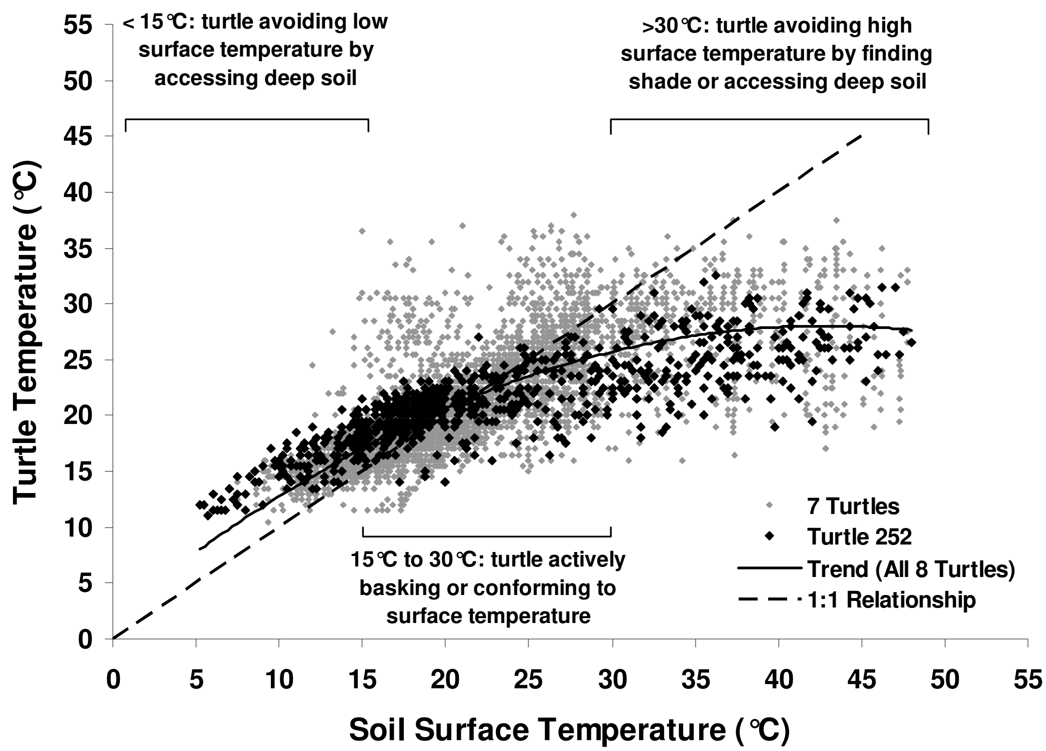

Figure 3.7. Relationship between bog turtle carapace temperatures and soil surface temperatures from 15 June to 30 July 2008 at four wetlands in Southwestern Virginia. Points represent each unique temperature pair measured at each 90-minute interval. Turtle carapace temperatures did not show a linear correlation with surface temperature, and showed that bog turtles may moderate their temperature by vertically adjusting their position relative to the soil surface. Turtle T252 used a drying habitat with minimal shade and appeared to bask less frequently than other turtles that used a saturated scrub shrub habitat with shade.

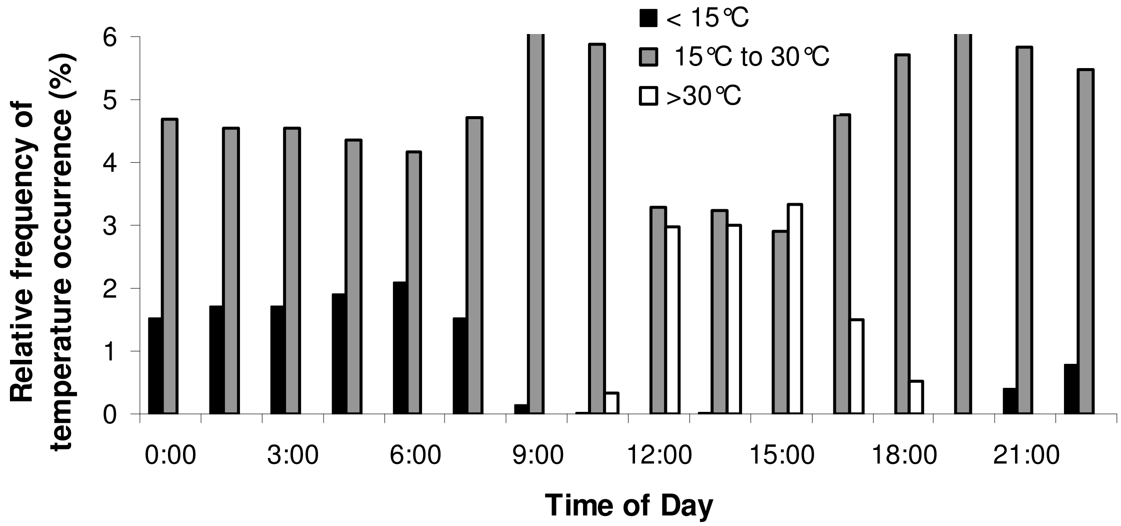

Figure 3.8. Relative frequency of occurrence by time of day for wetland specific soil surface temperatures measured at 90-minute increments (n=6016). Soil surface temperature ranges were defined by periods when soil temperatures were less than corresponding turtle carapace temperatures (<15°C), when soil surface temperatures roughly conformed to turtle temperatures (15°C to 30°C), and when soil surface temperatures exceeded turtle temperatures (>30°C).

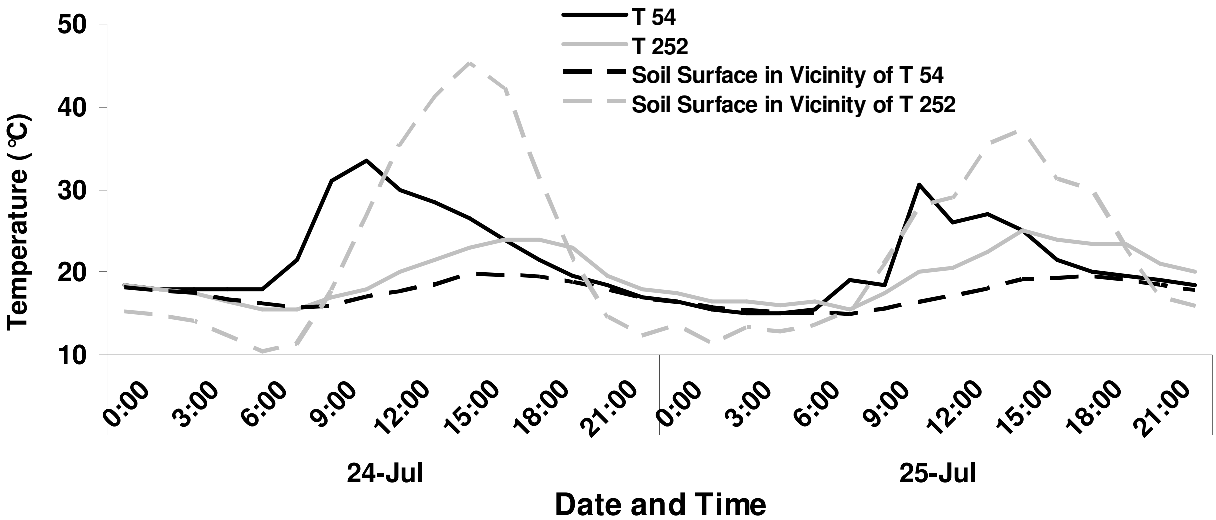

Figure 3.9. Average temperatures of the soil surface and the carapaces of turtles T54 and T252 throughout two typical sunny days in the summer of 2008. The graph shows differences in the thermal environment for turtles using a wetland exposed to full sun (T252) and a wetland with abundant shade (T54). Turtle T54 actively raised its temperature relative to substrate temperatures between 7:30 and 12:00 by basking. In contrast, T252 did not bask, and likely reached its maximum temperatures through its association with warmed soils.

Chapter 4: Short-interval bog turtle (*Glyptemys muhlenbergii*) activity, linear range, and near-stream movements during variable wetland hydrology

ABSTRACT

The landscape in the range of the bog turtle (*Glyptemys muhlenbergii*) in Southwestern Virginia provides an opportunity to evaluate cues for movement and activity and the pathways used for dispersal. Thrice-daily, repeated telemetry locations of 34 bog turtles over short intervals were used to measure how activity (m/h) was related to time of day, year, and wet and dry hydrology. Hydrology was defined as wet or dry by the depth to the water table. Paths of turtle movements ≥ 80 m were characterized as to whether they were confined to streams or not. Mixed model analysis indicated that turtles were much less active from 18:30 to 09:30 relative to the daytime and that turtles were most active during times when hydrology was categorized as wet during 2008 when moderate to severe drought was the dominant condition. Sex was not a factor in turtle activity. Turtles made large movements (≥ 80 m) more frequently during 2008, when drought conditions resulted in low water tables and reduced surface saturation. Median bog turtle linear ranges (min, max) were 93 m (22, 545) and 174 m (31, 965) for males and females, respectively. Individual bog turtles often clustered habitat use in two or more areas of their linear range, even using hibernacula as far as 314 m apart during successive winters. Turtle linear range was not correlated with turtle activity. Bog turtle paths during large movements were overwhelmingly within 80 m of USGS 7.5' mapped streams, and sometimes occurred directly in the stream along the bottom substrate. Movement paths crossed non-wetland areas, roads, and passed through culverts. Results suggest that drying conditions can stimulate semi-aquatic bog turtles to either remain inactive in sparsely available saturation or to move relatively long distances to find wetter conditions. Bog turtle areas of activity span across multiple core saturated areas. Conservation efforts should focus on allowing dispersal among habitats by reducing obstructions and risks to travel along streams.

Key Words: fen, drought, buffer, saturation, path, home range, Virginia, corridor, connectivity, dispersal

INTRODUCTION

The wetland fens occupied by bog turtles are characterized by groundwater supplied hydrology that results in nearly constant saturation of surface soils, without deep inundation (Arndt 1977, Bury 1979, Chase et al. 1989, Herman and Tryon 1997, Buhlmann et al. 1997, Carter et al. 1999, Ernst and Lovich 2009, Chapter 1). In the Southern Virginia Blue Ridge, the fens providing used and potential bog turtle habitats are present in headwater drainages, particularly in 1st through 3rd order streams (Buhlmann et al. 1997, Chapter 5), and form a mosaic of wetlands in a matrix of riparian forest and pasture. Wetlands in the range of the bog turtle are often degraded through anthropogenic disturbance such as draining, filling, pond construction, or other activities that can change hydrology (Bury 1979, Buhlmann et al. 1997, Herman and Tryon 1997, Klemens 2001). Further, fragmentation of the landscape matrix through road building, residential or commercial development, intensive farming, and forest succession can limit connectivity between occupied wetlands and other wetlands with high potential to provide new habitats. Researchers have frequently noted the importance of wetland connectivity for aquatic and semi-aquatic turtles (e.g. Gibbs 1993, Buhlmann et al. 1997, Carter et al. 2000, Joyal et al. 2001, Gibbons 2003, Roe and Georges 2007). Nonetheless, little is known about the movements that bridge the matrix between core habitats, especially for the bog turtle. In both the northern and southern range of the bog turtle, many local populations are considered isolated or fragmented, preventing habitat expansion by bog turtles (Klemens 2001, Pittman and Dorcas 2009). Habitats used by local bog turtle populations in Virginia are relatively less fragmented than those in other parts of the bog turtle's range (Buhlmann et al. 1997), providing an opportunity to investigate activity, its cues, and movement paths through the landscape.

The effect of hydrology on aquatic and semi-aquatic turtle movement varies. Turtles have been observed to make mass movements from drying habitats to wetter habitats (Gibbons 1983, Aresco 2005, Roe and Georges 2007), while other studies found that turtles aestivate or decrease their activity during dry periods (Rowe 2003, Remsberg et al. 2006). Bog turtles have been observed using streams during drought (Somers et al. 2007, Pittman and Dorcas 2009) and avoiding streams during normal conditions (Carter et al. 1999), but little is known about how activity and habitat use respond to wetland drying or wetting.

A useful metric of hydrology in groundwater-maintained wetlands without large areas of inundation is water table depth, which is relatively easy to measure and responsive to drought (Moorhead 2003). In bog turtle wetlands with a groundwater source, response of the water table may be delayed following a deficit in rainfall (Chapter 1). Therefore, water table depth may be a useful variable for evaluating the relationship between bog turtle habitat use and hydrology because it is less variable and more robust than short-event variables such as daily rainfall. Water table depth responds to anthropogenic factors that disrupt the water balance in a wetland; this provides further opportunities to evaluate relationships between hydrologic change and bog turtle activity and habitat use.

Activity and movement studies of turtles can reveal daily patterns of habitat use, including turtle response to environmental variables such as temperature, rainfall, or drought, and are important for developing conservation plans (Litzgus and Mousseau 2004, Rowe 2003, Smith and Iverson 2004). If activity is defined as the gross movement of an animal per unit time, then the calculation of activity is dependent on the time and the apparent net distance between location measurements. Net distances underestimate gross distance (Barton 1957, Chase et al. 1989, Carter et al. 2000), particularly for any animal that is confined within a limited-sized habitat or home range by territoriality, preference, or physical boundaries. For this reason, repeated, short-interval relocations using radio telemetry should provide a more accurate estimate of movement-defined activity than infrequent or opportunistic relocations, and can be used to evaluate activity levels throughout the day (Rowe 2003).

Bog turtles are known to be active in Virginia and North Carolina from April until November, yet occasional movements have been observed in March and December (Lovich et al. 1992, Ernst and Lovich 2009; Chapter 3). Based on their ability to capture turtles, Ernst and Barbour (1989) found that bog turtles appeared to be more active in the spring and early summer, with decreased activity during mid summers. Carter et al. (2000) found that Virginia bog turtles remained active through the summer, but that daily activity decreased somewhat with reduced rainfall that occurred in later summer and early fall. Some researchers have noted that bog turtles make a seasonal movement between hibernation areas and areas used for breeding, nesting, and foraging (Barton 1957, Whitlock 2002). Within the summer, bog turtles may be most active during morning daylight hours (Barton 1957, Arndt 1977, Ernst 1977).

Average bog turtle home ranges estimated in different field studies vary between 0.02 and 3.12 ha (Ernst 1977, Chase et al. 1989, Carter et al. 1999, Morrow et al. 2001b, Whitlock 2002, Pittman and Dorcas 2009). Sex does not appear to be a strong determinant of home range (Carter et al. 1999, Morrow et al. 2001b, Whitlock 2002). These home range studies used different methods of home range estimation, making comparisons difficult. Wetland size or degree of isolation from other wetlands may influence the probability of movement or the average distances moved. A landscape where wetland patches are small and isolated may result in a clumped habitat use pattern, which is not well-characterized using minimum convex polygon (MCP) home range estimators. Kernel density home range estimators are useful for identifying core use areas, but an arbitrary smoothing factor must be specified and the home range must be built from a large enough number of locations to converge on an accurate estimation. Kernel estimators for herpetofauna are especially sensitive to spatial autocorrelation because of their tendency for clumped habitat use (Row and Blouin-Demers 2006). Kernel estimators may predict a home range beyond what was actually observed for an individual. As a result of these issues, kernel estimators may give ambiguous results (Vokoun 2003, Row and Blouin-Demers 2006). These concomitant factors complicate spatial habitat analyses and suggest that using a more simplified metric may be appropriate, particularly when the main objective is to describe pathways used to connect core habitat areas or to evaluate if physical barriers or unsuitable conditions are preventing expansion of habitat use. For bog turtles whose habitats are frequently located in patches along riparian areas, a simplified home range metric is the basic linear range, defined as the greatest possible distance between any two locations recorded for an individual.

The routes most commonly used by bog turtles during apparent dispersals or migrations are unknown. There are numerous observations of long distance and inter-wetland movements by bog turtles, with multi-day movements as large as 750 m and year-long movements as large as 2,700 m (Buhlmann et al. 1997, Eckler et al. 1990, Somers et al. 2007, Carter et al. 2000). In unpublished data, one marked bog turtle in Virginia was found 6.3 km straight line distance from its original capture location (M. J. Pinder, Wildlife Diversity Division, Virginia Department of Game and Inland Fisheries, personal communication). In Virginia, 88% of wetlands known to be used by bog turtles occur within 56 m of streams identified on the USGS 7.5' quadrangle map series (Chapter 5). Given this occurrence, it follows that bog turtles may use areas near streams for travel. Long movements confined within stream valleys have been documented (Somers et al. 2007). Upland (non-wetland) movements that are distant from streams have also been recorded, such as the observation of Carter et al. (2000) of a bog turtle moving through a white pine (*Pinus strobus*) plantation. Bog turtles have the capacity for cross drainage movements, and frequently cross roads (Buhlmann et al. 1997). Road crossings are a significant source of mortality for many turtles and other herpetofauna, and such mortality can affect demographics of local or regional populations (Gibbs and Shriver 2002, Aresco 2005, Steen et al. 2006, Shepard et al. 2008, Langen et al. 2009).

I had several main objectives in this field study. First, I used radio telemetry over repeated, short-duration intervals of the day to evaluate if turtles were more active during wet periods than dry periods, and to evaluate how bog turtle activity differs throughout discrete intervals of the day. Second, I used activity and linear range data from individual turtles to evaluate whether more active turtles also had larger linear ranges and thus a higher potential for breeding dispersals or migrations. Finally, I used radio telemetry to evaluate the most probable path taken by turtles making large movements, defined in this study as any movement ≥ 80 m. Eighty meters is the approximate diameter of a 0.5 hectare wetland, the median size of wetlands used in this study. I expected that most large movements would occur near streams, with near-stream movements defined as being ≤ 80 m from a stream.

METHODS

Study Area

I conducted this investigation on turtles in six individual wetlands in Floyd County in the southern part of the Blue Ridge physiographic province of Virginia (Figure 4.1). Precise wetland locations are not reported because of the federal and state protected status of the bog turtle and the risk of collection and for the pet trade. The study wetlands, subsequently referred to as Wetland 1 through Wetland 6 (see Appendix A.1 for VDGIF site numbers), were spaced over a distance spanning 13.1 km. The average and median distances between adjacent wetlands used in the study were 2.7 and 1.3 km, respectively (range=0.7-8.5 km). The wetlands were between 0.3 and 1.3 ha in size (median=0.5 ha), were irregularly shaped with multiple projections, and had core areas of saturation because of irregular surface elevations and seepage areas.

Wetland sites contained flora typically associated with bog turtles (Morrow et al. 2001a, Ernst and Lovich 2009). Floral descriptions of bog turtle wetlands within the study area are available (Carter et al. 1999). Three out of the six study wetlands were identified on the U.S. Fish and Wildlife Service's National Wetland Inventory mapping series and are described as palustrine emergent (Cowardin et al. 1979). Hydrogeomorphic classifications have not been well described for wetlands in the Blue Ridge; however, the study wetlands appeared similar to the groundwater-supplied riparian depression, headwater floodplain, or toe-of-slope wetlands on 1st through 3rd order streams (Cole et al. 2008, Chapter 1). All study wetlands were located adjacent to or at the head of USGS 7.5' quadrangle map series identified streams (subsequently referred to as USGS streams). Groundwater was the primary hydrologic source for the study wetlands (Chapter 1). Valley slopes where the study wetlands occurred were between 0 and 3%. Topography outside of the stream valleys was variable and ranged from gently rolling pastures to ridges and hills with steep slopes.

Multiple adult bog turtles and nests have been observed on all six wetlands, while juvenile turtles have been captured at five of the six wetlands. Each study wetland contained between five and 68 bog turtles based on unpublished 1997 population assessments (that used Lincoln-Peterson estimators) or the total number of unique individual adult captures per wetland in 2007 through 2009. The landscape in the study area is a mosaic of farm fields and wood lots, and other bog turtle wetlands were present near the wetlands used in this study. Study wetlands were separated from other wetland areas (independent of inclusion in this study) by densely forested riparian areas, roads, or well-drained pastures. All study wetlands were historically used for livestock grazing, and most were used for grazing during the study period.

Water Table Measurements – Defining Sampling Period Hydrology as Wet or Dry

I used water table depth to describe hydrology conditions and to provide an explanatory variable for turtle movement. I installed three to eight shallow monitoring wells in each study wetland to measure water table depth. More wells were used on the larger wetlands and wetlands with complicated boundaries to monitor multiple groundwater seeps. I placed wells in saturated areas with deep soil away from the direct influence of streams and channelized flow.

Wells were constructed of 3.8-cm outside diameter PVC pipe with factory-cut 0.025-cm horizontal slots spaced at 0.5 cm over the entire length from the bottom end cap to the top of the riser. Boreholes used for well installation were dug using an 8.9-cm diameter mud auger. The annular space between the pipe and borehole was filled with medium-grade sand. Well depth was determined by refusal on bedrock or large gravel, or by 140 cm depth, whichever was shallower. The average well depth measured from the soil surface was 82 cm. I stood on top of plywood platforms with an approximate 45-cm hole in the center while digging boreholes and setting the wells to minimize disturbance to the wetland.

I hand recorded water table depth in water table wells every two to three days from May – August, every two weeks from September – October, and approximately once each month in November – April. Depth was determined with a tape measure and flashlight. I referenced all depths to the water table as the distance from the soil surface to the measured water surface in the well. Depth from the surface datum is negative. More details on monitoring well installation and hydrologic characteristics of bog turtle wetlands are available (Chapter 1).

Water table data were used to distinguish the hydrologic condition during sampling periods as either wet or dry. Wet conditions were defined as any time the water table was between -30.5 cm and the soil surface. The water table depth of -30.5 cm is a component for defining wetland hydrology by US Army Corp of Engineers methods (Wetland Training Institute, Inc. 1995). Dry conditions occurred when the water table was deeper than (less than) -30.5 cm. Monitoring wells within the same wetland were averaged as subsamples, and the resulting six wetland values were averaged to provide a grand average for each measurement date. I decided to use grand average, rather than wetland specific water table depth information, to define the hydrologic condition during sampling periods because the variability of water table depth was small among the study wetlands (Chapter 1). Over the 28 months that water table was measured, the standard error of the mean water table depth on the study wetlands was 1.0 cm. On account of the small variability among wetlands, defining wet and dry periods as a wetland-specific variable would not improve the inference that could be made from the data.

Precipitation and drought index data were collected in order to place water table conditions within context to more commonly used hydrology data. Precipitation data were obtained from four weather stations that were between 6 and 25 km from the study wetlands (National Weather Service 2010) (Chapter 1). Precipitation data were averaged by month and compared to long-term data tabulated from the 56 years of continuous data available at the weather stations. The severity of drought was examined using the Palmer Hydrological Drought Index (PHDI) developed by the National Weather Service. Data were downloaded for region 6 for the years 1895-2009 (National Climatic Data Center 2010). The PHDI index ranges from

-6.0 to 6.0. Negative values indicate dry conditions, with values between -3.0 to -4.0 indicating severe drought and values greater than -4.0 indicating extreme drought.

Radio Telemetry

All bog turtles used in this study were captured by hand or by trap. All new bog turtle captures were given a unique numerical shell notch assigned using the system consistent for all known captures in Virginia. I attached 3.8-g radio transmitters (model PD-2, Holohil Systems Ltd., Carp, Ontario) to the posterior plural scutes of the bog turtles using Devcon Plastic Welder™. Total weight of equipment attached to the carapace never exceeded more than 10% of the turtle's total body weight, and typically was in the range of 7 to 8%. Radios were attached to 45 turtles (23 female, 22 male) in 2008 and 27 turtles (13 female, 14 male) in 2009. Seventeen turtles (seven female, ten male) were used in both years, yielding a total of 55 radioed adult turtles (29 female and 26 male) over the study period.

I made locations using a handheld, scanning R410 receiver and a three-element, foldable Yagi antennae (Advanced Telemetry Systems, Isanti, Minnesota). Distances between radio locations were recorded as the straight line distance (nearest decimeter) between the previous and consecutive location. Locations were plotted on a Universal Transverse Mercator (UTM) grid by referencing turtle locations with a straight line distance and compass bearing to a survey control point with known UTM coordinates. Control point locations consisted of easy to find landmarks where GPS coordinates were recorded with a Garmin Map 76s unit (Garmin International, Inc., Olathe, Kansas). Accuracy estimates at the time of data collection were approximately 1.0 to 1.5 m. When turtles moved beyond approximately 100 m from a control point location, I recorded locations using a handheld GPS (accuracy $\leq$ 15 m).

Short-Interval Turtle Activity

I used a subset of radioed turtles from the greater pool of captured and radioed turtles to evaluate the effect of year, time of day, and hydrology on bog turtle activity. Turtle sample size for the activity objective included 20 turtles (ten female, ten male) in 2008 and 24 turtles (12 female, 12 male) in 2009. Ten turtles (four female, six male) were used in both years. Turtles were selected from each of the six wetlands, and I attempted to balance the number of turtles by sex at each wetland. Turtles were selected at random when the number of radioed turtles in a wetland exceeded the number needed for the activity study.

I defined activity as the net distance moved by an individual turtle divided by the number of hours passed (m/h) during a discrete interval of the day. Intervals of the day were bounded by radiotelemetry locations that occurred at average times of 09:30, 14:00, and 18:30 each study day. These intervals spanned approximately 15 hours (previous night's location time to morning location time), and 4.5 hours for the intervals ending at 14:00 and 18:30. These three intervals are subsequently called PM-AM, AM-PM, and PM. Two, two-person crews of technicians were coordinated to work simultaneously on different wetlands in order to maintain the turtle location schedule. The need to maintain the rigorous location schedule was a primary reason for only using a subset of total radioed turtles in the activity study, along with the goal of balancing turtle replicates among wetlands and between sexes.

In 2008 there were nine study days broken up into three, three-day sampling periods, while in 2009 there were 11 study days broken up into five, two-day sampling periods and an incomplete, one-day sampling period. Net distance could not be calculated for the first PM-AM interval of the day during each new sampling period, as there was no PM interval location available from the previous day. All turtle activity measurements occurred after nesting season between July 14 to August 31 in 2008 and July 13 to September 13 in 2009.   In total, 1326 radio locations and 1123 (480 in 2008 and 643 in 2009) activity events were recorded in the activity study. With the exception of six missing locations of a male in 2009 (the last six planned radiotelemetry locations), the activity dataset was completely balanced, providing the same number of observations per turtle each day and year of the study.

I visually confirmed the location of every turtle at each sampling event. At each point where I located a turtle, I collected data on hydrology, turtle depth, and whether or not a turtle moved or did not move between activity measures. I described the hydrological condition as either saturated or unsaturated. A location was defined as saturated if it consisted of open water or soil that was wet enough to drip by gravity if suspended, or similarly if a small hole created in the soil by the end of a broomstick immediately filled with water. I measured turtle depth by touching the turtle carapace with my fingertips and measuring my hand's penetration depth. A turtle was defined as submerged or buried if the top of its carapace was not visible because it was covered with mud. I recorded turtle depth as being at the surface (unburied), or as being in the 5 cm increment between the surface and 5 cm depth, 5 to 10 cm, 10 to 15 cm, 15 to 20 cm, or 20 to 25 cm. I also combined depth groups to simplify turtle depth data as being either unburied or buried. A movement was recorded for a turtle if the net distance between telemetry locations was greater than 50 cm. Movements less than 50 cm were considered the same as no movement because some turtles may have been stimulated to move by my telemetry activities (escaping behavior). Turtle locations were marked with a PVC stake so that movements could be easily recognized.

Linear Range of Bog Turtles and Near-Stream Use

In addition to short interval activity measurements, I used radio telemetry locations taken at intervals ≥ one day to investigate linear range of bog turtles. Telemetry began on March 9, 2008 and ended on September 17, 2009. Measurements were made opportunistically whenever possible on any bog turtle with a radio attached. For most turtles, locations occurred at least once a week during the months of May through September when bog turtles were most active. Locations were made approximately once each month from fall 2008 to spring 2009 for turtles overwintering with radios.

Throughout the linear range portion of the study, I frequently made "location checks" to verify the locations of turtles. Location checks were telemetry events when visual confirmation was not made with the turtles and the precise locations of turtles were not measured; instead, telemetry was used in the vicinity of the study wetland to verify that a turtle had not emigrated from the wetland since the previous data collection event. In 2009, location checks were used frequently to monitor turtle movement. I justified the use of location checks as they were easy to record, consumed less time, minimized destructive trampling within the wetland, and provided a signature as useful as visual confirmation of turtle location for identifying dispersal events from core activity areas. I would resume collection of regular location data if turtles began moving away from their previous location within a study wetland. In order to maintain radio contact, more frequent location data were recorded for any turtle making extremely large movements, as radio signals dissipated at distances greater than approximately 200 m.

Precise location data from 2008 and 2009 were combined and overlaid on a UTM grid to display on ArcGIS. I measured the greatest possible straight-line distance between any two locations recorded for each turtle using the "measure" tool on ArcMap. This distance measurement is subsequently referred to as the linear range of an individual bog turtle. Linear ranges were measured for all turtles accumulating at least 10 telemetry locations (53 turtles, 29 female and 24 male). Median and mean linear ranges were calculated from the entire data set of locations for that individual, i.e. from one year of data for most turtles and two years of data for the 14 turtles used in both study years. For the seven male and seven female turtles with at least 10 locations in both 2008 and 2009, I also evaluated how linear range differed by year. Linear range data for each of the 34 turtles (18 female and 16 male) that were also used in the activity study were compared to the same turtle's median and mean activity value using simple linear regression.

I used simple linear regression to test whether linear ranges were independent of the number of telemetry locations recorded for each turtle. I did not include bog turtles with > 35 locations in the regression because these turtles did not follow the typical telemetry schedule, and had an inflated number of locations for the following reasons: 1) They were being tracked more intensively to identify nesting behavior; 2) They were using non-typical habitat such as stream bottoms or non-wetland areas; or 3) They had moved away from core habitat areas and were being monitored more frequently so that they did not get out of radio signal range.

The path of large movements was examined to evaluate if most bog turtle movements are confined to areas near streams. I defined a large movement as any that was ≥ 80 m that occurred within a seven-day period or less. Eighty meters is the diameter of a circle with an area of 0.5 ha, approximating the median area of wetlands used in this study (Table 4.4). Seven days was an arbitrary time that reduced the likelihood of misclassifying the movement path between the end points of a large move. Large moves often had multiple telemetry locations within the seven-day period. Near-stream movements were recorded when all portions of the straight lines connecting telemetry location points were within 80 m of a USGS stream (Figure 4.2). I recorded when assumed movement paths (lines connecting sequential telemetry locations) crossed non-wetland areas, with a wetland area defined by the presence of wetland hydrology, hydric soils, and a dominance of hydrophytic vegetation (Wetland Training Institute, Inc. 1995).

Statistical Analysis

I used basic descriptive statistics (mean and standard deviation) to describe the water table data during the periods of the activity study. Water table depth was then used to assign hydrology as either wet or dry during each sampling period according to the previously discussed criteria. I used a linear mixed model (PROC MIXED, SAS Institute, Cary, NC) to evaluate the effects of interval of the day (INT), year (YEAR), sex (SEX), and hydrology (HYDRO) on activity. Individual turtles (TURTLE) were coded as a random effect, while all others factors were coded as fixed effects. To equally weight each turtle for the mixed model, all discrete activity values measured for a turtle were averaged by INT, YEAR, and HYDRO. This averaging effectively treated most of the activity events as subsamples, and resulted in one activity value for each combination of TURTLE, INT, YEAR, and HYDRO. The 10 turtles that were measured in both 2008 and 2009 were modeled as being independent by year, while the other 24 turtles only appeared in one year. Modeling turtles as a random effect enabled me to make inference on bog turtle activity in general even though some turtles were used in both study years. Activity values were natural log transformed to improve the assumption of normality of residuals during statistical tests, which were investigated in the modeling process. Before transforming, the scalar value of "1" was added to each activity value so that data could be used when turtles did not move (an activity of 0). The mixed model was evaluated using AIC_c scores as well as *P*-values of the fixed effects from the mixed model output. Potential models started with the *a priori* model with all fixed effects and no interactions; however, the global model and subsets with all possible combinations were also evaluated.

For habitat selection data over a period of interest, I first calculated the proportions of turtle locations during which an individual turtle was found buried or in saturated conditions. Similarly, to look at the prevalence of larger movements, I recorded the number of movements occurring within one interval of the day (AM-PM, PM-AM, or PM) that exceeding the arbitrary threshold of 25 m. Periods of interest included the years 2008 and 2009 and sampling periods that had wet and dry hydrologic conditions. To test for differences in habitat use or movement between years, I used a two-sample t-test to compare all turtles used in the activity study in 2008 (n=20) to the turtles used in 2009, but not used in 2008 (n=14). I used paired t-tests to compare turtle data between periods with wet and dry hydrology within 2008. I used simple linear regression to investigate the relation of linear range to number of radio locations and to turtle activity. Regression analysis was completed using MINITAB Student Release Version 14.11.1 (State College, PA). I log transformed dependent linear range data to improve the assumption of normality of residuals. A two-way ANOVA (Type III SS, SAS PROC GLM) was used to evaluate the effect of wetland site and turtle sex on linear ranges. Two-way ANOVA was also used to evaluate the effect of year and sex on the linear range of turtles that were tracked in both 2008 and 2009. I used an $\alpha \leq 0.1$ to indicate significance.

RESULTS

Water Table Measurements - Defining Sampling Period Hydrology as Wet or Dry

Average water table depth on the six study wetlands was greater and more variable in 2008 than it was in 2009, resulting in the identification of multiple sampling periods with hydrology conditions categorized as wet, and only one sampling period with hydrology categorized as dry (Figure 4.3). The depth to the water table during 14 July 2008 to 31 August 2008 (encompassing the period of the activity study) was based on 14 measurement events and was on average (±SE) -26.3 ± 3.13 cm. The three-day sampling period from 26 August 2008 to 28 August 2008 had water tables low enough to categorize hydrology as dry. Depth to the water table during this sampling period was -31.2 cm. The other two sampling periods during the 2008 activity study had hydrology categorized as wet, with water table depth more shallow than (greater than) -30.5 cm. Depth to the water table in 13 July 2009 to 13 September 2009 was based on 14 measurement events and was on average -4.3 ± 0.69 cm. All six, two-day sampling periods were categorized as wet in 2009. The average PHDI in 2008 was -2.84, indicating a moderate drought, and the average PHDI from August 2007 to July 2008 was -3.25, indicating severe drought conditions. Resumption of average to above average rainfall in 2009 corresponded to a water table rise, reflected in an average PHDI of 0.97, indicating normal conditions.

Turtle Activity

Dry hydrology conditions only occurred during one sampling period in 2008 and were not repeated in 2009. Accordingly, hydrology was coded in the model as HYDRO(YEAR) to find AIC_c values and least squares mean estimates. Mixed modeling suggested that bog turtle activity was strongly dependent upon INT, YEAR, and the interaction between INT and YEAR. The most highly supported model (AIC_c=216.9, w_i=0.476; Table 4.1) also found bog turtle activity to be dependent upon HYDRO(YEAR), but these results were driven by data from 2008 only. An equally supported model did not include the variable HYDRO(YEAR) (AIC_c=218.9, ΔAICc=2.0, w_i=0.175). Probability values generated through mixed modeling were consistent with AIC_c findings, and resulted in significant effects from all explanatory variables appearing in the top model (Table 4.2). SEX was not a significant factor in turtle activity.

Calculated means of the raw data and least squares mean estimates indicated how strongly dependent turtle activity was on the fixed factors included in the mixed model (Table 4.3). The significant interaction between INT and YEAR was also graphically evident, with more activity occurring during the AM-PM interval (09:30 - 14:00) in 2008 and more activity occurring in the PM interval (14:00 - 18:30) during 2009 (Figure 4.4). Due to this interaction, an overall difference between the AM-PM and the PM interval was not detected over the two-year study. Very little activity occurred during the PM-AM interval (18:30 - 09:30) relative to the other intervals that occurred during daylight hours, and this was consistent throughout the study. Based on means (±SE) of the raw data, activity was greater overall during the nine days measurements in 2008 that occurred during the drought (1.42 m/h ± 0.29) than it was during the 11 days of measurements in 2009 when regular rainfall patterns had returned (0.98 m/h ± 0.12). In 2008, mean activity calculated from the raw data indicated that activity was greater when HYDRO was wet (1.64 m/h ± 0.23) than when HYDRO was dry (1.42 m/h ± 0.29). Despite the effect of HYDRO during the 2008 sampling periods, greater activity was recorded when HYDRO was dry in 2008 than during 2009 when HYDRO was always wet. I interpret these results to mean that during an overall drought such as the one occurring during 2008, bog turtle activity was acutely stimulated by wet periods. Bog turtle activity was particularly increased in 2008 during the second sampling period (Wet 2) that had wet hydrology based on water table measurements. This sampling period followed a 9.9 cm rain event that brought water tables near the surface (Figure 4.3). The mean activity of the Wet 2 sampling period was 2.22 m/h ± 0.42. In 2009, water table also neared the surface when approximately 5.6 cm of rain fell between sampling periods Wet 4 and Wet 5 occurring on 19 July and 23-24 July, respectively. Bog turtle activity increased from 0.52 m/h ± 0.12 (Wet 4) to 1.14 m/h ± 0.17 (Wet 5) between those sampling periods.

Turtle-centered data measured from the 34 turtles used in the activity study indicated that bog turtles used saturated conditions (±SE) at 77% ± 3.7% of telemetry locations, but used this condition differently depending on the year, or whether it was a sampling period with wet or dry conditions during 2008. Use of saturated locations differed between 2008 (63% ± 5.8% of locations) and 2009 (89% ± 2.6% of locations) (*df*=32, *t*=3.57, *P*=0.001). In 2008, bog turtles were in saturated locations more often during sampling periods with wet hydrology (69% ± 5.3% of locations) than during sampling periods with dry hydrology (49% ± 8.7% of locations) (*df*=19, *t*=2.9, *P*=0.009). Similarly, bog turtles were found buried less frequently during times with reduced saturation. Overall, bog turtles were found buried during 64% ± 3.2% of locations. Bog turtles were found buried more frequently during the wetter 2009 (73% ± 3.9% of locations) than during the 2008 drought (55% ± 4.7% of locations) (*df*=32, *t*=2.81, *P*=0.008). In 2008, bog turtles were found to be buried more frequently during sampling periods with wet hydrology (62% ± 4.6% of locations) than during sampling periods with dry hydrology (41% ± 7.6% of locations) (*df*=19, *t*=2.93, *P*=0.009). On 1284 total observations, turtles were found at various depths, including the surface (34%), 0 to 5 cm (47%), 5 to 10 cm (15%), 10 to 15 cm (2.5%), 15 to 20 (0.7%), and 20 to 25 cm (0.8%). In total, 5% ± 0.8% of bog turtle movements that occurred within one interval of the day were ≥ 25 m. These larger moves were more frequent during the drought year of 2008 (8% ± 1.7% of moves) than during 2009 (3% ± 0.9% of moves) (*df*=32, *t*=2.15, *P*=0.039).

Spatial Extent of Turtle Habitat and Near-Stream Use

I did not find a correlation between turtle linear range and number of radio telemetry locations for turtles with between 10 and 35 locations ($F_{1,41}$=1.40, *P*=0.244) (Figure 4.5). This lack of correlation was important because it allowed me to use linear range data for turtles with relatively few radio locations. Average linear range (±SE) of the 53 individual turtles with 10 or more locations was 203 ± 28.4 m (median=113, range=22 – 956 m) (Table 4.4). Two-way ANOVA testing the dependence of linear range on wetland and sex was significant ($F_{6,46}$=5.48, *P*=0.0002). Wetland had a significant effect on linear range, as linear ranges on Wetland 5 were smaller than on other sites ($F_{5,46}$=5.18, P<0.001). Wetland 5 was not the smallest wetland in the study, but was surrounded by non-wetland on three sides and mature forest in the downstream direction. Support for a sex-based linear range difference was evident, with female ranges (mean=256 m) exceeding male ranges (mean=139 m) by 97 m ($F_{1,46}$=2.85, *P*=0.098).

Seven males and seven females had at least 10 locations in both 2008 and 2009. These turtles provided data on how the total linear range measured was dependent on individual years of the study (Table 4.5). Two-way ANOVA was used to test the dependence of linear ranges (natural log transformed to improve assumption of normality of residuals) on year and sex. Results indicated that linear range for both sexes was greater in 2008 than 2009 ($F_{1,24}$=25.23, P<0.001), but not dependent on sex ($F_{1,24}$=0.62, P =0.439). An interaction between year and sex was evident ($F_{1,24}$=9.55, P =0.005) because female turtles had a much larger range than males during the drought year of 2008, but a smaller linear range than males during 2009 when normal rainfall was measured.

Linear range was not correlated with median (Figure 4.6) or mean turtle activity. The slope of linear range (natural log transformed) versus median turtle activity was not significantly different than zero (slope=0.015, r^2=0.0, $F_{1,32}$= 0, P=0.952). The slope of linear range (natural log transformed) vs. mean turtle activity showed a stronger relationship (not shown) (slope=0.355, r^2=0.11, $F_{1,32}$=3.89, P=0.057). The stronger relationship of mean activity to linear range was not unexpected, as only one excessively large turtle movement was needed to result in a large range. This excessively large movement had the effect of making the mean activity for a given turtle much larger than its median activity.

Turtles made large movements (≥ 80 m that occurred in seven days or less) 46 times over the two-year study. Movement paths were overwhelmingly within the near-stream area, with only two movements exiting the 80-m near-stream area. It was frequent for bog turtles to move through non-wetland areas, most of which were still within 80 meters of a stream. Approximately 46% of large movements crossed non-wetland areas based on apparent straight line movements between radio locations (Table 4.6).

DISCUSSION

Turtle Activity During Sampling Periods with Wet and Dry Hydrology

Water table fluctuation within 2008 provided two sampling periods with wet hydrology, but only one period with dry hydrology. This data record limited the level of inference that could be drawn on the effect of hydrology on bog turtle activity. Due to persistent drought, average depth to the water table among six sites fluctuated from the ground surface to nearly -50 cm from May to July 2008. The magnitude of this water table drop was not achieved during the summer of 2007 or in 2009. These conditions led to inconsistent groundwater seepage in 2008 relative to 2009 (Chapter 1). Normal rainfall relative to long-term averages returned in 2009, raising the depth of the water table and reducing its variability. These hydrologic conditions were associated with greater turtle activity in 2008 than in 2009.

Higher water tables are associated with greater proportion of area covered by surface saturation (Chapter 1), attesting to the utility of water table depth as a useful metric for explaining how bog turtles are affected by wetland hydrology. Our data were consistent with previous findings that turtles select saturated areas (e.g. Chase et al. 1989, Carter et al. 1999), with turtles using saturated conditions at 77% of locations. During sampling periods with dry hydrology and during all of 2008 when the drought was most severe, bog turtles showed a significant decrease in both the probability of being found in saturated areas and the probability of being found below the soil surface. Field measurements in the vicinity of the groundwater wells on the six study wetlands showed approximately 7% of the wetland surface area being saturated at the peak of the drought in August 2008 compared to approximately 34% from June through September, 2009 (Chapter 1). Reduced availability of surface saturation may explain the observed decreases in the proportion of locations when turtles were found in saturated locations or buried. During times of wetland drying, bog turtles are faced with a tradeoff. On one hand, remaining sedentary within a limited saturated resource maximizes use of a dwindling resource and temporarily reduces exposure to high temperatures and predators (Roe and Georges 2008a). On the other hand, although acute risks may be associated with moving, crossing a drying habitat to find sufficiently saturated habitat may be a cost worth incurring if future risks are avoided or higher quality habitat is encountered (Southwood and Avens 2010).

The 10 cm rainfall event preceding the third sampling period in 2008 appeared to stimulate bog turtle activity. Bog turtles were more active during these three days than they were during any other sampling period of the study. It is unclear as to whether the rapid rise of water tables with associated increases in the availability of surface saturation, or simply the presence of rain, were associated with the observed increase in turtle activity. An apparent increase in activity due to rainfall (5.6 cm) or high water table was also recognized between the second (Wet 4) and third (Wet 5) sampling events in 2009. Based on depth to water table, conditions before Wet 4 were the driest experienced in 2009 (Figure 4.3). Rainfall events during an overall drought or moderately dry period may stimulate bog turtles to move. Rainfall following a drought may enable turtles to access newly wetted areas or return to areas that are generally considered high quality habitat during normal conditions (Roe and Georges 2008b).

Movements ≥ 25 m occurring within one interval of the day were more frequent during the drier summer of 2008. Of the 58 total movements occurring within one interval of the day that were ≥ 25 m, 37 of these occurred in 2008, while only 21 occurred in 2009. Year 2008 differed from 2009 in that water tables and surface saturation were more variable. These results indicate that reduced availability of saturated conditions may stimulate bog turtles to either reduce activity or to disperse across longer distances to find appropriate habitat.

Carter et al. (1999) measured the presence or absence of water at the previous locations of individual turtles and found that it was not a significant predictor for greater net turtle movement. Although I did not repeat Carter's methods, I expect that it would be hard to find significant effects on turtle movement with this metric because: 1) Bog turtles continue to use limited saturated areas even during drought; and 2) Although large movements are more probable during a drought, large movements are still so infrequent that an exceptionally large sample size would be needed to detect a significant turtle response.

Daily Timing of Bog Turtle Activity

The mixed model detected a significant interaction between INT and YEAR. This outcome is illustrated in Figure 4.4, which shows that bog turtle activity was greater during the AM-PM interval in 2008, while in 2009 turtles were more active during the PM. A biological interpretation of this finding is that bog turtles preferred to move when it was not overly hot and dry. During the drought of 2008, reduced temperatures and surface evaporation in the AM-PM interval relative to the PM interval may have provided a better opportunity for bog turtle movement. Hot conditions dominated during the PM interval, potentially making it more difficult for turtles to move between pockets of saturation used for cover and thermoregulation. The moist and associated cooler conditions in 2009 resulted in no limitation for afternoon movement as pockets of saturation were abundant.

Mixed model analysis also indicated a significant main effect of measurement interval, which was due to the diminished activity during the nighttime PM-AM interval relative to the primarily daytime AM-PM and PM intervals. Means activity values (±SE) from the raw data were 0.29 m/h ±0.03 during the PM-AM interval compared to 2.08 m/h ±0.28 and 1.60 m/h ±0.18 estimated for the AM-PM or PM intervals, respectively. A potential confounding aspect of this finding is the question of whether my practice of calculating activity by dividing the total distance moved between radio locations by the hours passed between locations caused a spurious mathematical outcome rather than a real one (Carter et al. 2000). The PM-AM interval encompassed approximately 15 hours compared to only 4.5 hours during the other intervals. I tested this finding by using total distance moved as the response variable in the same linear mixed model used to test the activity data. Model results using distance were consistent with those using activity, showing that distance moved was significantly smaller for the PM-AM interval ($F_{2,152}$=12.27, P<0.001). It is possible that activity concentrated in a very small area could explain the decreased net distances measured during the PM-AM interval. However, unpublished thread spool data that I measured on bog turtles during the PM-AM interval showed little activity. In other words, bog turtles were not accruing gross movement by dispensing a large distance of thread and moving back and forth within a small area. Some net movement did occur during the PM-AM interval, so further study is needed to identify the specific times at which movement is occurring during this long overnight and early morning interval.

Other researchers have observed much smaller daily rates of activity than those I observed in this study. Lovich et al. (1992) and Morrow et al. (2001b) observed activity rates between 1.1 m/day to 2.99 m/day, compared to 38.4 to 49.9 m/day (1.6 to 2.1 m/h) for daytime activity rates observed in this study. The discrepancy of these results may emphasize the importance of using short interval location data when estimating activity using telemetry (Carter et al. 2000, Row and Blouin-Demers 2006). Threadspool studies, though intensive, may be the superior way to characterize total activity because this method integrates total distance traveled. Using thread spools, summer bog turtle activity estimates over a 24-hour period were estimated at 26.5 m/day (Carter et al. 2000), 56.3 m/day (Barton 1957), and approximately 30 m/day (Chase et al. 1989). Using overall yearly activity means from the raw radiotelemetry data (Table 4.3), I calculated activity rates in this study as 36.7 m/day in 2008 and 23.8 m/day in 2009.

Linear Range and its Relation to Activity

Spatial habitat use by bog turtles resulted in elongated patterns which were easily evaluated for linear range. Notable linear ranges in previous studies include an 800 m (Somers et al. 2007) and a 556 m (Pittman and Dorcas 2009) range. Those ranges appeared to be extraordinary observations. In the case of the 800-m movement, the bog turtle had apparently already begun a large dispersal before being tracked, as it was found within the banks of a large stream in North Carolina by a fisherman, with no known wetlands in the vicinity. The 556 m range was recorded on one bog turtle captured in an isolated wetland in the North Carolina piedmont. The average range of the turtles (n=11) studied in that wetland was approximately 75 m (Pittman and Dorcas 2009). The relatively large sample size of my study (n=53) found an average linear range of 203 meters, with eight turtles having a range exceeding 400 meters. The linear habitat use of turtles over the lifetime of a bog turtle would be expected to surpass the short-term linear ranges measured in this two-year study.

The relatively large ranges measured in this study may indicate that large ranges in non-isolated local bog turtle populations may be more common than previously thought. Many of the singular and isolated observations of large linear ranges in other bog turtle studies may have been misidentified as rare dispersals when they are actually a part of a turtle's lifetime home range. Short studies that do not encompass an environmental perturbation such as drought or human-induced hydrologic change may not detect shifts in home range that occur when turtles disperse to find and use higher quality habitat. Because bog turtles often return to previously used activity areas, these movements may not qualify as one-time breeding dispersals. For long-lived bog turtles, lifetime home ranges may be considerably larger than ranges used during a shorter period on the order of a few years. Based on the linear range information gathered on turtles with at least 10 locations in both 2008 and 2009 (n=14), the large linear ranges measured in this study were a result of movements made during drought year of 2008 rather than during 2009 (Table 4.5). Although linear ranges were longer in 2008 than in 2009 for both sexes, females showed the largest decrease (mean difference of 449 m). It is uncertain whether these observations are related to reproduction, but they do attest to the importance of drought as a cue for movement.

The weakness of using the linear range metric measured in this study is that it does not discriminate between turtles crossing habitat or moving through habitat used for feeding, breeding, or cover. Observations indicated that spatial use for the majority of the turtles typically contained two or more clusters, rather than one cluster with singular, short-duration movements away from the cluster. Carter et al. (1999) also recognized multi-cluster home ranges, with between one and four clusters and an average of two clusters. For many turtles, a portion of habitat use occurred at the endpoints of large linear ranges, similar to the home range of male turtle 3226 (Figure 4.7). At least four turtles successfully hibernated in distant locations

(314 ± 38.5 m) along their linear range. The second largest range recorded in the study (Turtle 3227, 911 m), resulted from a single short duration movement when the turtle covered 736 m linear distance within a seven-day period. The turtle then returned to its starting point during a subsequent 12-day period, meaning the turtle moved approximately 3.2 m/h for a 19-day period. Interestingly, this remarkable rate of movement is still much slower than the top short-interval speed measured in this telemetry study, which resulted from a 130.5 m movement that occurred in just 4.8 hours (27 m/h).

Wetland site was the only variable having a statistical effect on linear home range. This was from the small average range (±SE) of 59.8 ± 7.4 m recorded for the 12 turtles located at Wetland 5. Wetland 5 was smaller than the mean wetland size, but primarily differed from the other study wetlands in that it was surrounded on three sides by roads and on the 4^{th} side by sloped uplands. There are no emergent wetlands within approximately 1,500 m downstream of Wetland 5, or 880 m over a ridge. Despite this, Wetland 5 continues to show juvenile recruitment and turtles appeared healthy. The small size and small ranges of turtle home range measured on Wetland 5 relative to other study wetlands suggests that turtle home ranges among turtles using different wetlands may not be comparable when the land use or vegetative cover surrounding the core habitat is not the same, or when the degree of isolation from other suitable wetland habitats differs.

Comparability of home range size among studies is further compromised because of the estimation techniques used for home range analyses. Row and Blouin-Demers (2006) found that kernel estimators were particularly variable for describing the home ranges of herpetofauna because of autocorrelation problems associated with clustered habitat use. Because of inaccurate and highly variable estimates found using kernel estimators, Row and Blouin-Demers (2006) suggested using MCP when comparisons of home ranges among studies is necessary. I found that former bog turtle studies providing MCP home range estimates use either the 95% MCP estimate (Carter et al. 1999, Morrow et al. 2001b), or do not specify how they calculated the MCP (e.g. Ernst 1977, Pittman and Dorcas 2009), which I assumed to be the 100% MCP. To maximize comparability of my turtle movement findings to past and future bog turtle studies, I calculated both the 95% and 100% MCP values for all 53 bog turtles included in the linear range study (Table 4.7). The largest bog turtle home ranges in this study greatly exceeded those reported in other studies. This study recorded maximum 95% MCP bog turtle home ranges of

4.7 ha (male) and 3.3 ha (female) and 100% MCP home ranges of 4.9 ha (male) and 7.8 ha (female). This compares to maximum 95% MCP home ranges of 1.36 ha (male) and 2.35 ha (female) recorded by Whitlock (2002), and 2.26 ha (male) and 1.09 ha (female) home ranges recorded by Carter et al. (1999). The mean 95% MCP home range of 0.58 ha (pooled between sexes) recorded in this study was similar to the 0.52 ha pooled home range (n=25 turtles) recorded by Carter et al. (1999) on some of the same wetlands. The pooled mean 100% MCP home range of 0.91 recorded in this study was smaller than the pooled (n=19 turtles) 100% MCP mean home range of 1.28 ha recorded by Ernst (1977).

Bog turtle activity was not a good predictor for the linear range of bog turtles. In other words, a highly active turtle appears no more likely to disperse or use a larger habitat than a less active turtle. Larger, though infrequent, movements occurred during the extremely dry events recorded during this study. Based on our results, heightened activity and associated large movements may be expected during major rewetting events following drought. This trend has been observed on a mass scale in a Florida lake for several species of fully aquatic turtles (Aresco 2005).

Movement Paths of Bog Turtles

Large turtle movements were confined primarily to areas near streams, as hypothesized. Only two of the 46 movements ≥ 80 m were in a direction that caused turtles to exit the 80 m wide near-stream area present on each side of a USGS stream. The first movement out of the near-stream area was observed when female turtle 3227 made a 127 m perpendicular move from the stream with a return after only one day. After returning, turtle 3227 began a much larger 736 m near-stream movement in seven days. The second movement out of the near-stream area was observed on female 55 and was 585 meters away from the origin wetland. This turtle crossed a major two-lane road before being found dead in a manicured residential lawn with apparent lethal damage from a domestic dog. One juvenile male turtle not in the radio telemetry study was found in 2008 on a two-lane road on the top of small ridge with no wetland areas visible from the road. Although our data on movements out of the near-stream area are sparse, it appears that bog turtles leaving the near-stream area may expose themselves to risks associated with more intensely managed and developed areas. Pittman and Dorcas (2009) observed a bog turtle death associated with a 556 m movement away from a stream. The return path of that turtle was apparently prevented by railroad tracks.

Forty-six percent of the movements that were ≥ 80 meters passed through non-wetland areas. Turtles were frequently observed in heavily grazed dry pastures and mature hardwood forests while on large movements within the near-stream area. Non-wetland movements within the near-stream area may also result in risks to bog turtles. Female turtle 237 died in 2008, most likely of over-heating after being flipped over and trodden by livestock. Turtle 237 was crossing an approximate 140 m long non-wetland riparian pasture area that it had successfully crossed at least three times in the previous month.

Some of the near-stream movements occurred directly within the banks of 1st and 2nd order streams. In these cases, I observed turtles crawling along the bottom of the stream. Male turtle 3226 was observed passing through two different large culverts with minimal water velocity and inlet and outlet inverts that were sunken below grade, thus allowing for passage without a vertical drop. These observations stress the importance of thoughtful culvert design that allows for safe and easy passage for bog turtles (Kaye et al. 2005). In-stream movements by bog turtles have been documented (Somers et al. 2007). Pittman and Dorcas (2009) observed sedentary bog turtles directly in North Carolina Piedmont streams in both winter and summer, and suggested that the heavy stream use could have been associated with the same severe drought observed in this study. I observed in-stream use both during and after the drought; however, more observations of stream use were made during the drought. Length of time in the stream was also more extensive during the drought, with one turtle spending two weeks under a cut bank in a 3rd order stream. Previous bog turtle habitat studies actually showed avoidance of streams relative to their availability during normal rainfall conditions (Carter et al. 1999).

The timing of large movements observed in this study of bog turtle movement paths were consistent with those observed in the activity study, with most of the longest movements occurring during the dry period and in 2008. These results originated from different data sources, with activity movements derived from short, intensive radio locations in late summer, while the study of travel pathways relied on opportunistic radio locations. Nonetheless, both attest to the high proportion of large movements measured during the drought. The majority of turtles with few locations that were used in this range analysis were tracked in 2008. This explains why range was found to be independent of the number of radio locations recorded, as nearly all of the large movements occurred in 2008.

Management implications

Careful protection and management of the core nesting, mating, and hibernation areas are not the only component of successful management of bog turtle habitat. The cues and strategies for movement through and between habitats must be understood. These movements may be associated with finding nest sites, dispersing to new habitats, or avoiding degraded or drying habitats. Further, it is uncertain whether the large linear ranges observed in this study indicate that the local populations are viable and highly adapted to living in a patchy and dynamic landscape, or whether these large linear ranges indicate low habitat suitability for completing all stages of life history. From a practical management standpoint, even if bog turtles are simply passing through areas of non-habitat or low quality habitat, these areas have consequences for safe and unobstructed movement. If turtles are experiencing high mortality while moving between habitats, a management strategy that protects isolated wetland habitats but does not address the connectivity between wetlands may result in the loss of individuals that are more likely to disperse. This would cause selection pressure for turtles that disperse less distance and have smaller ranges. This may reduce viability of local populations and eventually cause genetic defects (Shepard et al. 2008).

The predominance of near-stream movements indicates that bog turtle habitat management should not only focus on portions of the riparian area that qualify as a wetland, but also on any non-wetland areas that are near streams. All of the movements in this study, including those using the arbitrarily defined 80-m near-stream area, would be included in the 287 m buffer suggested by Semlitsch and Bodie (2003) to encompass the average maximum distances moved by a number of species of aquatic and semi-aquatic turtles. Federal laws associated with wetland and stream protection do not minimize activities in non-wetland areas, even if these activities occur directly adjacent to a stream. The Virginia Department of Forestry currently regulates a 50 foot buffer on each side of a stream or wetland where logging activities are limited (Virginia Department of Forestry 2002). Other buffer laws may be set by localities. The construction of roads (including gravel lanes) and storm water management facilities are examples of activities whose effect on bog turtles could be mitigated with properly enforced buffers. I suggest that buffers between 80 and 287 m would encompass most of the movements by bog turtles, many of which would undoubtedly be larger than those occurring within the observations made in this short study. Such buffer widths could also shield bog turtle wetlands from secondary impacts such as the deposition of excess sediments originating from erosion from upland areas while allowing for succession of vegetation core wetland areas within near-stream areas.

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Table 4.1. Results of competing models used to explain bog turtle activity (*v*) in Southwestern Virginia in 2008 and 2009 (k = # of parameters, AIC_c = second-order Akaike's Information Criteria for small sample sizes, ΔAIC_c = the change in AIC_c, and w_i = the relative amount of support for the top five models). All models included three random effects: TURTLE (the individual turtle generating the data), the intercept, and error. Shown for reference are the global model with all fixed effects and interaction terms and the model with the four fixed effect variables with no interaction terms.

Model	k	AIC_c	ΔAIC_c	w_i
Top five Models				
v(INT+ YEAR + HYDRO(YEAR) + INT x YEAR)	9	216.9	0	0.476
v(INT + YEAR + INT x YEAR)	8	218.9	2.0	0.175
v(INT + YEAR + HYDRO(YEAR) + SEX + INT x YEAR)	10	219.5	2.6	0.130
v(INT + YEAR + HYDRO(YEAR) + INT x Year + INT x HYDRO(YEAR))	11	219.6	2.7	0.123
v(INT l + YEAR + HYDRO(YEAR) + SEX + INT x YEAR + SEX x HYDRO(YEAR))	11	220.1	3.2	0.096
				$\Sigma = 1.0$
Global model with all interactions				
v(INT + YEAR + HYDRO(YEAR) + SEX + INT x YEAR + INT x HYDRO(YEAR) + SEX x HYDRO(YEAR) + SEX x INT + SEX x YEAR + INT x SEX x YEAR	18	227.2	10.3	-
Model with all variables of interest and no interactions				
v(INT + YEAR + HYDRO(YEAR) + SEX)	8	227.4	10.5	-

Table 4.2. Results of mixed model analysis testing the factors related to turtle activity in 2008 and 2009. Consistent with model results obtained using AIC_c, interval of the day (INT), YEAR, HYDRO(YEAR), and an interaction between INT and YEAR were significant (α=0.05). SEX did not influence activity.

Source	*df*	*F*	*P-value*
INT	2,152	60.76	<.0001
YEAR	1,152	13.74	0.0003
HYDRO(YEAR)	1,152	5.72	0.018
INT x YEAR	2,152	6.48	0.002

Table 4.3. Summary of turtle activities (n=34) calculated from raw data and from back-calculating activity from the least squares mean estimates of natural log transformed activity used in linear mixed modeling.

		----------------------Turtle activity (m/h)-------------------			
		Raw Data		LS means (back-calculated)	
Effect	Descriptor	Mean	SE	Median*	95% CL (lower, upper)
Interval of the day (INT)	AM-PM	2.08	0.279	1.42	1.137, 1.733
	PM	1.60	0.181	1.30	1.035, 1.603
	PM-AM	0.29	0.031	0.25	0.107, 0.415
YEAR	2008	1.53	0.183	1.11	0.881, 1.362
	2009	0.98	0.115	0.73	0.533, 0.951
HYDRO (YEAR)	Dry (2008)	1.42	0.287	0.95	0.707, 1.221
	Wet (2008)	1.64	0.229	1.28	1.001, 1.603
	Wet (2009)	0.98	0.115	0.73	0.533, 0.951
INT x YEAR	AM-PM x 2008	2.69	0.413	2.05	1.634, 2.534
	PM x 2008	1.58	0.250	1.31	0.992, 1.673
	PM-AM x 2008	0.32	0.044	0.33	0.149, 0.541
	AM-PM x 2009	1.08	0.128	0.91	0.615, 1.269
	PM x 2009	1.63	0.249	1.30	0.937, 1.721
	PM-AM x 2009	0.24	0.041	0.18	-0.007, 0.395

***Values back-calculated from natural log transformed means equate to the untransformed median.**

Table 4.4. Turtle linear range (n=53) descriptive statistics by sex on each of six study wetlands for all turtles with at least 10 total locations. Linear range was defined as the greatest possible straight-line distance between any two locations recorded for each turtle. Two-way ANOVA (Type III sum of squares) testing the dependence of linear range (natural log transformed to improve assumption of normality of residuals) on site and sex showed that both site ($F_{5,46}$=5.18, P=0.001) and sex ($F_{1,46}$=2.95, P=0.098) were significant factors explaining linear range.

				---------Linear range (m)---------			
Wetland	VDGIF site #	Wetland Size (ha)	Turtles (n)	Mean	SD	Min	Max
1	1	0.48	4 F	303	253	82	543
			7 M	86	46	36	157
2	3	0.58	3 F	266	220	82	510
			1 M	241	-	-	-
3	28	1.27	6 F	337	332	113	965
			2 M	97	0.7	96	97
4	18, 2	0.50	9 F	290	265	41	911
			4 M	172	71	66	221
5*	19	0.44	5 F	69	31	31	101
			7 M	53	22	22	90
6	84	0.27	2 F	215	168	96	333
			3 M	416	121	349	545
Total	-	-	29 F	256	244	31	965
			24 M	139	128	22	545
Overall	-	-†	53	203	207	22	965

***Turtle ranges in Wetland 5 were significantly different and smaller than in other five wetlands. (Tukey post hoc test controlling for experiment wide Type 1 error, α=0.05).**
† Median wetland size = 0.49 ha and mean wetland size = 0.59 ha.

Table 4.5. Linear ranges (±SE) of the 14 bog turtles (seven male, seven female) that had at least 10 locations in both 2008 and 2009. Mean linear ranges by year and sex as well as overall means are provided. Linear range was defined as the greatest possible straight-line distance between any two locations recorded for each turtle. Two-way ANOVA was used to test the dependence of linear range (natural log transformed to improve assumption of normality of residuals) on year and sex. Results indicated that linear range for both sexes was greater in 2008 than 2009 ($F_{1,24}$=25.23, P<0.001), but not dependent on sex ($F_{1,24}$=0.62, P=0.439). An interaction between year and sex was evident ($F_{1,24}$=9.55, P=0.005) because female turtles had larger linear ranges than males during the drought year of 2008, but smaller linear ranges than males during 2009 when normal rainfall was measured.

		Mean linear range (±SE) (m)	
	N	2008	2009
Males	7	192 (±43.0)	130 (±39.0)
Females	7	509 (±118.0)	60 (±11.3)
Both sexes	14	350 (±74.7)	95 (±21.8)

Table 4.6. Summary of large turtle movements observed from radio telemetry locations in 2008 and 2009. Large moves, defined as any movement ≥ 80 m that took place within a seven-day period, were more likely to occur near streams (within 80 meters of a USGS 7.5' quadrangle map-identified stream) than away from a stream. Paths of large movements frequently crossed areas of non-wetland, with wetland areas defined by the three criteria method (Wetland Training Institute, Inc. 1995).

				Number of turtle movements		
Year	Sex	n	Telemetry events	≥ 80 m	Near stream	Crossing non-wetland
2008	F	24	701	31	29/31	18/31
	M	21	533	10	10/10	1/10
Total 2008	-	45	1234	41	39/41	19/41
2009	F	13	289	1	1/1	1/1
	M	13	321	4	4/4	1/4
Total 2009		26	610	5	5/5	2/5
Overall		71	1844	46	44/46 (96%)	21/46 (46%)

Table 4.7. Median and mean number of locations, linear range, and home range area for each of 53 bog turtles included in study. Linear range was defined as the greatest possible straight-line distance between any two locations recorded for each turtle. The 100% and 95% minimum convex polygon (MCP) home range areas were calculated to enable comparison with earlier bog turtle studies. Combined means (±SE) are provided at the bottom of the table.

		Number of Locations			Linear Range (m)			100% MCP (ha)			95% MCP (ha)		
	n	Mean	Med	Range	Mean	Med	Range	Mean	Med	Range	Mean	Med	Range
Males	24	21.9	17	10–46	139	93	22–545	0.50	0.17	0.01–4.9	0.40	0.10	0.01–4.7
Females	29	24.6	23	10–50	256	174	31–965	1.24	0.44	0.02–7.8	0.73	0.24	0.02–3.3
Combined	53	23.4 (±1.6)	18	10–50	203 (±28)	113	22–965	0.91 (±0.22)	0.29	0.01–7.8	0.58 (±0.13)	0.18	0.01–4.7

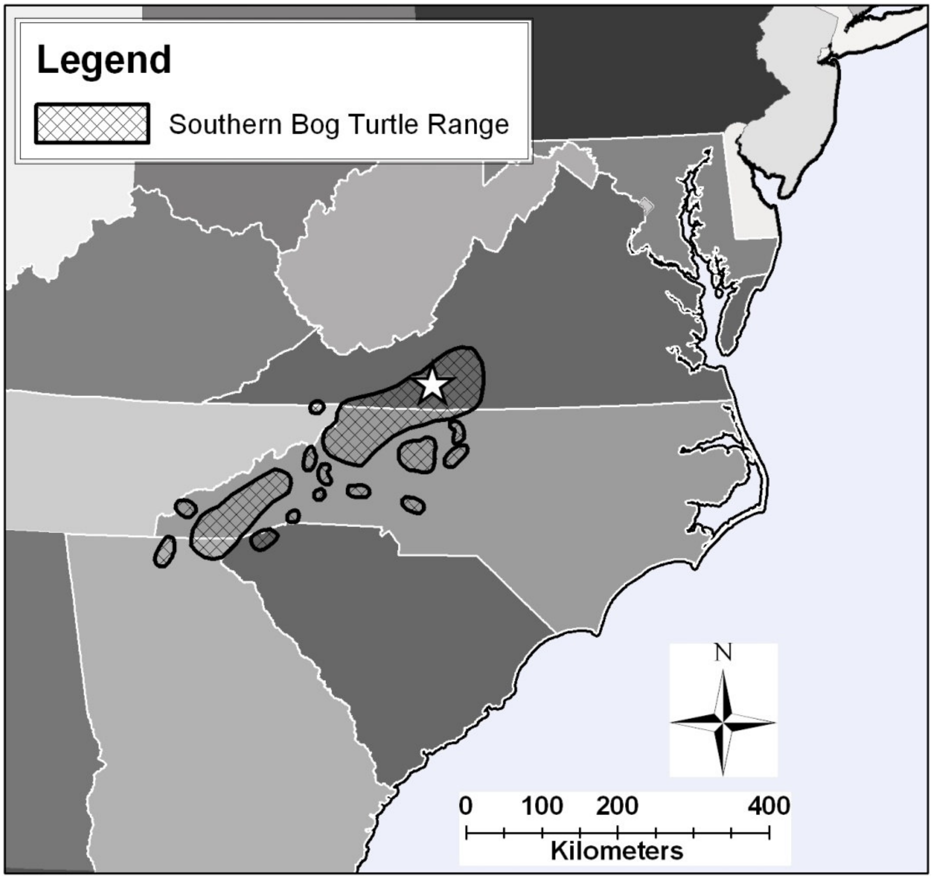

Figure 4.1. Study location in the Blue Ridge Physiographic Province of Southwestern Virginia. Shown is the southern range of the bog turtle (Natureserve 2009).

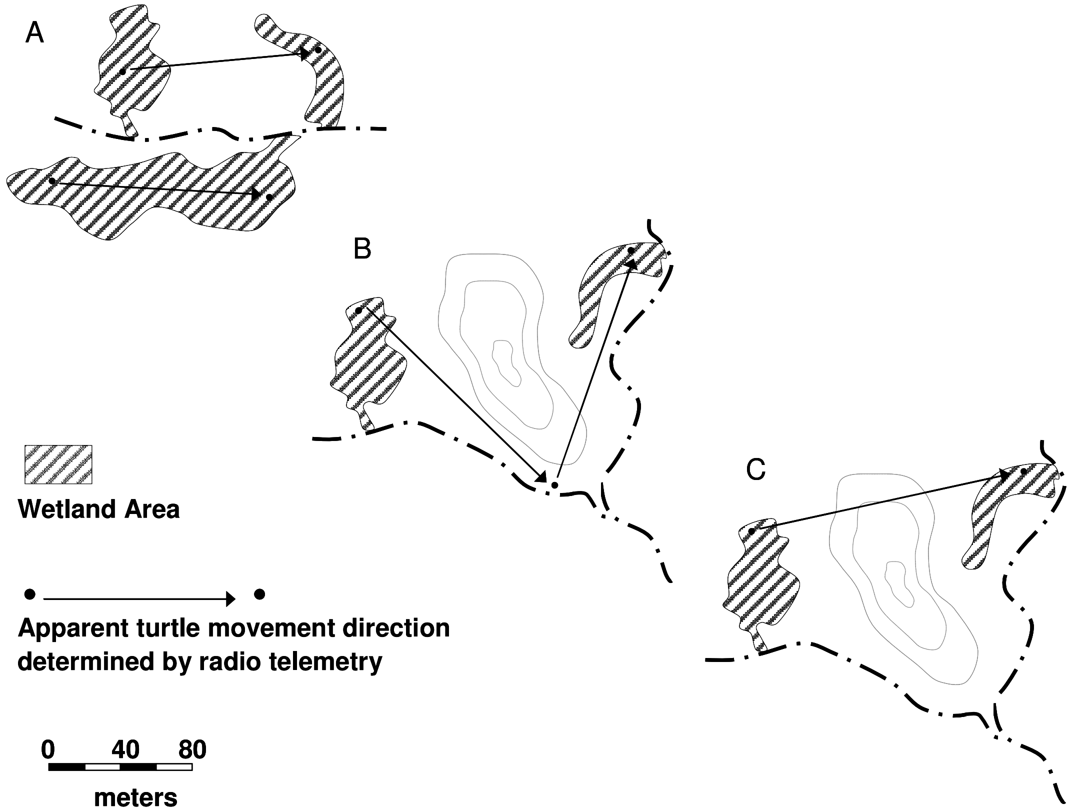

Figure 4.2. Hypothetical scenarios of bog turtle movement paths across the landscape. Scenarios A and B are "near-stream" movements where straight line connections between two or more telemetry locations remain within 80 m of a USGS 7.5' identified stream. "Near-stream" movements may pass through non-wetland areas. Scenario C is not a "near-stream" movement. In this study, all observed turtle movements over 80 m needed to be completed within a seven-day period to reduce the chance of misclassifying the pathway.

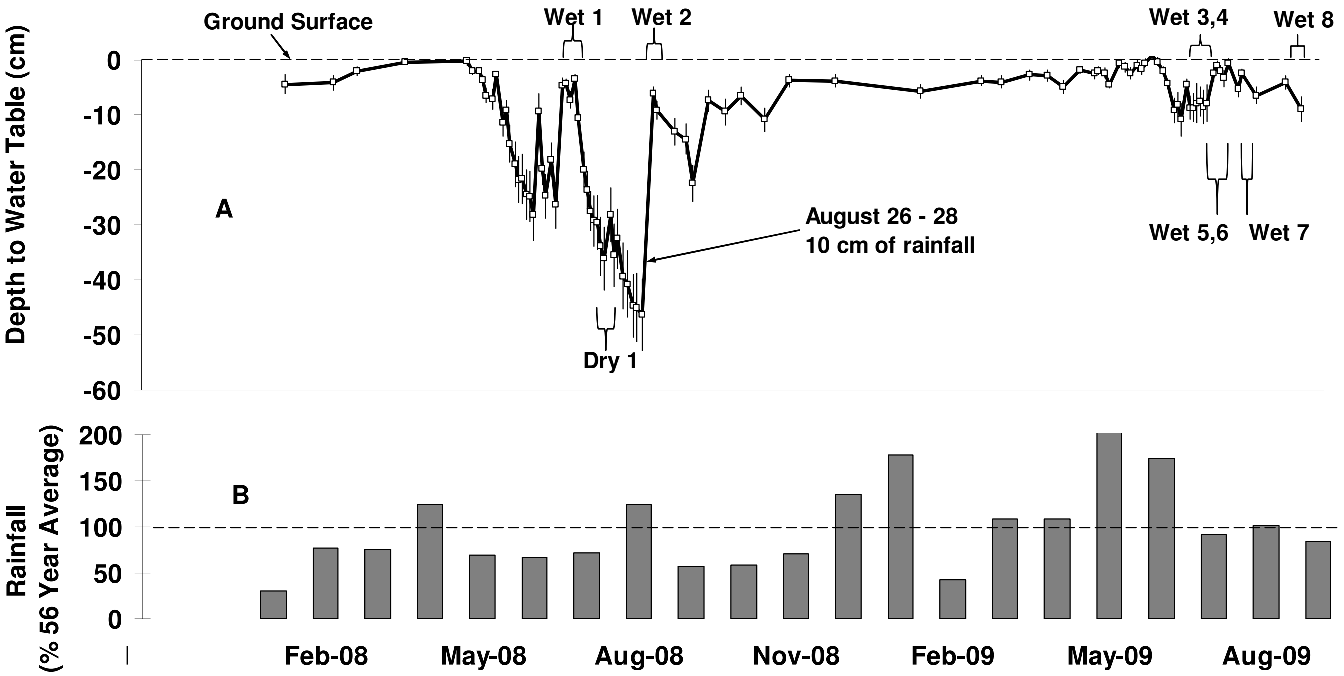

Figure 4.3. (A) Average depth to the water table for the six study wetlands from January 2008 through September 2009. (B) Monthly precipitation during the study relative to the long-term average. Depth to the water table was used to define hydrologic conditions as either wet or dry in the activity study. The activity study was broken into three sampling periods during the summer of 2008 and six sampling periods during the summer of 2009. Dry hydrologic conditions occurred if the water table was lower than -30.5 cm (depth datum negative from the surface), otherwise conditions during the sampling period were wet.

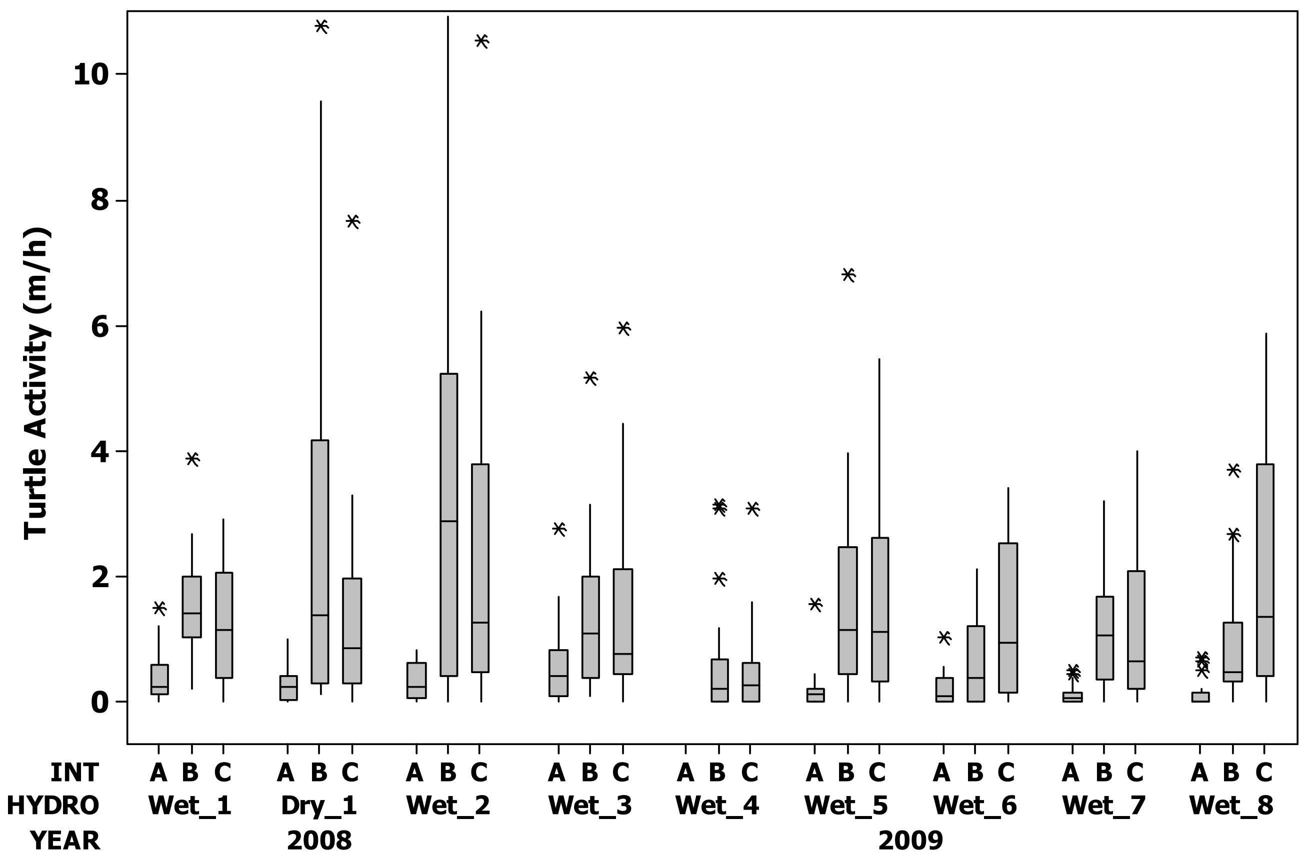

Figure 4.4. Box and whisker plot of average activity (m/h) for adult bog turtles in 2008 (n=20) and 2009 (n=24). Hydrology during sampling periods were defined by the depth to water table, while the interval of the day (INT) was the time from 18:30 to 09:30 (shown as "A", PM-AM in text), 09:30 to 14:00 ("B", AM-PM in text), or 14:00 to 18:30 ("C", PM in text). Note the increased activity during the second wet (Wet_2) sampling period in 2008 following a 10 cm rain event. Observations of 17.2 m/h (Wet_2), 13.5 m/h (Wet_3), and 19.5 m/h (Wet_6) not shown on plot to improve scale on y-axis.

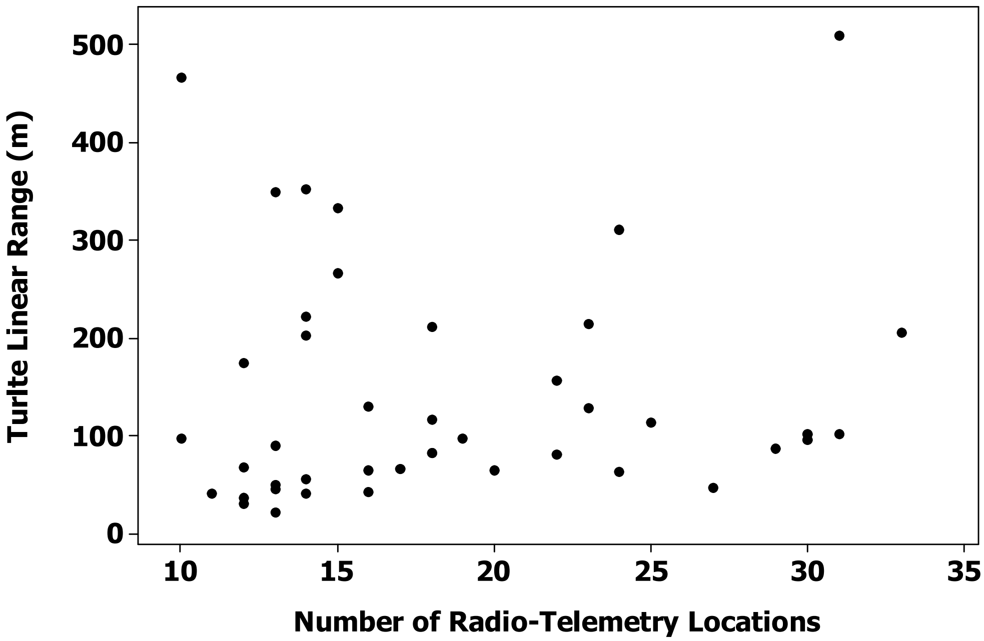

Figure 4.5. Scatter plot of linear range vs. number of radio telemetry locations recorded for turtles (n=43). A statistical test with the hypothesis of non-zero slope indicated that linear range (natural log transformed to improve assumption of normality of residuals) was not dependent on the number of radio locations ($F_{1,41}$=1.40, *P*=0.244). Consequently, I was able to include linear ranges from turtles with as few as 10 locations in linear range analyses.

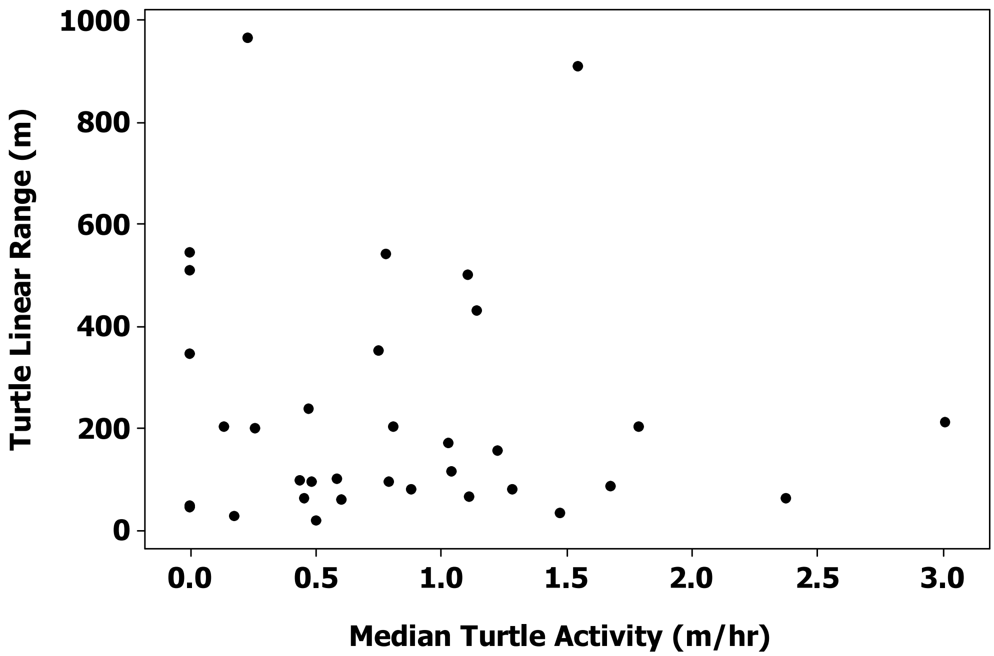

Figure 4.6. Scatter plot of bog turtle linear range versus median turtle activity recorded for 34 individual turtles (n=18 female, n=16 male) over one or both years of the activity study. Linear range was the greatest straight-line distance between any two turtle locations. Activity was the distance moved by a turtle over an hour averaged across all sampling periods. A test of regression slope with the null hypothesis that the slope=0 could not be rejected using natural log transformed (to improve assumption of normality of residuals) range data ($F_{1,32}$=0.00, P=0.952).

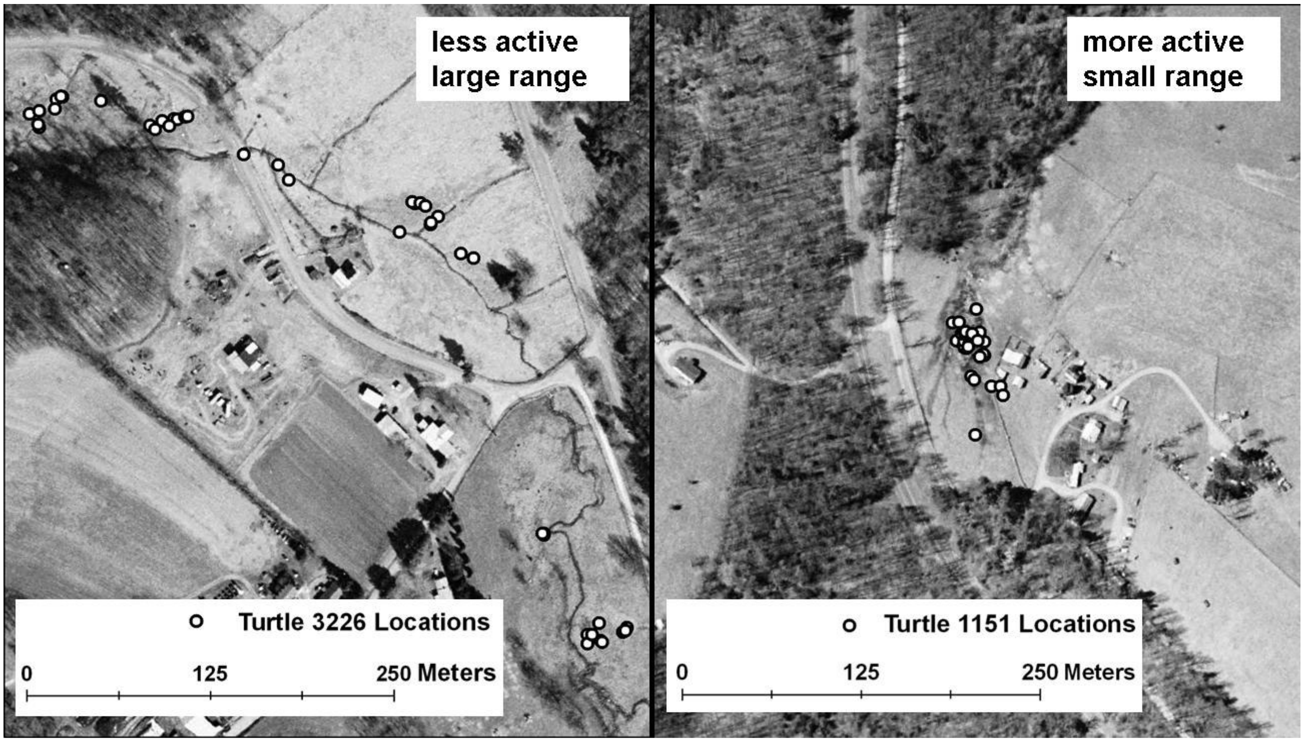

Figure 4.7. Point locations recorded for two bog turtles overlaid on identically-scaled aerial photography of two different wetlands in Southwestern Virginia. Turtle 3226 (male) had a 545 m linear range and a mean and median activity of 1.3 m/h and 0 m/h, respectively. Turtle 1151 (female) had an 87 m linear range and a mean and median activity of 2.2 m/h and 1.7 m/h, respectively. Turtle 3226 was observed moving directly along the bottom of a USGS 7.5' quadrangle map-identified 1st order stream, through road culverts, and hibernated in different locations separated by 300 m during two different winters.

Chapter 5: Using readily available GIS data to model bog turtle (*Glyptemys muhlenbergii*) habitat distribution with field validation

ABSTRACT

Field surveys conducted to detect the presence of the bog turtle (*Glyptemys muhlenbergii*) are expensive and time-consuming, and management decisions are difficult considering the uncertainty associated with distinguishing between true negative and false negative outcomes. Using commonly available GIS data to model the landscape factors associated with occupied bog turtle wetlands may improve our survey success in Southwestern Virginia, where only a fraction of occupied wetlands have been identified. In an approximate 1410 km^2 area, I compared hydric soil, National Wetland Indicator (NWI) wetlands, land cover, topographic wetness index inverse, and stream order data collected on bog turtle occupied wetlands (n=50) to the same variables collected on apparently unoccupied (previously field surveyed) wetlands (n=48) or random areas (n=74) generated along stream networks. Logistic regression modeling with stepwise variable selection determined that the topographic wetness index inverse, percentage of low vegetation, and presence of 3rd order streams were successful at discriminating occupied areas from random areas (percent concordance 82.5%), while all variables were ineffective at differentiating occupied and apparently unoccupied areas (percent concordance 61.3%). I used significant regression coefficients to create a resource selection function (RSF) layer displaying the relative probability of high quality bog turtle habitat over the landscape. The accuracy and efficacy of the predictive RSF layer was tested by determining RSF scores on an independent set of bog turtle field survey data. Occupied wetlands (n=14) identified in the independent field surveys had significantly higher RSF values than wetlands (n=77) where bog turtles were not detected (MW=2301, P=0.002). A confusion matrix and associated receiver operating characteristics (ROC) curve were used to investigate the source of prediction error. This model has the potential to quickly rule out large portions of the landscape as potential bog turtle habitat in the study area, allowing biologists to allocate survey effort more efficiently.

***Key Words*:** Virginia, NWI, SSURGO, NLCD, topographic wetness index, stream order, hydric soil, landscape, logistic regression, fen

INTRODUCTION

The core range of the bog turtle (*Glyptemys muhlenbergii*) in the Southeastern United States extends along the Blue Ridge of Virginia and North Carolina. Throughout this range, the proportion of wetlands occupied by bog turtles is low, and occupied wetlands are separated by well-drained agricultural fields, areas of dense and mature forests, moderate to steep slopes, and wetlands that are not occupied by bog turtles. Protocols for bog turtle surveys require that considerable person-hours be spent in the field over multiple events that coincide with the bog turtle activity season (Klemens 2001). Time-consuming bog turtle surveys still have the potential to result in a false negative outcome for turtle presence because bog turtles are small, have inconspicuous coloration, move away from humans, and spend much of their time submerged in mud (Somers and Mansfield-Jones 2008).

Considering the high costs of field-run bog turtle surveys, developing less field intensive methods to discriminate initially between potential bog turtle habitat and non-habitat is crucial. Habitat distribution and resource selection models for a wide range of wildlife species have been created with binary data of used and unused areas. These models are frequently evaluated using logistic regression and implemented with Geographic Information Systems (GIS) (Compton et al. 2002, O'Brien et al. 2005, White et al. 2005, Baskaran et al. 2006, Welch and Eversole 2006, Suzuki et al. 2008). Widely available landscape-level GIS data offer an opportunity to develop habitat distribution models without extensive field collection of habitat variables.

Soils, wetland, and land cover GIS data are available from the Soil Survey Geographic Database (SSURGO), the National Wetland Inventory (NWI), and the 2001 National Land Cover Database (NLCD). Hydrology data are available through the National Hydrography Dataset (NHD) or can be derived from Digital Elevation Model (DEM) data. These data sources can be used to create variables that may explain bog turtle habitat distribution, and offer consistent large-scale coverage while also being linked to biologically relevant aspects of the species. Although species distribution models may have prediction capacity without explicit biotic data, models using explanatory variables that can be ecologically justified are most useful because they can identify causal factors (Guthery et al. 2005, Soberon 2010).

Existing bog turtle habitat studies have recognized the importance of hydric soils (Pitts 1978, Carter et al. 1999), open canopy vegetation (Morrow et al. 2001, Tesauro and Ehrenfeld 2007), and wetland position within the landscape (Buhlmann et al. 1997). All known bog turtle wetlands have wetlands with hydric soils present due to the nearly continuous saturation in the upper soil (Pitts 1978). Many bog turtle wetlands occur in headwater areas or in narrow valleys adjacent to small streams (Buhlmann et al. 1997). Many of the wetland areas typical of the type used by bog turtles may be too small to be identified as a hydric soil in the SSURGO database or as a NWI polygon (Stolt and Baker 1995). The proportion of bog turtle wetlands intersecting hydric soil or NWI polygons is unknown.

Bog turtles require sunlight for basking and nesting (Ernst and Lovich 2009), and are frequently associated with wet meadows grazed by livestock (Klemens 2001). When wetlands occupied by bog turtles do not occur in wide-open pasture, vegetation types with frequent openings to allow the penetration of sunlight would be expected. The 2001 NLCD categorizes land cover into entirely open land uses such as grassland/herbaceous or pasture/hay, while also identifying land covers with a high potential for openings, such as scrub/shrub vegetation. Further, the NLCD identifies land uses that may be useful to exclude from possible bog turtle habitats, including completely forested areas and developed areas.

Topographic wetness indices derived from DEM data result in a continuous landscape surface that can identify areas of the landscape that have moist soils and elevated groundwater tables indicative of wetland areas (Beven and Kirkby 1979, Sorensen et al. 2006). In general, wetness indices use DEM data to identify higher potential for wet areas at locations having low slopes while simultaneously having a large accumulated drainage area. Several forms of the topographic wetness index have been described, and these forms vary in how slope and accumulated drainage area are calculated (Sorensen et al. 2006). Wet areas identified by the topographic wetness index have been found to correlate well with discretely identified wetland areas in New Brunswick, Canada (Murphy et al. 2007). As small, discrete wetland areas are often underestimated in the Blue Ridge of Virginia (Stolt and Baker 1995), the topographic wetness index may have the potential to identify wet areas occupied by bog turtles that are not already identified in existing wetland databases.

Stream order may be an important proxy for describing the type of landscape positions where bog turtle wetlands occur. Stream order is a function of upstream area and topography, and streams of a similar order can be expected to have similarities within a given geology and land use. Most bog turtle wetlands are located in headwater areas or adjacent to small streams (Buhlmann et al. 1997). Hydrology in bog turtle wetlands is primarily groundwater driven, and the hydrologic gradients moving through the wetlands are generally independent of and not parallel to stream flow (Chapter 1). Further, flooding is not frequent in bog turtle wetlands (Chapter 1). The geomorphology of the landscape may control the potential for groundwater seeps to occur in low slope positions. For example, valley geomorphology must be at a minimum wide enough to allow for the physical space required for a flowing wetland area that is outside of the hydrologic influence of the stream.

The classification of unused and available areas is important for developing and interpreting an accurate logistic regression model of resource use (Keating and Cherry 2004, Johnson et al. 2006, Baasch et al. 2010). When unused areas are incorrectly assigned, or when random locations are assigned to represent unused areas, absolute probability of use as estimated by logistic regression coefficients may not be valid (Keating and Cherry 2004). Although estimates of absolute probability of resource use may not be possible when random locations are used, it is possible to make inference on relative use of resource units to each other (Manley et al. 2002). When areas are considered available that are truly unused or have no potential for use, logistic model results may overestimate the ability of the model to discriminate a used location from a random one (Baasch et al. 2010). Explicitly defining availability and the unused resource units is an essential factor in developing logistic models. Thus, logistic resource selection models continue to be used and can provide robust results, even with randomly selected areas of non-use (Johnson et al. 2006). To maximize a model's predictive power, they should be tested for prediction errors, preferably with independent field data not used to train the model (Fielding and Bell 1997, Baskaran et al. 2006, Gude et al. 2009).

The purpose of this investigation was to use a set of GIS-derived variables in a logistic regression framework to model the landscape factors that discriminate between occupied bog turtle wetland habitats and unused areas (non-habitat). To find a balance between a useful, accurate model and the need to statistically discriminate between used and unused areas, I trained the model by comparing used and unused areas with three different scenarios. The scenarios included the following comparisons: 1) Bog turtle occupied areas against field surveyed areas that were apparently unoccupied; 2) Bog turtle occupied areas against random areas in the known range of the bog turtle species that were near streams and had $\leq 14\%$ slopes; and 3) Bog turtle occupied areas against random areas in the known range of the bog turtle species that were near streams on any slope class. Finally, I field tested the model's prediction ability using an independent data set.

METHODS

Study Area and Data Sets Used for Model Training

I conducted this investigation in a study area encompassing parts of five counties in the Southern Blue Ridge physiographic province of Virginia (Figure 5.1). The study area was approximately 93 km long and was 25 km wide at the widest point. Total area was approximately 1410 km^2. The landscape in the study area is a mosaic of farm fields, wood lots, roads, and some small developed areas. The National Park System's Blue Ridge Parkway passes through the eastern part of the study area.

I defined the perimeter of the study area using several factors. The primary factor defining the study area was the known locations of occupied (n=50) and unoccupied / unknown bog turtle wetlands (n=48) in Virginia. These locations were known before starting the study by using a wildlife database compiled and maintained by the Virginia Department of Game and Inland Fisheries (VDGIF). To ensure accuracy before modeling began, the point locations of database wetlands were confirmed by agency staff by aerial photography or by physically travelling to the wetland to ensure that the point locations were centered on the wetlands. Another factor limiting the study area was the availability of GIS elevation data with consistent resolution. The final defining factor was the desire to extend the study area into a portion of Carroll County, VA in advance of a highway project. This area had no known bog turtle occupied wetlands before this study began, but contained numerous wetlands that appeared by visual inspection to be potential high quality habitat.

I set the size and shape of the experimental unit for this analysis as a 1-ha round plot (radius=56.4 m). I based the dimensions upon personal experience and existing literature describing typical bog turtle wetland sizes in Virginia (Buhlmann et al. 1997). I subsequently use the term "plot" to indicate a 1-ha wetland or any other landscape location used for modeling. Plot terminology is used because although some locations in the development of this model were confirmed wetlands meeting established criteria (Wetland Training Institute, Inc. 1995), other locations were randomly generated from within the study area and may not actually meet wetland criteria.

GIS Data Acquisition and Preparing Explanatory Variables

I acquired five layers of spatial data for the study area and overlaid them in the ArcMap 9.2 application of ArcGIS (ESRI Redlands, CA, USA). These data sources included SSURGO data (Soil Survey Staff 2009) for the five counties included in the study area, NWI wetland polygons (Cowardin et al. 1979, United States Fish and Wildlife Service 2009), seamless 2001 30 x 30 m NLCD data (Homer et al. 2004), 10 x 10 m DEM data (United States Geological Survey 2008), and high resolution NHD (United States Geological Survey 2009). The NWI and DEM data were downloaded as 7.5 minute quadrangles and subsequently merged or joined by the mosaic command in Arc Toolbox. To prepare the data for use as explanatory variables, each layer was converted to raster data with a consistent 10 m resolution using the methods described below.

There were three different hydric soil series present on bog turtle occupied wetlands (Chapter 2), but not all of these hydric soil series were used in each county soil survey covering the study area. Therefore, certain soil series had an "undefined" availability through parts of the study area, so they did not offer a useful categorical variable for model building. For this reason, I simplified soil information into hydric and non-hydric categories rather than creating the model with existing categorical soil series. Soil map unit polygons from all counties were merged, converted to 10 m x 10 m raster, and classified as a "1" for hydric and "0" as non-hydric. Hydric inclusion soils were considered as non-hydric because, by definition, inclusions are small in size, dispersed spatially throughout a map unit, and only comprise ≤ 10% of the total map unit area.

Wetland data in the NWI were converted to 10 m x 10 m raster and classified as "1" for present and "0" for absent. The 14 categories of land cover type depicted in the 30 m resolution 2001 NCLD raster data set were converted to a binary system, with low vegetation (pasture/hay, crops, grassland, scrub shrub) and wetland coverage (woody wetlands and emergent wetlands) classified as "1" and other areas (developed areas, barren land and mature forests types) classified as "0." I resampled the 30 x 30 m NLCD to achieve 10 x 10 m resolution. This resampling procedure did not add any additional information to the NLCD data, as it only split each original 900 m^2 cell into 9, 100 m^2 cells with the same cover type. I modeled pasture/hay and crops together because these land cover types are all typical of farm areas in the region. Farm fields in the study area are typically small and dissected by numerous drainages because of the hilly topography. Further, wetland areas are frequently too small to be identified specifically as wetlands (Stolt and Baker 1995). Therefore, it is feasible that wetland areas could be present in low vegetation cropped areas identified in the 2001 NLCD.

The topographic wetness index was created from 10 x 10 m DEM data. A typical way to calculate the topographic wetness index of a given raster is to take the natural log of the ratio of the upslope drainage area to the local slope (Sorenson et al. 2006). This method can result in a mathematical inconvenience with undefined raster calculations caused by numerous zero values in the denominator of the ratio. To compensate for this, I used the free hydrological modeling extension TauDEM 3.1 (David Tarboton, Utah State University, USA) to calculate the topographic wetness index inverse. The topographic wetness index inverse uses the ratio of the local slope to the upslope drainage area to model the potential for an area to be wet. The topographic wetness index inverse has values that are greater than or equal to zero, with smaller values indicating wetter areas.

I used the DEM data to develop a stream network within the study area, and then determined the Strahler stream order for any drainages flowing through sample plots. Strahler stream order is a categorical way of defining a stream size, with 1st order streams occurring at the headwater positions of a drainage and higher order stream occurring downstream. Before I worked with DEM data to create a stream network, I created a depressionless DEM. Digital Elevation Models often have natural low spots (such as a sinkhole) that cause problems with any subsequent surface flow algorithms developed from the DEM data. I repaired any depressions in the DEM using the “fill” function in the “hydrologic analysis” tool set in ArcMap. The practice of filling depressions is standard for any surface hydrology analysis in GIS. For example, creating a depressionless DEM is one of the intermediate processes that occur when finding the topographic wetness index inverse using the TauDEM 3.1 modeling extension.

To create the stream network from the depressionless DEM, I used ArcMap’s “hydrologic analysis” tools to determine flow direction and create a continuous flow accumulation surface throughout the study area. To set a threshold for flow accumulation, I used a 14-ha threshold value because it resulted in a stream network that approximated the NHD stream network with regard to the upstream origin of streams. The NHD stream network corresponds exactly to the stream networks depicted on USGS 7.5’ quadrangle maps. Setting a 14-ha threshold for flow accumulation resulted in a binary classification where raster cells with at least 14 ha of upstream area receive a value of “1” and all others receive a “0.” After reclassification, I used ArcMap's "stream order" function to determine the Strahler stream order for all streams that were 4^{th} order or smaller.

Given the widespread availability of USGS 7.5' quadrangle maps, there would have been practical benefits to use the NHD identified streams (same as USGS streams) rather than DEM-derived streams to determine stream order; however, I experienced considerable setbacks in finding an efficient and automated way to determine stream order from the vector stream data in the NHD. Nonetheless, the DEM-derived stream network procedure was considered acceptable because it is a consistent and easily reproducible method to create a stream network.

Once I processed the data layers, they were available for data extraction using the 1-ha plot experimental unit. For hydric soil and NWI data, the experimental unit could only result in a binary outcome (not to be confused with the raster unit, which was also binary). In other words, only one raster cell in the 1-ha plot with a value of "1" was needed to result in a presence outcome at the plot scale. For vegetation data originating from the NLCD 2001 cover, the experimental unit could result in any number between 0 and 1. This value was the simple average of the 100 raster cells in the 1-ha plot. Topographic wetness index inverse in the experimental unit was the average of the 100 raster cells in the 1-ha plot. Stream order values at the experimental unit scale took the value of the highest order stream present, represented by at least one pixel within the 1-ha plot (Table 5.1).

Modeling Process and Statistics

To develop a model with the best predictive ability, I considered three modeling scenarios (Table 5.2). Each modeling scenario used the set of occupied bog turtle wetland plots (n=50), but used one of three different sets of 1-ha plots for the unused plots. Modeling Scenario 1 compared occupied wetland plots to the unoccupied / unknown wetland plots (n=48) identified in the VDGIF wildlife database. Unoccupied / unknown wetland plots are those areas that appeared to be suitable bog turtle habitat to some biologists, but were surveyed at least once with no bog turtle detections. Scenarios 2 and 3 compared occupied wetland plots to randomly generated 1-ha plots. Sample size of random plots was 74 for both Scenarios 2 and 3. Comparison of occupied to random areas is frequently used in logistic regression modeling (Compton et al. 2002, O'Brien et al. 2005, White et al. 2005, Baskaran et al. 2006). Although there is a small probability that random areas are actually occupied, this strategy has little effect on the results on the model outcome, as long as predictions using the generated regression coefficients are not interpreted as absolute occupancy probabilities (Manly et al. 2002, Keating and Cherry 2004, Johnson et al. 2006). However, it is important to carefully define the available areas where random points may occur to develop an accurate model (Compton et al. 2002, Baasch et al. 2010)

I limited random plot generation (availability) in modeling Scenarios 2 and 3 to areas within 56.4 meters of NHD-identified streams. This distance was equal to the radius of a 1-ha plot. I applied this constraint to random plot generation because I found in a preliminary analysis that the center points of 88% of the 50 occupied wetlands plots were within 56.4 m to NHD streams, indicating that bog turtle wetlands are usually near flowing drainages. Random plots in Scenario 2 were further constrained by slopes ≤ 14%, which prevented random plots on steep and often rocky areas. Random plots in Scenario 3 were near streams but had no slope constraints. I applied these constraints in order to prevent random site generation on areas of the study area that had little potential of supporting bog turtles, effectively limiting availability of unused areas (such as ridge tops or steep slopes). Although this strategy had the potential to reduce the statistical effect size between occupied and random plots, it enabled me to improve the probability of finding real and meaningful habitat differences.

I used ArcMap zonal statistics to extract independent variable raster data from within all 1-ha plots in the occupied, unoccupied / unknown, and randomly generated data sets. Zonal statistics are used when summaries of raster data are desired from within vector data polygons, in this case 1-ha plots. I multiplied all topographic wetness index inverse values by 10,000 to increase their values to approximately 1. This scaling helped me to interpret the odds ratio in the model output. I used PROC LOGISTIC (SAS Institute, Cary, NC) to model the extracted plot data in each scenario. I tested two multi-variable model sets for each scenario. The first model set included the global model with all independent variables and an intercept (nine parameters, no interactions). The second model set included the best model as determined using stepwise selection with a variable entry $\alpha=0.2$ and a variable retaining $\alpha=0.1$. I used percent concordance, which is analogous to the area under the curve (AUC) of the Receiver Operating Characteristic curve (ROC), to diagnose the model fit of each scenario. I also used Akaike's Information Criterion for small sample sizes (AIC*c*) to compare the global model with the stepwise-selected model within each unique scenario. Using this diagnostic, I identified that scenario which was most useful for further analysis and for creating a predictive surface layer for bog turtle habitat.

I used the logistic regression results from the most supported modeling scenario for further analyses, and discontinued analysis of the inferior two scenarios. I used basic descriptive statistics to determine average variable values and determined the regression coefficients for all variables retained in the stepwise selected top model. Regression coefficients were used to create a continuous predictive surface, subsequently referred to as the resource selection function layer, or RSF layer (Manly et al. 2002). It would not have been accurate to simply create the RSF by applying the regression coefficients to each 10 x 10 m pixel of the independent variable layers because the original logistic regression to find the coefficients was completed using mean raster values of 1-ha plots (100 pixels). To account for this matter of scale, I needed to complete an intermediate step by using neighborhood focal statistics on the significant independent variable raster layers. Neighborhood focal statistics are used on raster data when the desire is to create a new raster layer where new raster values are based on calculations with that location's (the focal point's) nearest neighbors. Each raster cell in the new layer was calculated by averaging raster values in the surrounding 100 cell "neighborhood" of the old layer. This calculation was completed in every single raster cell in the study area, resulting in a new 10 x 10 m raster layer for each significant independent variable. Each cell in this layer was therefore representative of the 1-ha area surrounding it. I then used the raster calculator to create a final predictive resource selection function layer using the following:

$$\text{Resource selection function at a given raster cell} = \frac{e^{\text{logit}}}{1 + e^{\text{logit}}} \qquad \text{(eq. 1)}$$

where:

$$\text{logit} = B_0 + B_1 X_1 + B_2 X_2 + \ldots + B_k X_k \qquad \text{(eq. 2)}$$

where:

B_k = the logistic regression coeffiecent for the k$^{\text{th}}$ independent variable

X_k = the value of the k$^{\text{th}}$ independent variable at a given raster cell

Field Testing the Model

I tested the prediction ability of the RSF layer by evaluating how well it differentiated between an independent set of bog turtle occupied and unoccupied / unknown wetlands. In the summer of 2009, the VDGIF initiated wetland surveys at 77 wetlands within the study area in Carroll County where bog turtle status was unknown. The wetland sites selected for bog turtle field surveys were selected from brief visual roadside surveys. These roadside surveys identified candidate wetlands that looked as if they would provide high quality habitat based on their prevalent herbaceous vegetation and abundant surface saturation without a great deal of inundation.

Survey activities consisted of approximately 1.5 total person hours of hand searching by probing with a wooden pole and peering through vegetation. If turtles were not captured using the probing technique, permission was asked to set traps overnight. Traps were set on 19 different wetlands for a total of 58,314 trap-hours. Other data recorded during the survey were related to habitat assessment scoring criteria previously developed by the VDGIF. This assessment, termed the Site Quality Analysis (SQA), consisted of 13 questions, each with a ranked scoring system (Carter 1998) (Table 5.3). The scoring system was based upon best professional judgment. The SQA questionnaire was completed by VDGIF personnel as part of the survey process for every visited wetland. An overall wetland score was calculated by summing the scores from all of the questions.

Locations of each of the 77 field-tested wetlands (grouped into occupied and unoccupied / unknown plots) were overlaid on the predictive RSF layer to begin the last part of the model validation process. Once again, I created a 56.4 m radius buffer around the point locations and used zonal statistics to calculate the average RSF value within the 1-ha plot. For additional comparisons useful for assessing the utility of the model, I also extracted the average RSF for the original random plots (n=74) used to create the predictive model. Finally, I generated an entirely new set (n=320) of random 1-ha plots from anywhere within the study area (not constrained to areas near streams) and extracted the RSF values. The average RSF values for each data set were ranked and plotted in a cumulative probability plot. I created an ROC curve using the field-tested occupied and unoccupied / unknown wetlands. To create the curve, I used an error matrix and calculated the true positive rate and the false positive rate at incremental threshold levels of the RSF (Fielding and Bell 1997). I calculated the AUC of the ROC plot manually by dividing the curve into discrete trapezoids and summing the areas.

RESULTS

Selection of Best Model Scenario

Percent concordance indicated that model Scenario 3 provided the best discrimination between occupied and unused plots (Table 5.2), while Scenarios 1 and 2 were less effective. Only vegetation was a significant variable in model Scenario 1 comparing bog turtle occupied plots to unoccupied / unknown plots. The top (stepwise selected) and global model in Scenario 1 had a concordance of 61.3% and 71.5%, respectively, indicating that the stepwise selected model was not much better than chance at discriminating between groups of plots. Scenario 2 was not much better than Scenario 1 at discriminating between occupied and random plots near streams of slopes ≤ 14%. In this scenario, the variables NWI wetland and 2nd and 3rd order streams were selected in the top model. The stepwise selected model had a concordance of 62.1%. The over-parametized global model improved the concordance to 75.8%. Model Scenario 3 (comparing occupied plots and random plots near streams) contained topographic wetness index inverse, vegetation, and 3rd order streams as significant variables, and resulted in a concordance of 82.5%. Concordance above 80% is considered to have an excellent ability to discriminate the data (Hosmer and Lemeshow 2000). The concordance of the top stepwise selected model was nearly as high as that of the global model (83.6%). The AIC_c score for the top model was smaller (130.91) than the global AIC_c (138.38). These diagnostics indicated that the stepwise selected model in Scenario 3 was the simplest model able to discriminate between used and random points in the data.

Variable Selection and Creation of the RSF

Stepwise logistic regression using Scenario 3 resulted in a top model with three significant variables: topographic wetness index inverse, vegetation, and 3rd order streams. With the intercept, the top model contained 4 parameters (Table 5.4). The Hosmer and Lemeshow test of the logistic regression on the top model was not significant (χ^2=5.119, *df*=8, *P*=0.7448) (Hosmer and Lemeshow 2000). A finding of non-significance on the test indicated that the model adequately fit the data. Plots with bog turtles had smaller values of the topographic wetness index inverse (negative regression coefficient), indicating areas with low slopes and large upstream drainage areas. Plots with bog turtles had a greater proportion of low vegetation (positive regression coefficient). Finally, plots with bog turtles were associated with 3rd order streams, resulting in a positive regression coefficient. The significant regression coefficients in the top model resulted in a predictive RSF layer that ranged from 0 to 0.69. The RSF did not range between 0 and 1, apparently because the negative intercept shifted the RSF curve. Despite the shifted logistic curve, the continuous RSF layer differentiated the landscape resource units and provided a measure of relative probability of finding high quality bog turtle habitat to test in the field (Figure 5.2).

I calculated average values of all the modeled independent variables, regardless of their level of significance or inclusion in the top model (Table 5.5). Vegetation / land use on occupied sites was 58.4% covered by low growing vegetation, pasture, or cropland as compared to 25.4% on random unoccupied / unknown plots. A 3rd order stream was present in 34% of the occupied plots compared to 18% of the random unoccupied / unknown plots.

Several variables differed in their average values grouped by occupancy status, yet did not show up in the top model. Fewer 1st and 4th order streams and more 2nd order streams were present on occupied plots than random unoccupied / unknown plots. Hydric soils were present on more than 50% of both occupancy groups, but were present on a higher proportion of occupied plots. Twenty- eight (28) percent of occupied plots contained an NWI-identified wetland compared to only 7% of random unoccupied / unknown plots. The NWI wetland was close to remaining in the top model, and had a *P*-value = 0.16 before it was removed at the last step of the stepwise selection.

Field Testing the Model

Field surveys of 77 wetlands in the summer of 2009 resulted in the identification of 14 previously unknown bog turtle occupied wetlands and 63 unoccupied / unknown wetlands. All 63 wetlands were surveyed without detecting turtles, but because detection rates from a single visit must be less than 100%, I classify wetlands as unoccupied / unknown. These wetlands were used to test the modeled RSF layer that was trained using the coefficients from the logistic regression model. Average and median RSF values within the 1-ha field validation plots were larger for the 14 occupied wetlands than they were for the 63 unoccupied / unknown wetlands

(Table 5.6). A non-parametric Mann-Whitney test showed this difference to be significant (median difference=0.064, *MW*=2301, *P*=0.002). Field-derived SQA values showed similar trends to model-derived RSF values, with SQA scores higher on occupied wetlands than on unoccupied / unknown wetlands (median difference=8.3, *MW*=2250, *P*=0.003). Although both the RSF and SQA values were significantly higher on occupied sites, a regression of RSF vs. SQA values did not show a positive correlation (Figure 5.3). A test of regression slope with a null hypothesis that the slope=0 could not be rejected using natural log transformed data (to improve the assumption of normality of residuals) ($F_{1,75}$, P=0.839, r=-0.024).

The ability of the GIS model to differentiate between occupied plots and unoccupied / unknown plots identified during the field validation was evident using a plot of cumulative percent probability vs. ranked RSF values (Figure 5.4). This cumulative probability plot indicates the cumulative number of 1-ha plots that have RSF values below a given threshold. As RSF values increase along the x-axis, the number of 1-ha plots that are less than or greater than the RSF value can be tabulated in order to determine which 1-ha plots are correctly (or incorrectly) classified. Occupied plots were also easily differentiated from the random plots near streams used in building model Scenario 3 as well as random plots generated anywhere (including areas not along streams) within the modeling study area.

An ROC plot of the true positive versus false positive rate of the field validation data indicated that the RSF layer was somewhat useful for discriminating between bog turtle occupied areas and unoccupied / unknown areas within the study area (Figure 5.5). The AUC=0.70, which indicated that there was 70% chance that the RSF was higher for any randomly selected occupied plot than for an unoccupied / random plot. It is important to point out that the field test and ROC diagnostics were completed for the field test data comparing actual wetland areas that looked like potential bog turtle habitats from road surveys, rather than for data consistent with those used to train the model that included occupied and random areas near streams that may not even occur in an actual wetland area. The source of the testing data also explains why the ROC plot from the field data had a smaller AUC (70%) than the % concordance (82.5%) achieved in the training data set. Greatest overall modeling classification accuracy was achieved when RSF cutoff thresholds were high. In other words, when RSF values were high, there were very few false positive classifications of bog turtle habitat. Lower RSF threshold values had lower overall accuracy because more plots were classified as occupied when they were truly unoccupied /

unknown; however, lower RSF threshold values also resulted in higher model sensitivity because they were more likely to correctly classify occupied plots.

DISCUSSION

Performance of Model Scenarios 1 and 2

I established in model Scenario 1 that it was difficult to differentiate known occupied wetland plots from previously searched unoccupied / unknown wetland plots. This result indicated that either: 1) the apparent statistical disparity between occupied and unoccupied / unknown plots is not great enough to be modeled with GIS variables, or; 2) the survey effort used to establish the *a priori* unoccupied criteria was not sufficient. Based on the effective performance of the GIS variables to discriminate between occupied and unoccupied wetlands in the field test, there is evidence that occupancy status was incorrectly assigned to the *a priori* unoccupied wetlands used in Scenario 1. Bog turtles are known to be difficult to detect in surveys (Klemens 2001, Somers and Mansfield-Jones 2008).

The inability of model Scenario 2 to identify occupied areas could only be attributed to a lack of consistent differences between the candidate data sets. The slope ≤14% constraint was intended to rule out a large portion of the study area as available at the onset of the modeling process, but also had the effect of randomly selecting areas that were very similar to known bog turtle occupied areas. Incidentally, many of the initial randomly selected 1-ha plots with the ≤14% slope constraint actually intersected with known bog turtle occupied areas and needed to be removed from the data set to maintain statistical independence. For this reason, and the poor concordance of the regression, Scenario 2 was not considered a good modeling option. Despite the poor performances of Scenarios 1 and 2, they were both useful for interpreting the relative prediction ability of model Scenario 3. The disparity between used and unused data in resource modeling is a function of the modeling area defined as available, and this disparity affects the apparent predictive success of the final model (Baasch et al. 2010). An iterative process to define available habitat such as the one used in this analysis may be effective in some habitat modeling situations because it results in better understanding of the potential for the explanatory variables to discriminate between used and unused areas.

Predictive Capacity of GIS Explanatory Variables

The percent cover of low vegetation as determined by the 2001 NCLD variable was a significant predictor of bog turtle presence in Scenario 3. On average, 58.4% of cover on occupied plots was the low vegetation type, compared to 25.4% on random plots with no slope constraint. The actual availability of the low vegetation type within the area created by a 56.4 m buffer on each side of all USGS 7.5' quadrangle mapped streams in the study area was 31%. These results indicate that the open canopy conditions observed in many bog turtle occupied wetlands are disproportionately high relative to their availability on the landscape. As this variable could be related to forest succession, these vegetation results would be useful to re-evaluate as land cover data sets are released in the future.

Occupied wetlands in Scenario 3 were likely to occur near streams (88% near streams), and when streams were present near occupied wetlands, they tended to be in valley landscape positions with 3rd order streams. Although not significant, 2nd order streams were represented more in the occupied data set, while 1st and 4th order streams were underrepresented in the occupied data set. To further demonstrate the disproportionate occurrence of the streams within the 50 occupied plots, I compared them to the total availability of streams by order in the study area (Table 5.7). Stream availability was calculated by the number of pixels in the study area occupied by streams of orders 1 through 4. A goodness of fit test showed that the distribution of stream orders identified near occupied plots was disproportionate to the availability of streams throughout the study area landscape (χ^2=27.7, *df*=3, *P*<0.001). To standardize these stream order findings and make them more relevant for management, I compared stream orders determined from the DEM-derived stream network to the stream orders determined from the USGS 7.5' quadrangle map. This comparison was made using the streams located within the 50 occupied plots (Table 5.7). Stream orders for the USGS mapped streams were determined manually. I also plotted the USGS-mapped stream order versus the DEM-derived stream order (Figure 5.6). From the plot it is easy to see that stream orders identified on the DEM-derived stream network were smaller than the orders for the same streams as depicted on a USGS 7.5' quadrangle map. A Spearman rank correlation coefficient of the two datasets was 0.752. It is important to account for this difference between datasets, as identifying the location of streams with a given order is dependent upon this information. Bog turtle occupied plots tended to occur in valley landscape positions with small to mid-sized streams. Although less frequent, bog turtle occupied wetlands also occurred within headwater positions where 1st order streams or no streams are identified on the USGS map. A qualitative field observation was that bog turtle wetlands often occurred at the junction of streams, probably because these areas were gently sloped with accumulated water.

The topographic wetness index inverse indicated that occupied areas were more likely to have moist soils and higher water tables than the random areas near streams. The topographic wetness index inverse effectively ruled out high habitat potential for ridge tops and steeply to moderately sloped areas, which are unlikely to support wetland hydrology. The importance of the topographic wetness index inverse to identify where wetlands may occur on the landscape should not be undervalued, particularly since the other variables capable of identifying parts of the landscape where wetlands occur, presence of hydric soils and NWI wetland, were not significant. The ability for the topographic wetness index inverse to predict high surface water tables was not specifically validated in this modeling exercise, yet I would expect to find this condition consistently in the areas with the lowest index values. Sorensen et al (2006) found that the local slope algorithm identical to the one used in TauDEM 3.1 performed well at identifying high groundwater tables as compared to alternative slope algorithms such as that suggested by Hjerdt et al. (2004). The algorithm used by Hjerdt et al. (2004) effectively calculates slope according to larger-scale landscape features, and has been useful for predicting soil and vegetation characteristics as opposed to local water table hydrology (Sorensen et al. 2006).

The statistical non-significance of the hydric soil and NWI wetland variables was an important outcome of this investigation, as personal communication with other bog turtle researchers led me to expect these variables to be useful predictors at the onset of this investigation. The presence of hydric soils was not capable of discriminating between occupied and unoccupied / unknown plots because both groups were likely to contain hydric soils. However, as 74% of bog turtle occupied plots intersected hydric soils, the absence of hydric soils may preclude bog turtle presence in some areas. It is important to note that the identification of hydric series boundaries differs by county, so managers should use discretion and consider whether their county of interest tends to overestimate or underestimate hydric map units. The NWI wetland variable had some power to discriminate between occupied and unoccupied / random plots, yet NWI polygons were not frequently identified in plots of either occupancy group. These results indicated that large false negative errors could result if NWI identified wetlands were used in future predictive models. Stolt and Baker (1995) used standard wetland delineation practices (Wetland Training Institute, Inc. 1995) to delineate wetlands in two 2.5' quadrangles located within the boundaries of the bog turtle study area and found that only 9.7% of the delineated wetlands were identified by NWI mapping. The authors noted that most of the unmapped wetlands occurred in woodlands, but also that many of the unmapped wetlands occurred at 0.2 to 0.6 ha seeps positioned in floodplains and at the heads of drainages. These landscape positions commonly support bog turtle habitats.

Balancing Model Classification Error

In modeling habitat, if too large of an area is classified as having a high potential for occupancy, the model is less useful because there will be a high false positive rate. The lack of differentiation between wetland plots in Scenarios 1 and 2 forced me to extract variable information from other areas within the study area, including potential non-wetland areas near streams, in order to have discriminatory power to identify bog turtle occupied areas. This spatial expansion of the model building data set improved discriminatory power and enabled the creation of a predictive RSF layer, but also had the statistical effect of increasing the areal proportion of the study area that was potentially bog turtle habitat (increasing false positive rate). Within the RSF layer constructed using modeling Scenario 3, the areal proportion of highly predicted habitat was also an important consideration. Using the raster calculator, I found that areas with an RSF threshold value of 0.3 or greater only comprised 3.3% of the study area. An RSF value of 0.25 and 0.2 comprised 7.9% and 15.9%, respectively. As a comparison of this land area, the total area within the 56.4 m buffer on NHD streams was approximately 17.7%. When I increase the threshold of the RSF value on the ROC curve, I decrease the areal extent of highly predicted area, decrease our false positive rate, and simultaneously decrease the true positive rate. At an RSF value of 0.25 the true positive rate was 50% (i.e. 50% of the occupied wetlands had RSF scores higher than 0.25), the false positive rate was 22%, with a total accuracy of 73%. Although the establishment of this RSF threshold is somewhat arbitrary, it greatly reduces the amount of area that needs to be searched, maintains an acceptable true positive rate, and limits false negatives.

The RSF over-estimated (resulted in false positives) the habitat potential on large streams (4th order and greater) that had large, flat floodplains. These areas tended to appear suitable in the topographic wetness index inverse due to their low slope and large upstream areas. These areas also had the low vegetation type typical of bog turtle habitats. If this model exercise were repeated, I would exclude these high order streams from the study area earlier in the modeling process. Although bog turtle wetlands must certainly become inundated with moving water during the largest floods, I did not observe flooding in the seepage areas of the occupied wetlands, even during the largest rains (Chapter 1). I expect that high order streams with large flood events could potentially disrupt turtle nesting, and the lower organic matter soils associated with large floodplains are not typical of occupied habitats (Chapter 2). Wetlands on large floodplains are likely to differ from many occupied wetlands because hydrology sources on floodplains are typically overbank flooding while hydrology on lower order streams are associated with groundwater sources (Brinson 1993).

A consistent qualitative observation I made in the field is that many areas that scored high RSF values but were unoccupied / unknown or showed little potential to be occupied (false positives) contained streams and wetlands that were modified from their natural state. In these misclassified areas, streams were frequently incised, either from bank erosion by livestock or channelization by humans (Buhlmann et al. 1997). Many of the misclassified wetlands had also been ditched, or did not support water tables as close to the surface as would be expected because incised or ditched streams presumably facilitated drainage in the area. Often, ditched wetlands and channelized streams are discernable in aerial photographs, so photography may be able to screen for these human modifications when putting this model into practice.

Future Work and Management Implications

Although the explanatory variables used to develop this habitat model may have implied mechanistic links to the biology of bog turtles, the model is primarily correlative (Kearney 2006). This model also does not account for interactions with other organisms, including humans and domesticated animals. With exception to vegetation cover, the variables used in this model are relatively stable over time. I expect that vegetative cover in the study area would be influenced by anthropogenic factors; therefore, succession of vegetation and land use should be considered in future models. The ability for bog turtles to move through the landscape may be controlled by land use and conditions near streams (Chapter 4). This model evaluates conditions of habitats bog turtles are currently using, and may not depict the conditions that bog turtles used historically or will use in the future.

This model appears to be moderately successful at discriminating between occupied and unoccupied / unknown areas of the landscape. Bog turtle managers could therefore use the model to improve their survey success for finding new bog turtle wetlands or to more easily rule out areas of non-habitat. This model has similarities to models that were designed specifically for the purpose of identifying potential areas for wetland restoration (Russell et al. 1997, White and Fennessy 2005). Those models used various combinations of the topographic wetness index inverse, land cover, hydric soils, and position relative to various sized streams to identify places where restoration could be achieved. This model may be a good resource to identify appropriate areas for wetland restorations related to bog turtle habitat. The riparian areas identified in this model with high RSF values, but where wetland ditching or stream channelization have altered the normal hydrology, would be notable candidate areas for restoration. Wetland restoration activities designed to improve the potential for bog turtle habitat should consider whether the candidate area has a good groundwater hydrology source, is not currently occupied by bog turtles, and is within dispersal distance to known bog turtle wetlands. I do not recommend large-scale wetland restoration activities on occupied wetlands because grading and soil moving equipment can disturb soils, potentially changing soil conditions related to organic carbon and particle size (Bruland and Richardson 2005, Bruland and Richardson 2006, Stolt et al. 2000). Thus, large-scale restoration may result in direct mortality of turtles by equipment use or disturbing soils in hibernation and activity areas that are important for bog turtle habitat use (Chapters 3 and 4). Smaller scale restoration activities, such as stream bank stabilization and placement of small structures to elevate the water table could be feasible in wetlands already occupied by bog turtles, as these activities would have less chance of negatively impacting resident turtles than large-scale restoration. Restoration occurring on currently unoccupied wetlands within dispersal distance of bog turtle occupied wetlands provides an opportunity to research if availability of high-quality habitat controls bog turtle wetland use.

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Table 5.1. Overview of the explanatory variables and their data sources used for logistic modeling of bog turtle habitat.

Variable	Source of data	Overview of data processing	Possible values
NWI Wetland	NWI, 1977 to present (vector)	Multiple quadrangles merged and polygons converted to raster layer.	Binary 1, 0 1 = present in 1-ha plot
Hydric Soil	SSURGO (vector)	Multiple counties merged, hydric series identified, polygons changed to raster.	Binary 1, 0 1 = present in 1-ha plot
Vegetation	NLCD, 2001 (raster, 30 x 30 m)	14 categories reclassified to 2. 1 = pasture, cropland, or wetland 0 = other (developed or forest). Resampled to 10 x 10 m. Averaged pixel values (n=100) in 1-ha plot.	Continuous values between 0-1
Stream Order*	DEM (raster, 10 x 10 m)	Created a 14 ha flow accumulation layer. Reclassified to show streams as present or not. Reclassified by Strahler stream order. 1 pixel in 1-ha plot indicates presence.	Nominal 1^{st}, 2^{nd}, 3^{rd}, 4^{th} present in 1-ha plot
Topographic wetness index inverse	DEM (raster, 10 x 10 m)	Used TauDEM 3.1 for processing. TauDEM divides the slope of drainage by catchment area. Multiplied by scalar value of 10,000 and averaged pixel values (n=100) in 1-ha plot.	Continuous values ≤ 0

*** NHD stream data were used in random plot generation, but were not used as a model variable. Stream orders for model were derived from DEM.**

Table 5.2. Description of model scenarios tested for ability to discriminate between occupied and unoccupied / unknown plots using the GIS variables listed in Table 5.1. The AIC_c values are only comparable within the same model scenario, as sample sizes among scenarios differ. All top models were selected using stepwise regression in SAS, with an entry α=0.2 and a retaining α=0.1. All Global models include nine total parameters (eight variables and the intercept). Only the top model from Scenario 3, which performed the best with the fewest variables, was used in further analysis and to create a predictive model for the study area.

Logistic model scenarios	Concordance	AIC_c	Parameters in top model	Action taken
Scenario 1: Bog turtle occupied (n=50) and *a priori* unoccupied (n=48) wetlands selected from Virginia wildlife database	Top = 61.3% Global = 71.5%	Top = 136.02 Global = 142.41	Intercept vegetation	Models not considered useful for predicting bog turtle occupancy. No further analysis made.
Scenario 2: Bog turtle occupied (n=50) wetlands from Virginia wildlife database and randomly selected 1-ha plots (n=74) within 56.4 meters of USGS 7.5-minute map indentified streams. Random plots on ≤ 14% slopes.	Top = 62.1% Global = 75.8%	Top = 152.24 Global = 160.82	Intercept NWI wetland 2^{nd} order stream 3^{rd} order stream	
Scenario 3: Bog turtle occupied (n=50) wetlands from Virginia wildlife database and randomly selected 1-ha plots (n=74) within 56.4 meters of USGS 7.5-minute map indentified streams. Random plots on any slope.	Top = 82.5% Global = 83.6%	Top = 130.91 Global = 138.38	Intercept wetness index vegetation 3^{rd} order stream	Explanatory ability of model considered adequate. Coefficients retained for creating predictive raster layer.

Table 5.3. Variables and scoring criteria used in the Site Quality Analysis (SQA). The SQA was designed by the Virginia Department of Game and Inland Fisheries to rank bog turtle habitat quality (Carter 1998), and was used to score wetlands visited during the field-testing of the logistic model.

Rating weight	Excellent	Good	Fair	Poor
Site Area Total = 14	>5 ha = 7.0	2-5 ha = 4.6	1-2 ha = 2.4	>1 ha = 0
Site Shape Total = 5	Circular = 2.5	Oval/Ellipsoid = 1.7	Sinuous = 0.9	Linear = 0
Site Hydrology Total = 18	Abundant water >3 springheads, high density (3/m^2) of surface water pockets = 9.0	Adequate water, 2-3 springheads, good density (2/ m^2) of surface water pockets = 5.9	Little water, 1 springhead, low density (1/ m^2) of surface water pockets = 3.1	No surface water present, no springheads (<0.5/ m^2) = 0
Substance Quality Total = 20	Abundant (>75% of total area), mucky soil rich in organics, black/rust in color, to a depth of 1 m or more = 10.0	Soft substrate (25-75% total area) present containing some organics, dark brown/red in color, to a depth of at least 0.5 m in places = 6.6	Small (<25% total area), scattered areas of coarse/silty mud with no organics, light brown/red in color), never deeper than 0.25m = 3.4	Hard, compacted substrate ,few areas of soft silt or muck present = 0
Intrapatch Isolation Total = 8	Contiguous core area of suitable habitat, no recent ditches, mowing, or barriers to average movements = 4.0	Habitat is contained within fewer than three cores, recent ditches make up <25% of total habitat, occasional mowing = 2.6	Habitat comprised of many small habitat patches, recent ditches 25-75% of total area, mowing or other factors may serve to isolate patches = 1.4	Ditched/drained wetland, habitat restricted to ditches, unsuitable habitat between = 0
Successional Stage Total = 14	Young wetland, typical poor fen, bog, or wet meadow habitat, woody plants <25%, <75% of ground area is shaded = 7.0	Woody plants comprise 25-50% of habitat, mostly open canopy (25-75% of ground area is shaded) = 4.6	Woody plants dominate some areas, open canopy reduced (75-95% of ground area is shaded) = 2.4	Patches of wetland vegetation rare, young trees present, heavily shaded (>95% shade) = 0
Proximal Impacts Total = 10	Little or no grazing, no neighboring development within 1 km = 5.0	<25% of wetland vegetation removed by grazing or mowing, roads at least 0.5 km from core habitat = 3.3	25-75% of wetland vegetation removed by grazing or mowing, roads closer than 0.5 km = 1.7	Feedlot, wetland barren in places, noticeable impacts from roads or heavy machinery = 0
Dispersal Potential Total = 10	Unrestricted movement possibilities, no potential barriers = 5.0	Movement likely out of site, <2 potential barriers = 3.3	Movement possible, but infrequent, barriers likely restrict movement (3-5) = 1.7	Isolated from neighboring sites, successful dispersal very unlikely = 0
Recruitment Potential Total = 10	>3 large (l m^2) hummocks of pristine mosses and sedge clumps = 5.0	Several potential nesting areas (2-3) = 3.3	At least one area suitable for nesting = 1.7	Successful nesting unlikely, little or no suitable habitat = 0
Drought Tolerance Total = 20	Abundance of water, vegetation lusher than surrounding areas, persistent water likely = 10.0	Abundant water, but unevenly distributed, areas of habitat will dry seasonally = 6.6	Few patches of water, vegetation lower than other areas, will dry in drought years = 3.4	Sparse water at best, vegetation low, water never abundant and absolutely absent in later summer = 0
Development Threats Total = 16	Potential for disturbance is remote, no roads or dwellings visible = 8.0	Site is partially visible from roads, dwellings farther than 1 km = 5.3	Roads or development 100-1000 m away = 2.7	Encroaching development < 100 m away, has observed impacts on site = 0
Community Diversity Total = 12	Large number (>20) of native wetland plant genera = 6.0	Adequate number (10-20) of native wetland plant genera = 4.0	Small number (5-10) of native wetland plant genera = 2.0	Virtual monoculture (0-5) of native wetland plants = 0
Pristine Indicators Total = 14	2 or more species, relatively abundant, indicate openness = 7.0	At least one species relatively abundant = 4.6	At least one species, but uncommon = 2.4	No species present that indicate historic openness = 0

Table 5.4. Logistic regression coefficients for explanatory variables remaining in the top model identifying potential habitat for bog turtles. These coefficients were used to calculate a continuous predictive Resource Selection Function (RSF).

Variable	Coefficient estimate	SE	Odds ratio estimate	Odds ratio 95% confidence limits
Intercept	-0.490	0.588	NA	NA
Wetness index inverse	-0.055	0.0205	0.947	(0.91, 0.99)
Vegetation	0.021	0.00707	1.022	(1.01, 1.04)
3rd order stream	1.25	0.5471	3.498	(1.20, 10.2)

Table 5.5. Average values of all explanatory variables tested in modeling Scenario 3. Topographic wetness index inverse and % coverage of low vegetation (vegetation) were continuous variables; mean values for these variables are calculated from the 100, 10 x 10 m cells present in each 1-ha sampling plot. The mean for the remaining binary variables can be interpreted as the proportion of 1-ha plots with the variable present. Stream orders were modeled as individual binary variables.

	Occupied plots (n=50)		Random plots (n=74)	
Variable	Mean	SE	Mean	SE
Wetness index inverse *	13.4	1.097	32.4	3.367
Vegetation*	58.4	4.804	25.4	3.597
3rd order stream*	0.34	0.068	0.18	0.043
1st order stream	0.16	0.052	0.30	0.053
2nd order stream	0.36	0.069	0.20	0.047
4th order stream	0.04	0.028	0.09	0.034
Hydric soil	0.74	0.063	0.55	0.058
NWI wetland	0.28	0.064	0.07	0.029

***Variables supported in top model and coefficients used to create predictive RSF layer.**

Table 5.6. Model-developed resource selection function (RSF) and Site Quality Analysis (SQA) values measured from an independent set of 77 field-surveyed locations. The SQA values were calculated over the entire wetland at the time of the site visit, while RSF values were extracted from ArcMap using a 1-ha circular plot with the center point placed in the center of the wetland.

Occupancy group	n	Model-derived RSF values			Field-derived SQA values		
		Mean*	Median	SE	Mean**	Median	SE
Occupied	14	0.28	0.25	0.013	55.3	56.1	2.2
Unoccupied / Unknown	63	0.21	0.19	0.033	47.0	48.1	1.4

***Difference between occupancy groups significant using a Mann-Whitney test (*MW*=2301, *P*=0.002)**
****Difference between occupancy group significant using a Mann-Whitney test (*MW*=2250, *P*=0.003)**

Table 5.7. Stream orders present in occupied 1-ha wetland plots. The frequency of stream sizes was disproportionate with the availability of stream sizes based on a pixel count of 1st through 4th order streams in the study area. Stream order information was calculated from a 14-ha flow accumulation threshold using hydrology tools in ArcMap 9.2.

Data set	Strahler order of stream					Total
	0 (no stream)	1st	2nd	3rd	4th	
Pixel count in study area (DEM - derived streams)	NA	101,456 (51)	51,437 (26)	31,108 (15)	16,897 (8)	200,898 (100)
DEM - derived streams	5 (10)	8 (16)	18 (36)	17 (34)	2 (4)	50 (100)
USGS 7.5 - minute quadrangle streams	6 (12)	21 (42)	12 (24)	11 (22)	0 (0)	50 (100)

***Larger order stream counted when two or more streams occurred in the same 1-ha plot.**

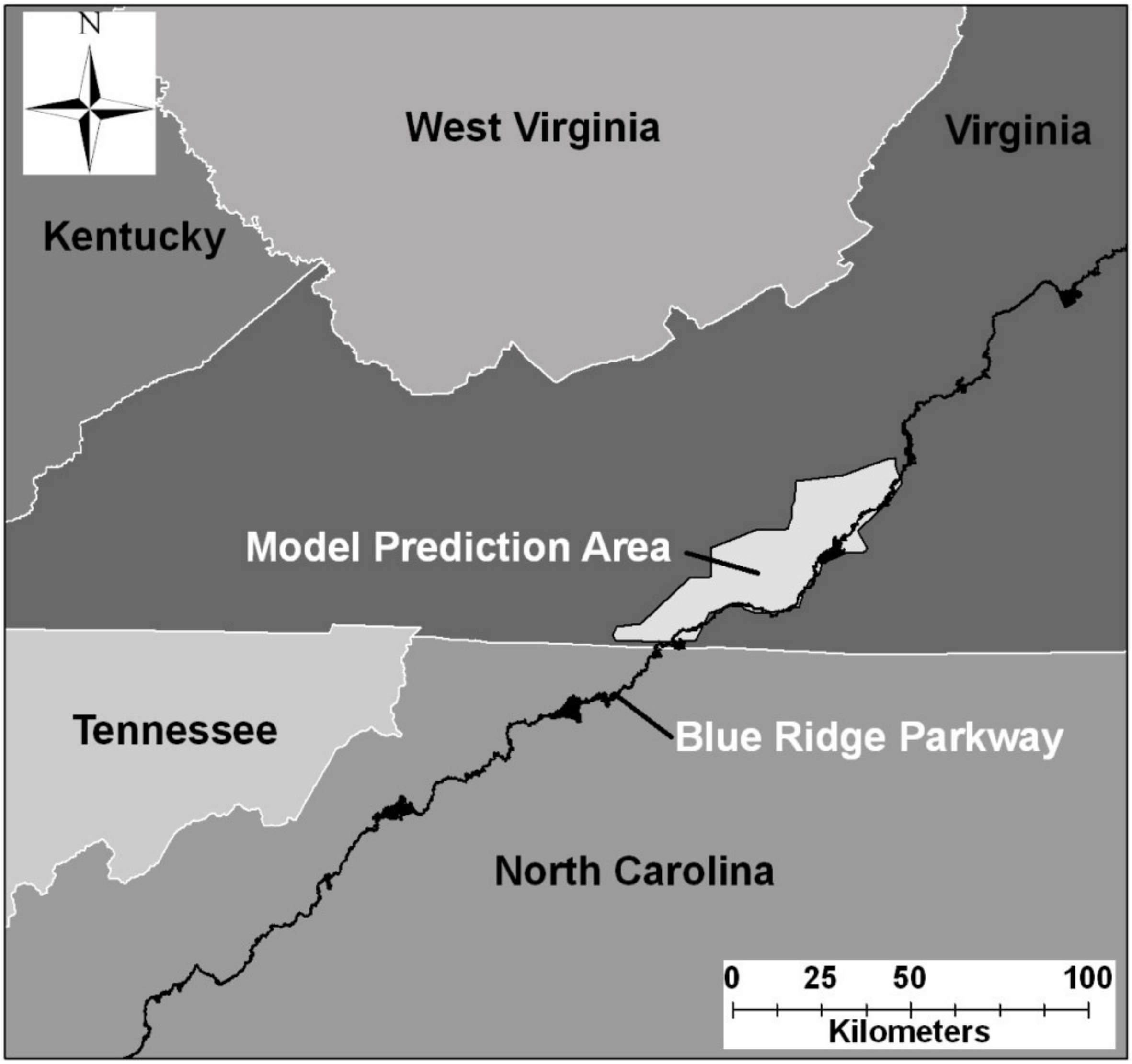

Figure 5.1. Study area in the Southern Blue Ridge of Virginia. The model study area included parts of five counties and encompassed approximately 1410 km^2.

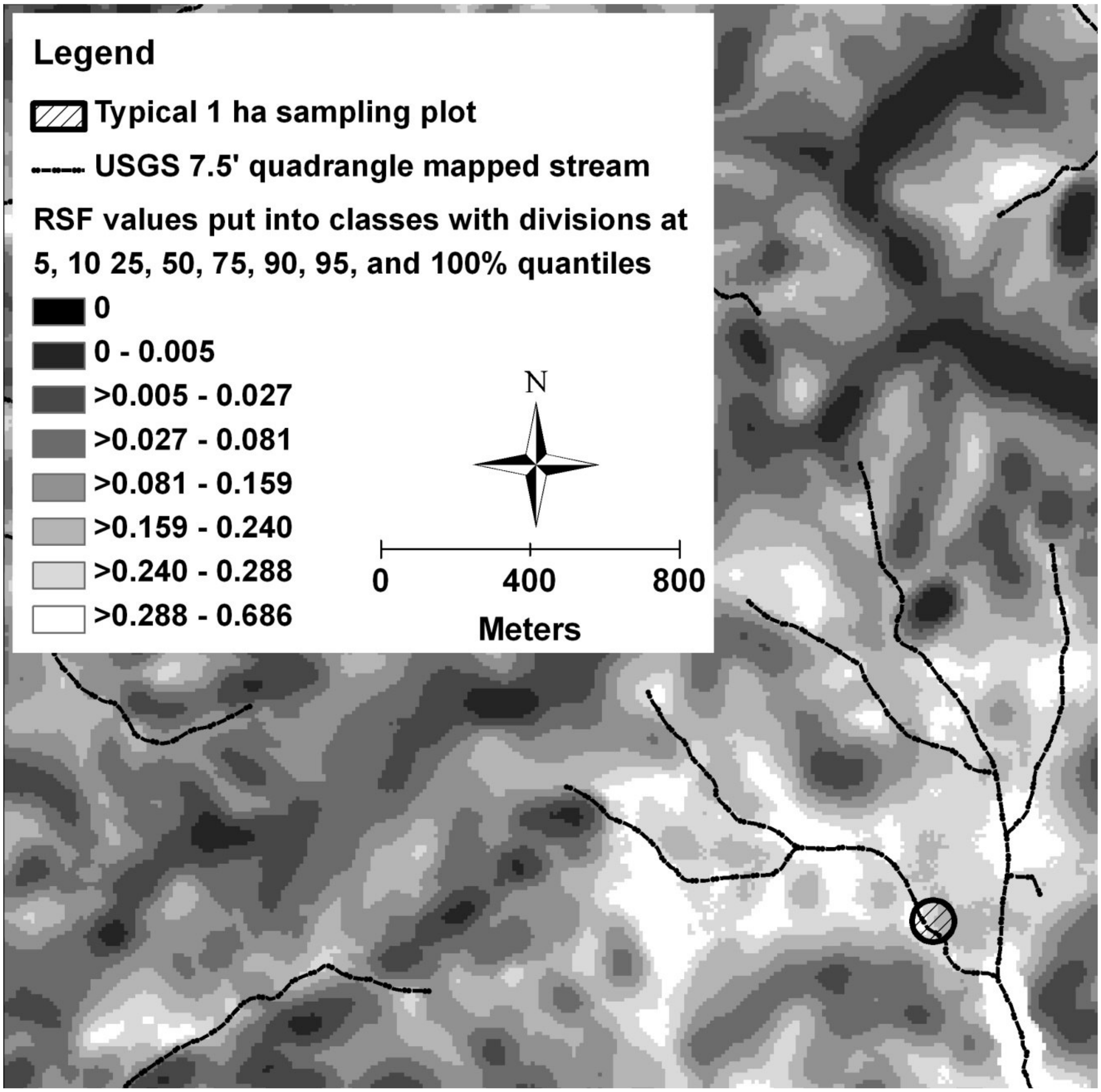

Figure 5.2. Graphic showing a small, typical portion of the resource selection function (RSF) layer predicting relative probability of high-quality bog turtle habitat over the landscape. The RSF layer was built from the variables topographic wetness index inverse, vegetation, and 3rd order streams that were determined to be significant predictors of bog turtle habitat. Note the increased RSF values associated with 3rd order streams. Shown is a typical 1-ha plot used during the process of sampling pixels in both the model building and model validation processes.

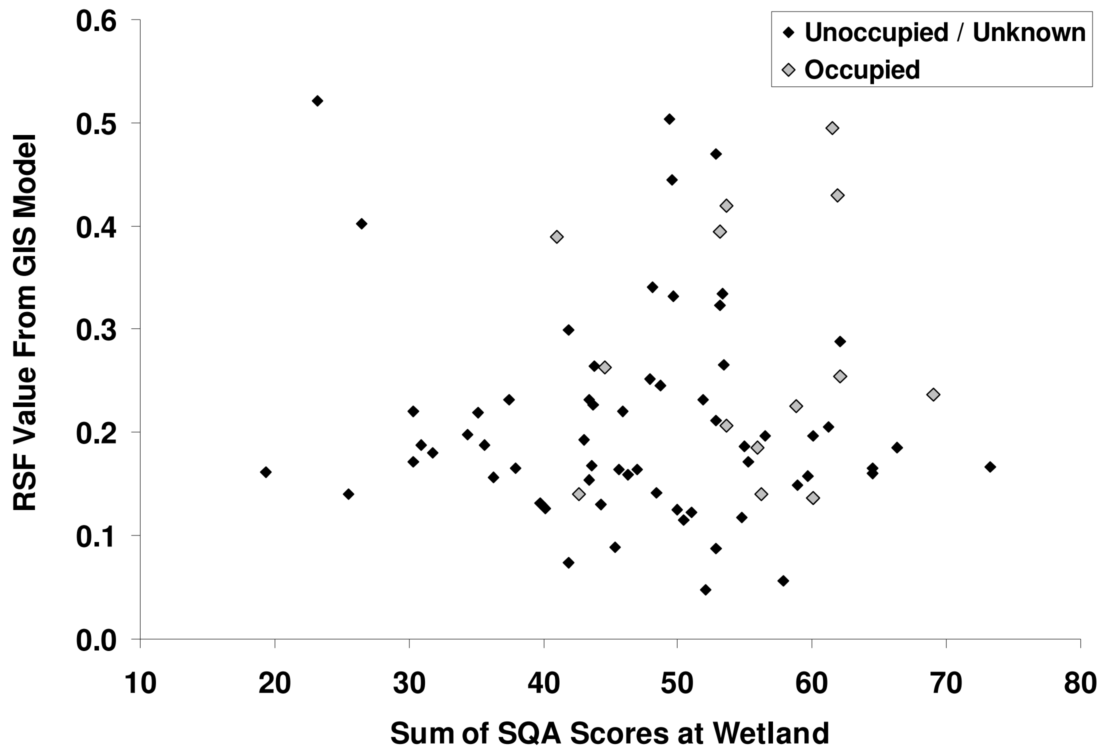

Figure 5.3. Relationship between field-derived Site Quality Analysis (SQA) scores and model-derived resource selection function (RSF) values. A test of regression slope with a null hypothesis that the slope =0 could not be rejected using natural log transformed (to improve assumption of normality of residuals) data ($F_{1,75}$,=0.04, P=0.839, r=-0.024).

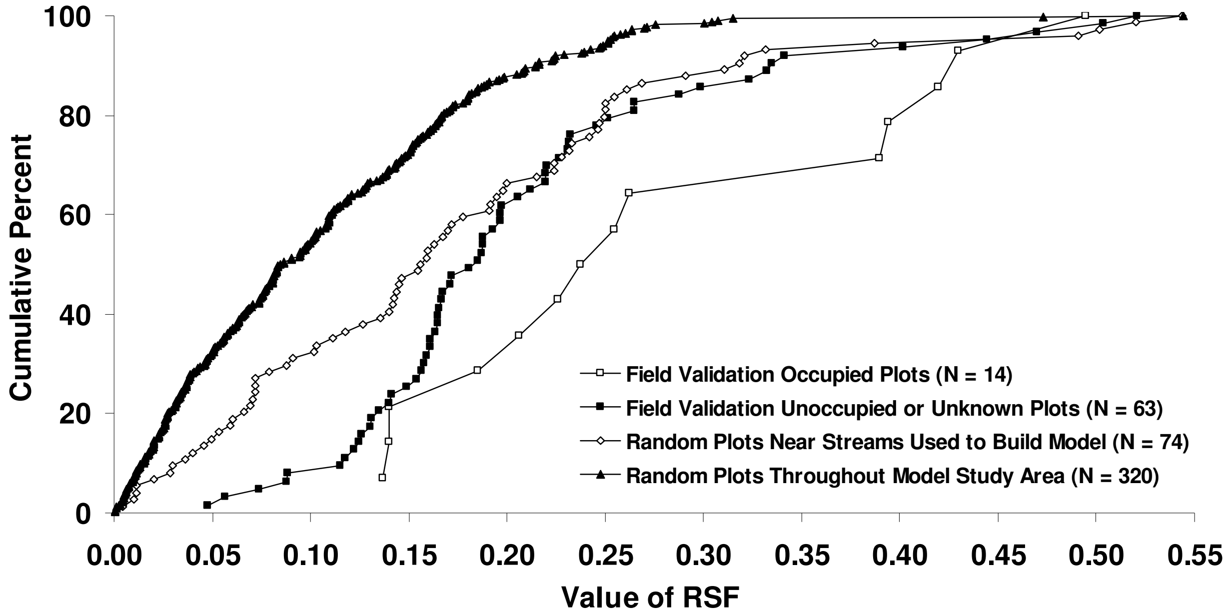

Figure 5.4. Cumulative probability distribution of resource selection function (RSF) values evaluated for four different sets of 1-ha plots. Field validation plots were independent of the model training data and were used to test the prediction ability of the logistic model. The set of "random plots near streams used to build model" differ from both the "field validation occupied plots" and "field validation unoccupied or unknown plots" used to field test the model because model building used randomly generated 1-ha plots near streams (including some non-wetland areas), while field validation plots were areas meeting wetland criteria that were chosen because they appeared to provide bog turtle habitat from a brief road survey. "Random plots throughout model study area" differed from all the other data sets because it contained mostly areas of non-wetland distant from streams.

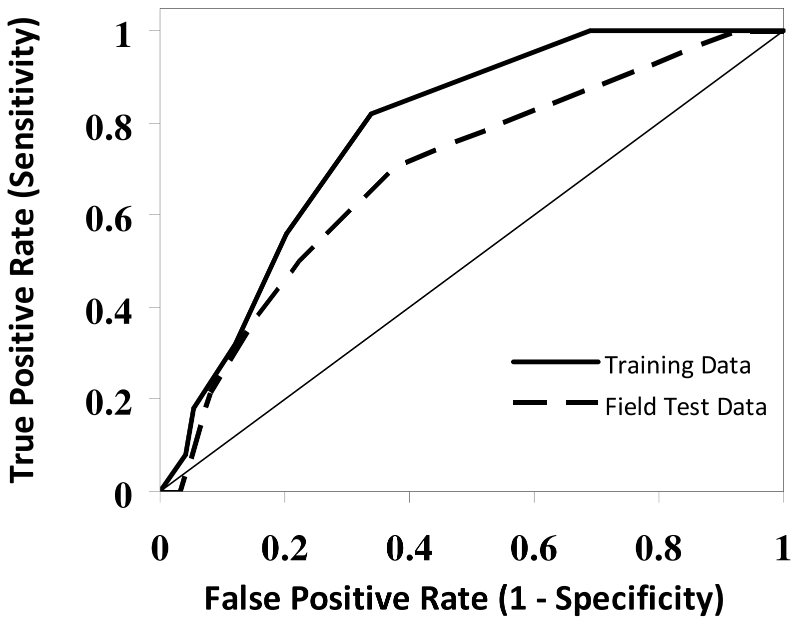

Figure 5.5. Receiver operating characteristics (ROC) curve for field tested data (n=77, occupied =14, unoccupied / unknown =63) and model training data (n=124, occupied =50, random =74). The area under the curve (AUC) for the field-tested data was 0.70, while the AUC for the training data was 0.83. The 1:1 line (AUC 0.5) would indicate chance performance of the model. The discrepancy between field-test and training data occurred because the field-test data were 1-ha plots placed over actual wetlands selected from road surveys, while the training data were randomly generated 1-ha plots along USGS 7.5' quadrangle identified streams.

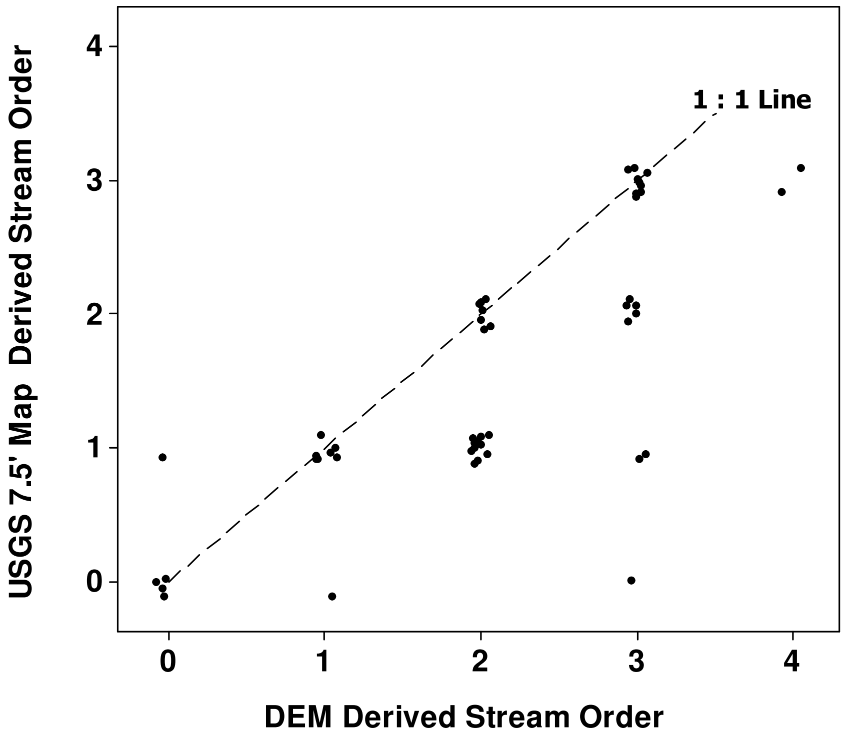

Figure 5.6. Relationship of stream order determined from a DEM-derived stream network with a flow accumulation threshold of 14-ha and stream order determined from USGS 7.5' quadrangle identified streams. Streams were all within 1-ha circular plots centered on top of bog turtle occupied wetlands (n=50). Data points are randomly offset to a small degree in the x and y direction in order to reveal overlapping points. The Spearman rank correlation coefficient between the data was 0.752.

Chapter 6: Managing bog turtle (*Glyptemys muhlenbergii*) habitat in Virginia

ABSTRACT

Making management recommendations is an important and challenging aspect of being a natural resources scientist. The management of the bog turtle (*Glyptemys muhlenbergii*) in Southwestern Virginia is complicated because the wetlands used by the species are dynamic habitats that are influenced by human activities such as agriculture, development, and draining and filling. I make general management recommendations based on three years of field studies in bog turtle wetlands, an evaluation of the Site Quality Analysis currently in use by the VDGIF, and a review of the literature. High quality bog turtle wetlands are characterized by nearly constant saturation at the surface, and bog turtles select saturated areas even when their availability is reduced. Managing bog turtle wetlands must emphasize the maintenance of high subsurface water tables, while avoiding inundation. Educating landowners and enforcing existing wetland laws regarding ditching and draining wetlands must occur to maintain wetland hydrology for bog turtles. Activities that reduce recharge areas and pressure heads in local and regional aquifers have the potential to reduce discharge from seeps supplying water to wetland habitats. Maintaining connectivity among wetlands in the range of the bog turtle is important and best achieved by allowing safe passage through areas near streams where bog turtles frequently travel. How to manage livestock grazing in bog turtle wetlands remains a debatable issue. The hooves of grazing livestock alter the structure and physical composition of soils in bog turtle wetlands. Bog turtles frequently use the micro-habitats created by livestock hooves, particularly in marginally wet conditions when saturation is hard to access because of surface drying. Identifying bog turtle habitats is an important aspect for management, and can be facilitated by using GIS to recognize landscape positions where wetlands are likely to occur.

***Key Words*:** water table, soil, wetland, fen, hydrology, saturation, dredge, fill, connectivity

OBJECTIVE

Scientific studies of species and their habitats are useful because they provide basic information about the species' ecology as well as information about management strategies that may help conserve the species. The ecology of the bog turtle (*Glyptemys muhlenbergii*) is not well understood, and as a result, the best management strategies to conserve it are unclear. The bog turtle lives in wetlands that almost always have a history of former human activities including cultivation of hay and row crops, livestock grazing, development, wetland draining, and various modification to the hydrologic and sediment budget. As a result, successful bog turtle habitat management must account for the ecology of the species while also considering how human activities are involved.

Considerable uncertainty exists when evaluating how natural systems work, even after careful and reproducible studies. This uncertainty, coupled with social and political forces, makes it challenging for scientists to make objective management decisions (Sullivan et al. 2006). With these challenges in mind, the objective of this chapter is to provide management recommendations related to bog turtle habitat. These recommendations are derived from these following sources: 1) the empirical results of the field studies reported in Chapters 1 through 5; 2) my unpublished observations of bog turtle wetlands in the Blue Ridge of Virginia and North Carolina; 3) my former experience as an MS student characterizing shallow groundwater hydrology under agricultural systems; 4) my experiences as a wetland scientist, at which time I delineated the jurisdictional bounds of freshwater wetland areas according to the laws set forth in Section 404 of the Clean Water Act and shared these results with the Army Corps of Engineers (COE) and State Agencies; and 5) my values and ethics in regard to wetland areas and the wildlife that uses them. Briefly stated, I acknowledge as fact that freshwater wetlands are areas of high biodiversity, they improve water quality and moderate water quantity, and people enjoy the aesthetics of wetlands. The Government of the United States and the Supreme Court have made laws and repeatedly upheld rulings that are intended to protect wetlands. Given this legal framework, I believe that these laws need to be enforced in areas such as Southwestern Virginia, where rural land use, relatively low human population density, and few enforcement personnel have resulted in weaker application of wetland laws relative to other parts of the state (personal experience with wetland delineation and Section 404 permitting in Northern Shenandoah Valley). It is important for me to state these values up front, as they have undoubtedly been a part of my path toward becoming a scientist and could have been a factor in how I designed and reported my empirical studies. Sullivan et al. (2006) believe that it is important for scientists to be open about their underlying values, particularly when making management recommendations which are inherently value-driven. When I speak of wetland law in this document, I do not believe that I am switching roles from a scientist to a supporter of a particular policy, which can corrupt principles that are important to effective science (Lackey 2007). Instead, I am stating facts about existing laws where clear guidance for implementation has been provided since 1987 (Wetland Training Institute, Inc. 1995).

In this management chapter, I discuss general management recommendations that are related to the maintenance of habitat and prevention of impacts to habitat that will render them incapable of supporting wetland hydrology. These management topics include the following: 1) managing wetland hydrology and saturated soils; 2) maintaining connectivity between wetlands; 3) regulating agricultural land use and livestock grazing; 4) remotely identifying wetlands with good habitat potential; and 5) demanding enforcement of existing laws regulating dredge and fill of wetlands. As each management topic is covered, I will provide a short discussion as to how my findings are related to bog turtle management and how these ideas integrate with current strategies for bog turtle management.

MANAGING WETLAND HYDROLOGY AND SATURATED SOILS

The presence of high water tables and saturation in bog turtle wetlands has been documented (e.g. Arndt 1977, Bury 1979, Chase et al. 1989, Carter et al. 1999, Ernst and Lovich 2009). High water tables are a product of groundwater-maintained hydrology, and show little variability even after drought periods (Chapter 1). Bog turtles overwhelmingly choose saturated conditions, even when they are limited in availability (Carter 1999 et al. 1999, Chapter 4). Surface saturation is the aspect of hydrology that is most relevant to the ability for bog turtles to submerge themselves in shallow soil (Chapter 1). Surface saturation may also be related to the selection of bog turtle nest sites, with Whitlock (2002) finding that 18 of 22 (82%) bog turtle nests occurred within 50 cm of standing water. Based on the association of bog turtles with high water tables and saturation, a management goal is to maintain these conditions. Maintenance of hydrology includes preventing the excessive lowering and rising of water tables in occupied wetlands or wetlands that have the potential to become bog turtle habitat.

My findings suggest that high water tables are a factor discriminating between wetlands used by bog turtles for breeding and wetlands where no turtles were encountered (Chapter 1). Wetlands used by bog turtles had higher water tables and more saturation than wetlands where no turtles were encountered. Measurements of turtle habitat use indicated that lowering the water table as little as 15 cm on average in the core saturated areas of wetlands used for breeding could impact bog turtles, forcing them to adjust behavior or move to other areas with higher water tables. Bog turtles were found submerged at depths between the soil surface and 15 cm for 96 % of 1284 summer locations (Chapter 4), and observations and temperature signatures measured during winter also showed that turtles frequently hibernated at similar depths. Without saturation at the soil surface, avoiding high heat in the summer could be more difficult for bog turtles. Temperatures on the soil surface reached 45ºC, which likely exceeds the critical thermal maximum of bog turtles. Critical thermal maxima for the closely related wood turtle (*Glyptemys insculpta*) and the spotted turtle (*Clemmys guttata*) are both 41°C (Hutchison et al. 1966). In winter, maintaining body temperatures above freezing may not be possible for bog turtles without saturation in the upper soil because ambient air temperatures rapidly fluctuate around freezing in Virginia (Chapter 3).

Water table reductions in the relatively small, gently sloped wetlands used by bog turtles can be caused by several factors. Wetland ditching is an obvious method, and this practice is still common in the region (personal observation). Stream incision is also a factor. Incision can occur from stream channelization, increased flow volume and velocity from impermeable surfaces upstream, or easily eroded, unstable stream banks, a condition often created by heavy livestock grazing in streams (Zeckoski et al. 2007). Wetland ditching and incision of streams adjacent to bog turtle wetlands results in lateral groundwater flow gradients. These gradients have the potential to overpower the vertical upward gradients that are characteristic of wetland seepage areas in bog turtle wetlands (Chapter 1).

Activities occurring outside of the immediate vicinity of occupied wetlands also have the potential to reduce water tables in wetlands. Creation of impermeable surfaces in the groundwater recharge area for bog turtle wetlands may result in loss of head pressures controlling discharge into seepage wetlands (Brennan et al. 2001). Further, seeps originating from deeper groundwater sources may be a factor in the hydrologic budget of bog turtle wetlands. Should local or regional water tables drop from the pumping of groundwater for agricultural, residential, or industrial purposes, discharge from seeps could be reduced. More research is needed to determine where recharge occurs for the hydrology discharging into bog turtle wetlands.

Inundation, flood water, and excessively high water tables can have negative effects on bog turtles. High velocity surface flow and the cycles of erosion and deposition associated with surface flow can alter the silt and sandy loam textures and high organic carbon contents associated with bog turtle occupied wetlands (Chapter 2). Storm water outflows into a bog turtle wetland in New Jersey were associated with the eventual extirpation of the local turtle population using the wetland (Torok 1994). Channelized (as opposed to sheet flow or groundwater flow) inflow from surrounding areas can bring in sediment and also be a vector for the immigration of invasive plant species. Even when it is associated with low velocity surface hydrology, inundation can directly affect bog turtles and their nests. Bog turtles frequently bask on vegetation protruding above the water surface, and successful bog turtle nests are always above the water line. Inundation associated with widely fluctuating water tables and elevated water tables would drown turtle embryos in the nest. Elevated water tables in winter could affect hatchlings, as bog turtles spend their first winter in the nest or in the vicinity of the nest (Ernst and Lovich 2009). Turtle nesting is often associated with sphagnum moss, which is associated with high organic matter levels (Mitchell 1994, Moore et al. 2007). It is uncertain as to how quickly female bog turtles will find appropriate alternative nesting areas to adjust to hydrologic changes. In the only known population viability analysis completed for bog turtles, Whitlock (2002) found that bog turtle populations were only stable when 97% of adult females, 83% of juveniles, and 32% of eggs and hatchlings less than one year old survived annually, and when 100% of female turtles nested annually. These figures were dependent on the specific demographics of the study population in Massachusetts and Connecticut, but they attest to the importance of high survival rates of all life stages of bog turtles, including eggs and hatchlings.

Culvert construction can alter normal hydrology in several ways, sometimes resulting in inundation on the upstream end and a water table drop on the downstream end. Culverts associated with relativity small projects, such as the culverts installed under gravel roads or driveways, can have a large effect on hydrology. Upstream, culverts can cause inundation, particularly when the invert (the inside bottom of a culvert) of the intake pipe is not buried below grade. Downstream, the outlet of the pipe can facilitate channelized flow because of higher erosion rates associated with turbulent flow and elevation drops from pipes not buried below grade. An informative technical review of culverts and their effects on movement of aquatic wildlife has been prepared by the Maine Department of Transportation (2008).

Maintaining high water tables can be achieved by prohibiting ditching and reducing erosion rates of stream banks. Overgrazing wetlands can be a factor in excessive erosion of stream banks (Zeckoski et al. 2007). When the origin of down-cutting into seepage areas are at eroded stream banks, restoration projects may be warranted to stabilize the stream banks and to bring water tables in the effected seepage area to former levels. Permits from the COE and / or the state of Virginia are technically required before such restoration activities within a wetland begins, and the activities should be completed by qualified individuals that can survey water table and soil surface elevations before and after the activity. The problems associated with excess inundation discussed above should be avoided when restoration plans include raising the water table. Those responsible for designing wetland restorations should avoid the assumption that more water is better. The degree to which water tables should be raised is entirely dependent on wetland specific qualities, such as the degree to which water tables have been lowered by previous drainage activities and the slope and width of valley where the restoration is planned. I suggest that a basic restoration design strategy is to bring the water table up to an elevation that maximizes the area where the soil is saturated to the surface, while minimizing the area of inundation. Inundation should be avoided in seepage areas that are showing upwelling of water; however, small elevation gains of the water table above the mean soil surface elevation (on the order of 5 cm) will not harm most seepage areas because the variable topography on the surface will prevent complete inundation and allow some spots for basking and nesting. Sediment deposition and plant material will eventually result in buildup of the soil surface below the inundation. A good discussion of procedures associated with restoration of bog turtle wetlands is provided in Somers et al. (2000).

MAINTAINING CONNECTIVITY BETWEEN WETLANDS

Most bog turtle habitats and wetlands in Floyd and Carroll counties, Virginia appear to be located within known dispersal distances of other wetlands used by bog turtles. Furthermore, many wetlands that are currently unused by bog turtles are present along the streams and drainages in the region. These conditions allowed me to evaluate how turtles move through the landscape. Bog turtles have been observed moving along both streams and over ridges, but the most dominant pathways were unknown. I found that bog turtles moving through the landscape primarily used paths that are within 80 m of USGS 7.5’ quadrangle streams. These findings were determined from 46 movements that exceeded 80 m in length, 96% of which were confined to near-stream areas (defined as being ≤ 80 m to a stream). These turtles were at times moving between areas of core wetland habitat, and other times were moving temporarily into wooded areas along streams for unknown purposes. Bog turtles were much more likely to make long movements during the severe drought conditions observed in 2008 than they were during the normal rainfall conditions in 2009 (Chapter 4). The average movements made by turtles during this investigation surpassed those observed by Carter et al. (2000) on many of the same study wetlands. That study occurred during normal rainfall conditions.

From a management standpoint, the most economical conservation and land preservation activities for bog turtles should occur along streams. Although bog turtles may not spend a great deal of time along the near-stream areas spanning their core home range areas, moving through them can present risks to bog turtles. The habitat extending between core turtle home range areas is often minimally saturated, providing fewer opportunities for turtles to find cover and thermoregulate. I found that bog turtles crossed non-wetland areas with no surface saturation 48 % of the time while traveling through near-stream areas. Land use varied within the 80-m near-stream areas used by bog turtles. Many of the areas were grazed pastures, while other areas were wooded. Some turtles moving near stream areas may encounter manicured lawns in residential areas. Similar to wood turtles (*Glyptemys insculpta*) (Natural Resources Conservation Service 2010), bog turtles may be at risk of being struck by mowing equipment. Traveling through manicured lawns increases the visibility of bog turtles, making them more likely to be picked up by humans, spotted by predators, or attacked by domestic dogs. One turtle in the study was apparently killed by a domestic dog after it entered a residential property during a long movement away from its original wetland. Another bog turtle crossing heavily grazed pasture was found dead following apparent overheating after being flipped over and possibly trodden by livestock.

In this study, turtles crossed through culverts and over roads during their long movements. Being struck by vehicles can be a source of mortality for turtles crossing roads, and dead bog turtles have been observed on the Blue Ridge Parkway (Tom Davis, National Park Service, personal communication). Ideally, new road construction should be avoided in areas with bog turtle wetlands. In Pennsylvania (where impacts to the habitat of the federally threatened bog turtle must be avoided under the Endangered Species Act), the biological opinion provided by the U.S. Fish and Wildlife Service resulted in the construction of a road that completely spanned the bog turtle habitat (McElhenny and Brookens 2004). At the very least, roads built in the vicinity of bog turtle wetlands should not have curbs, as turtles are not able to move over them. Safe passage at stream crossings should be promoted. Wide culverts without steep gradients between the inlet and outlet result in low water velocity, which is preferable for facilitating safe and effective bog turtle movement. The presence and availability of culverts allowing easy passage may promote movement of turtles under rather than across roads. The topic of designing culverts with acceptable velocities and dimensions to facilitate the passage of aquatic wildlife is discussed by the Maine Department of Transportation (2008).

Establishing and maintaining positive relationships with private landowners is an important aspect of maintaining good connectivity among bog turtle occupied wetland habitats. I have the opinion that landowners should be informed about the potential presence of the rare bog turtle on their property. Avoiding the subject may leave landowners suspicious about the modes and motives for conservation of the bog turtle in Virginia. Most landowners are somewhat aware that a rare turtle is present in the area, and providing information about the turtle enables landowners to talk with their neighbors and other people in the community about the species. Interestingly, following bog turtles using radio telemetry moving onto unfamiliar properties was an effective motivation to knock on doors and meet new landowners. Most of these owners were willing to let me access their property, and some landowners were excited about the rare turtle using their property.

REGULATING AGRICULTURAL LAND USE AND LIVESTOCK GRAZING

Most existing bog turtle wetlands in Virginia continue to be used for agricultural purposes, primarily beef livestock grazing. A debate among bog turtle biologists is the importance of livestock grazing for maintaining bog turtle wetlands, and this debate still remains open. Grazing bog turtle wetlands is used as a management tool for preventing vegetative succession from herbaceous to woody vegetation (Tesauro 2001, Phu 2008). Grazing activity may also be associated with modifying soil, making it more or less conducive for bog turtle use. Grazing in wetlands is implicated in increased erosion rates and degradation of water quality.

My observations of soil structure and bog turtle behavior suggest that livestock grazing does change bog turtle habitats. In the wetlands with the highest and most stable water tables, soils generally remain saturated and are of low strength. Low strength soils enable bog turtles to easily submerge themselves in mud. In consistently saturated areas, grazing livestock may serve to break up the soil structure held together by the fibrous roots of herbaceous vegetation. Despite this possibility, I do not expect that the grazing of livestock on consistently saturated soil is as important for maintaining low strength soils as it is in marginally wet areas. Marginally wet areas occur either along the perimeter of permanently saturated areas, or in wetlands that are just inherently less wet than others. In marginally wet areas, mean water tables may not remain between the surface and 15 cm of depth all times of the year as they do in the wetter areas. When hot and dry weather conditions prevail in marginally wet areas, evaporation from the soil surface can occur more rapidly than rates of upward capillary action can replace moisture, resulting in a hardened surface soil crust. This process can occur even if the water table is relatively near the soil surface. Under these conditions, the hoof activity of livestock appears to create holes in the surface that provide micro-habitats for turtles where turtles can access water and mud. Excessive grazing (defined as grazing to the point when the quantity of vegetation is reduced to a level resulting in damage to plant roots and increased plant death) should be avoided, as this would likely result in more direct sun exposure to bare soil. Based on qualitative observations, I suggest that evaporative losses on the uppermost portion of sun-exposed surface are more likely to cause a surface crust relative to areas where herbaceous vegetation is present. Although evapotranspiration from herbaceous vegetation may convey more volume of water to the atmosphere than evaporation from bare soil, much of the water from plant evapotranspiration probably originates from deeper root-zone depths where water is plentiful rather than the soil surface. Excessive grazing should also be avoided because it may result in compaction in incompletely saturated soils, particularly when clay content is high.

On longer time scales, the hoof action of livestock can modify soil structure in marginally wet areas by pushing green plant matter and roots deeper into the soil where decomposition is slow. Under moderate to light grazing management, marginally wet soils can have increased organic carbon content, and related increases in water holding capacity. All of these changes result in a soil that is more easily accessed by bog turtles because soil strength is lower in soils with high water content and high organic carbon contents (To and Kay 2005).

In the northern range of the bog turtle, grazing is a management tool used primarily for control of woody vegetation (Tesauro 2001, Phu 2008). On these wetlands, sheep or goats are the dominant grazers. I suggest that if micro-topography and vertical mixing are important on marginally wet areas, sheep and goats do not have the weight or foot size to create the type of holes used by bog turtles. If land use changes are made in bog turtle wetlands that result in removing livestock from permanent grazing access, allowing temporary access to large livestock may be important. If woody vegetation control is the primary issue, than sheep or goats may be effective. If creating micro-habitat is also desired, even a few large livestock may be effective at modifying soils if they are forced to graze in the marginally wet areas.

There are several serious concerns about grazing livestock in wetlands. One concern is that grazing can result in erosion of stream banks directly through physical disturbance and indirectly through removal of vegetation that stabilize banks (Zeckoski 2007). As discussed earlier, this could result in lowering the water table in adjacent bog turtle wetlands. High input of fecal bacteria into surface waterways are another serious concern associated with livestock grazing. Many streams downstream of known bog turtle wetlands exceed the Total Maximum Daily Loads allowed for fecal coliform (The Louis Berger Group, Inc. 2002). Removing livestock from stream and wetlands using fencing is an effective method of reducing fecal inputs into waterways. For ideal management with respect to fecal contamination in bog turtle wetlands, livestock could be excluded from streams and stream banks and allowed access to wetland areas. However, based on the small size of most of the bog turtle wetlands I have visited in Virginia, this strategy of fencing is not feasible. Although hydrologically disconnected from stream areas, most bog turtle wetlands are very close to streams. Thus, excluding livestock from streams would simultaneously exclude livestock from bog turtle wetlands. If fecal coliform levels are a primary concern, grazing management in bog turtle wetlands should occur in early spring when there is high base flow available for dilution. Heavy grazing should be avoided in late spring and early summer when bog turtles are nesting. Unfortunately, this suggested timing is probably not consistent with the grazing needs of the typical rancher, who would probably desire to graze livestock in the wetland in the summer and early fall when less forage is available in other areas.

Research should continue to determine how important the grazing of livestock is for bog turtle wetlands and preventing vegetative succession. I do not think that all grazing studies must be completed on wetlands occupied by bog turtles to prove useful information on vegetative succession. Rather, studies could occur on wetlands regardless of bog turtle occupancy, as long as they have similar hydrology, soils, and vegetation structure as wetlands used by bog turtles. Keeping careful records of grazing intensity (head counts, area of paddocks, rotation schedules) is a most challenging, yet key component in studying effects of grazing in wetlands. Assessment of vegetation should be completed using vegetative transects as well as aerial photography. I recommend that replication of any future grazing studies be at the wetland scale, rather than small plots, as larger areas are better able to integrate spatial shifts in grazing pressure and minimize edge effects of fencing. Non-grazed wetland areas could be experimentally created by identifying wetlands where total exclusion of livestock has been achieved. A potential source for such wetlands could be formerly grazed areas that are enrolled in the United States Department of Agriculture's Conservation Reserve Enhancement Program (CREP), as these areas currently exclude all grazing (United States Department of Agriculture 2007). Should CREP areas be used for studying vegetation, it must be understood that riparian plantings need to be curtailed so that accurate data on natural succession could be obtained. This would be in violation of current CREP requirements. Such a large-scale vegetation study would be challenging, but would be a great opportunity to better understand succession processes in wetlands. Furthermore, the necessary collaboration with the Natural Resources Conservation Service (NRCS) would be a leap forward in gaining a potentially influential partner in bog turtle conservation on privately owned agricultural lands. Finally, careful design of large scale grazing field studies could present opportunities to partner with other research groups to simultaneously study succession while monitoring the relation of grazing to erosion and water quality.

REMOTELY IDENTIFYING WETLANDS WITH GOOD HABITAT POTENTIAL

In chapter 5, I used commonly available GIS variables to predict areas of the landscape with a high probability of providing high quality bog turtle habitat. Several important findings related to management were revealed. Hydric soils were not good predictors of high quality bog turtle habitat because hydric soils were so abundant over the landscape that they could not differentiate bog turtle habitat from non-habitat. However, hydric soils may be useful for ruling out areas that are not wetland areas at all. Wetlands identified on the National Wetland Indicator (NWI) maps were more common on bog turtle wetlands (28%) compared to random areas near streams (7%). Unfortunately, since the occurrence of NWI wetlands on bog turtle wetlands was so low, using only NWI areas to identify potential bog turtle habitats would result in many false negative predictions. According to the 2001 National Land Cover Database, vegetation in areas predicted as high quality bog turtle habitat was significantly less tall (herbaceous vs. large woody) than the proportion of vegetation available near streams. These findings suggest that bog turtles' requirement for open-canopied areas for nesting and thermoregulation is related to their selection of wetland habitats.

The topographic wetness index inverse was useful for identifying low areas near streams with a high likelihood of elevated water tables. The topographic wetness index inverse often predicted false positive wet areas in valley positions with channelized streams and drained wetlands. These landscape positions would be candidate areas to restore wetland conditions for bog turtles, or simply for restoration as part of required mitigation associated with Section 404 permits in the area.

Forty-four (44) of 50 (88%) known occupied wetlands in Virginia occurred within 56 meters of a USGS 7.5' quadrangle identified stream. The majority of these streams were 2nd and 3rd order streams as calculated on a 14 ha DEM-derived flow accumulation network (analogous to approximately 1st and 2nd order streams on a USGS 7.5' map). I reiterate that bog turtle wetland hydrology was not supplied by the streams passing through the wetlands, rather, stream order was an important feature describing the valley size and drainage position where bog turtle wetlands occur. Bog turtle wetlands were not found near streams greater than 3rd order (both DEM-derived and USGS-identified streams). The reason that bog turtle wetlands may occur near small to mid-sized streams is that these valley positions are more likely to support groundwater maintained hydrology rather than overbank flooding hydrology (Brinson 1993). Bog turtles may not be found as frequently near 1st order streams because these areas have a higher probability of drying because of reduced recharge areas relative to 2nd and 3rd order streams. Wetlands occurring along 1st order streams may also be less likely to be reached by dispersal events since these wetlands are further distances up the drainage from source populations.

During field-testing of my predictive model in Carroll County, Virginia, I found that 1-ha plots centered over actual bog turtle occupied wetlands had higher model scores than 1-ha plots centered over wetlands that were unoccupied or unknown. Scores from the Site Quality Analysis (SQA) followed the same trend. Despite the ability for both of these techniques to differentiate occupied wetlands from unoccupied or unknown wetlands, scores from the techniques were not correlated (Chapter 5). This non-correlation indicated that these habitat evaluation techniques were not measuring the same wetland properties. Indeed, two out of three of the GIS-derived variables (topographic wetness index inverse and presence of 3rd order streams) used to develop the model output were reflective of large-scale landscape features. The SQA features were developed from wetland-specific habitat measurements. Given the different performance of the two habitat evaluation techniques, combining them is difficult. A positive aspect of the GIS technique is the ability to use the model over a large scale, while a weakness is that the user must be adequately trained to operate the model. Another benefit of the GIS technique is that it accurately reflects the true variability seen over the landscape because it is developed from both used and non-used areas. A positive aspect of the SQA is its ability to be used intuitively on ground level, while a weakness is that the categorical questions used to assess habitat are not statistically weighted. Without a statistically-based system to weight the questions, the relative importance of each question to rank bog turtle habitats is unknown. In addition, some of the categorical questions in the SQA may not well-represent the true variability seen in bog turtle wetlands. For example, the first question in the SQA is based on wetland size. The SQA provides a score of "7.0" for a wetland > 5 ha and a score of "0" for wetlands < 1 ha. Field testing of wetlands in Carroll County identified 14 occupied wetlands. Of these wetlands, 12 were < 1 ha, and only one was > 5 ha. The importance of wetland size for bog turtle occupancy and demography must be investigated. Further, many small wetlands are part of a complex of wetlands, and it is unclear when one wetland ends and another begins. The methods used to assign wetland size are not generally standardized, and I believe that most wetland areas are overestimated because they include non-wetland areas. I suggest that when reliable estimates of wetland areas are desired (rather than the area of a complex of wetlands), the 3-criteria method should be used to delineate wetland boundaries (Wetland Training Institute, Inc. 1995).

DEMANDING ENFORCEMENT OF SECTION 404 OF THE CLEAN WATER ACT

Section 404 of the Clean Water Act regulates dredging and filling of jurisdictional waters of the United States. Regulation of some freshwater areas has been controversial due to the lack of a surface water connection to navigable waters of the United States (Downing et al. 2003). Surface water connections to navigable waters of the United States from most or all Virginia bog turtle wetlands are clearly evident and easy to establish and delineate. In my experience working with four different Regional offices of the COE (including the Norfolk office responsible for regulating all Virginia waters), I would not have suggested an isolated condition for any of the wetlands included in my detailed study of bog turtle wetlands. Operating a bulldozer or backhoe in jurisdictional waters of the United States is a regulated activity.

Exceptions to Section 404 do exist for farming operations that have used, and maintained, active drainage procedures in the 10 years before present. Indeed, many ditching activities in the Blue Ridge of Virginia are protected by this “grandfather clause.” Most ditching activities that I have observed do not fall under this clause because either the wetlands are not in farm use, or there is no evidence that the farm has been activity maintaining the ditches at least once every 10 years. Many people involved with natural resource management make a false assumption that any activity is permissible on wetlands located on private properties used for farming.

Why are laws regulating wetland dredging and filling important? These laws are generally important because they protect our water quality, water quantity, soil resources, and aquatic environments. Dredging and filling wetlands do not just affect areas in the immediate vicinity; they can also impact downstream areas. The rapid disturbance of sediments can result in a load of material that is too large to be transported within the channel. The result can be sediment deposition either on the bottom of the stream, or in the floodplain of the stream following overbank flow. Sedimentation over wetland surface soils can increase the proportion of coarse material on the surface, changing the physical qualities of the soil (Chapter 2). Coarse soils with little organic matter may reduce the quality of hibernation areas and even increase the risk of freeze damage to hibernating turtles (Costanzo et al. 1998).

In a more narrow view, by protecting wetland areas from drainage, bog turtle habitats will be protected by default. The management of bog turtle wetlands will improve, or arguably have at least a feasible chance of being effective in Virginia, only if all sectors of society become educated about existing federal and state wetland law. Constant debate about navigable waters has unnecessarily eroded wetland enforcement throughout the country. It appears that in Southwestern Virginia, wetland regulation has been rendered ineffective by confusion over how to interpret wetland laws and uncertainty as to whom the wetland laws apply, such as in the cases of lands used for agricultural or strip mining areas. In many situations, citizens may contest that wetland laws should not apply to them because of private property rights. State agency personnel, county engineering departments, and the people working for the federal agencies that are responsible for providing wetlands expertise need to be educated about which wetland activities are legal and which are not. Just as important, someone needs to hold enforcement agencies accountable for their responsibilities so that they, in turn, can hold accountable those responsible for infractions of wetland law.

Having written records of wetlands on private lands is the first step in identifying and monitoring how wetland ecosystems are changing over time because management activities that are causing negative impacts to wetlands are difficult to identify or avoid without prior site information. A potential screen for the presence of wetlands or the identification of illegal wetland activities may occur most practically during the sale of a property or during the application for a county building permit. During property sales or refinancing, banks often require a brief on-site visit (sometimes called a transaction screening) or a complete Phase I Environmental Site Assessment by an environmental scientist in order to locate any features of a property that could be considered as an environmental liability. Interestingly, noting the presence of wetland areas is desirable to lending institutions because they are viewed as a liability that lowers the property value (the same way as a floodplain would) because wetland acreage is not easily improved. When applying for a building permit, soil scientists often visit properties to determine if soils on the property have adequate permeability to safely accommodate a septic system. The presence of wetlands should be noted by the soil scientists in their site visit paperwork and retained in each county's building permits department. Finally, farmers that participate in federal cost sharing programs or subsidies are required to have a farm plan approved and filed by the NRCS. This farm plan should identify wetland areas.

Once Section 404 laws protecting wetlands from dredging and filling are consistently applied in the Virginia range of the bog turtle, the next challenging management activity will be to apply appropriate mitigation procedures in response to permitted wetland impacts. Mitigation activities must explicitly recognize the more stringent habitat limitations of wetlands providing habitat to bog turtles relative to the broad requirements needed to simply qualify as a wetland area. Under federal law, wetland restoration areas or created wetlands designed to mitigate permitted wetland impacts usually do not need to resemble the hydroperiod, and thus ecological function, of the impacted wetland as long as the mitigated area meets wetland criteria (Lewis 2001). The non-specific nature of wetland mitigation requirements has the potential to negatively impact bog turtle habitats in Virginia. As inevitable wetland impacts occur in the bog turtle's range, wetlands with a hydroperiod typical of bog turtle occupied wetlands could shift to wetlands with a less persistent hydroperiod, a more variable hydroperiod, or excessive inundation. This potential shift in wetland types could occur even while adhering to stated federal goals of no net wetland losses. Future wetland impacts in the range of the bog turtle must recognize the specific hydrologic conditions present in wetlands used by the species, as these conditions are difficult to recreate in the mitigation process.

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Conclusions

In the southern portion of its range, the bog turtle (*Glyptemys muhlenbergii*) is considered rare and is a species of conservation concern. All three of the definitions of rarity discussed in the well-known paper by Rabinowitz (1981) appear to apply to the bog turtle. The species has a small and disjunct range, is found at low densities in many of its habitats, and has specific habitat requirements. In this dissertation, I focused on how specific habitat requirements are an element of bog turtle rarity. Specifically, I evaluated how specific hydrologic and soil conditions are related to bog turtle habitat use and bog turtle behavior.

Overall, my findings emphasize the role of hydrology as a dominant factor in the habitat and ecology the bog turtle. Hydrology, described in terms of depth to the water table and extent of surface soil saturation, was found to differ between wetlands that were used or unused by bog turtles. These results suggest that bog turtle selection of wetland habitats, and ultimately occupancy rates, are related to hydrologic conditions. Bog turtle movement and activity were found to respond to changes in hydrology. Other habitat variables such as soil and vegetation are ultimately controlled through pathways originating from wetland hydrology (Mitsch and Gosselink 1993). It follows that hydrology is a principle variable to consider when evaluating bog turtle habitat use, describing the effect of weather and climate on bog turtle behavior, anticipating effects of land use changes in or around bog turtle wetlands, and employing management actions in bog turtle wetlands. Hydrology has the potential to differ as a response to drought and long-term climate changes, thus it is important to assess the persistence of wetland hydrology based on a monitoring design using repeated measurement events rather than a single observation.

In chapter 1, I found that water tables measured in wetlands used by bog turtles remained at a higher elevation and were more resilient to drought than water tables measured in unused wetlands. In wetlands used by breeding bog turtles, the water table remained within 15 cm of the surface for 24 of the 28 study months compared to 19 months in wetlands with no turtle encounters. The difference measured in water table elevation between used and unused wetlands was greatest during and after the drought of 2007 and 2008. The extent of surface saturation in the wettest portions of the wetland was found to be inversely related to water table depth (i.e. a deeper water table results in less surface saturation). Low water tables resulted in reduced availability of saturation, particularly on wetlands with no turtle encounters. During fall 2008 and spring 2009, these wetlands contained approximately 25% less saturated area near groundwater wells than did wetlands where breeding occurred.

Organic carbon contents averaged (± SE) 8.8% ± 0.66% in the surface soils of the most consistently wet portions of the study wetlands (Chapter 2). Although this carbon content was not great enough to qualify as organic material (requirement for organic soils), these elevated organic carbon levels are a direct result of persistent saturation made possible by groundwater discharge. Results suggested that somewhat higher organic carbon is present in wetlands used by bog turtles compared to unused wetlands. It is difficult to isolate soil conditions from hydrologic conditions in wetlands because hydric soils are by definition formed under the influence of persistent saturation. For example, bog turtles were found to select areas with lower strength soils than were randomly available in the study wetlands. Lower strength soils are associated with soils with high moisture contents and greater organic matter (To and Kay 2005).

The biological relevance of high water tables to bog turtles was discussed in Chapters 3 and 4. Using radiotelemetry, I found that active and hibernating bog turtles were almost always found at soil depths between 15 cm and the soil surface. During summer activity, bog turtles selected saturated locations 77% of the time. Bog turtles continued to select saturated locations when this resource was limited in availability. In winter, hibernating bog turtles remained below the water table, where temperatures remained above freezing and higher than nearby unsaturated wetland areas. During the summer when surface areas exposed to full sun reached temperatures exceeding 45°C, bog turtles avoided potentially lethal temperatures by accessing shade and saturated areas. Critical thermal maxima for the closely related wood turtle (*Glyptemys insculpta*) and the spotted turtle (*Clemmys guttata*) are both 41°C (Hutchison et al. 1966).

Movement and activity of bog turtles responded to water table hydrology (Chapter 4). Bog turtles were most active when conditions were wet and water tables were near the surface, but the likelihood of making a large move was greater during the driest conditions when water tables were deepest. When large turtle movements occurred, nearly all of the movement paths were confined to areas near streams. Furthermore, bog turtles frequently entered flowing streams or saturated ditches, particularly during the drought. These findings imply that bog turtle selection for saturated areas is strong enough to result in inter-wetland movements to seek saturated soils or to use atypical saturated habitats such as flowing streams or ditches when surface hydrology is limited. The occurrence of inter-wetland movement along streams indicates that a landscape approach, rather than a wetland by wetland approach, should be a consideration when establishing conservation measures for the bog turtle. The acknowledgement that fragmentation can hinder inter-wetland movement of bog turtles is not a new concept (Buhlmann et al. 1997). Nonetheless, my finding that most inter-wetland movements occur along streams implies that management incentives that conserve and protect near-stream areas will be the most effective at counteracting the effects of fragmentation.

An important goal in this dissertation was to ensure that my findings could be applied to wetlands beyond those actually included in the study. A related goal was to allow the results to be relevant among both wildlife scientists and wetland scientists. To achieve this, I used standard methods for characterizing water tables and soils including shallow groundwater monitoring wells, soil taxonomy, organic carbon content, and particle size analyses. This standardization is important because it allows for direct comparisons among wetlands included in future studies. By describing the vertical hydrodynamics of the water table, the presence of upward vertical gradients, and the presence of bog turtle wetlands in riparian depression, toe of slope, and headwater riparian landscape positions (Chapters 1 and 5), I was able to compare my findings to all wetlands in the landscape using the hydrogeomorphic (HGM) classification system (Brinson 1993, United States Department of Agriculture 2008). Although HGM classifications have not been used in the Blue Ridge of Virginia, generalizing HGM results among regions is useful and has been successful in other studies (Cole et al. 2008).

Why is broad comparability of my findings important? In this study, water table conditions measured in wetlands used by bog turtles were compellingly different from conditions in morphologically similar wetlands not used by bog turtles. Even greater differences in water table hydrology would be found if wetlands used by bog turtles were compared to the larger set of wetlands available in the species' range in Virginia, especially wetlands with different landscape positions and hydrology sources. I found that the mean depth to the water table of wetlands with breeding bog turtle populations during June through September 2009 was within 4.9 cm of the soil surface. In comparison, an area meeting minimum wetland criteria must only have water table elevations within 30.5 cm of the surface for two weeks of the growing season, which occurs between approximately May and October (Wetland Training Institute 1995). It follows that many wetland areas in the range of the bog turtle have hydrology that is much less persistent and more variable than the wetlands used by bog turtles. Broadly speaking, wetlands along large stream and river systems that receive hydrology from over bank flooding and in-stream wetlands are examples of locations where hydrology would differ greatly from the groundwater driven headwater riparian depression wetlands more typical of where bog turtles are found.

Under federal law, wetland restoration areas or created wetlands designed to mitigate permitted wetland impacts do not need to resemble the hydroperiod, and thus ecological function, of the impacted wetland as long as the mitigated area meets wetland criteria (Lewis 2001). The non-specific nature of wetland mitigation requirements has the potential to negatively impact bog turtle habitats in Virginia. As inevitable wetland impacts occur in the bog turtle's range, wetlands with a hydroperiod typical of bog turtle occupied wetlands could shift to wetlands with a less persistent hydroperiod, a more variable hydroperiod, or excessive inundation. This potential shift in wetland types could occur even while adhering to stated federal goals of no net wetland losses. Future wetland impacts in the range of the bog turtle must recognize the specific hydrologic conditions present in wetlands used by the species, as these conditions are difficult to recreate in the mitigation process.

Bog turtle habitat management that focuses on protection and conservation of areas near streams appears to offer the most straightforward and comprehensive strategy for bog turtle conservation. Conservation activities near streams such as preventing building of roads and structures should facilitate safe passage of turtles between habitats while accommodating habitat transitions and hydrologic changes occurring on the landscape. Wetland managers and bog turtle biologists should be prepared to adapt to the inevitable spatial changes to hydrology that will occur throughout the landscape as vegetative succession, sediment dynamics, cycles of beaver dam construction, and human activities (including creation of impervious surfaces or installation of wells that could affect the groundwater supply) occur in and around bog turtle wetlands. These hydrologic changes may result in home range shifts along streams or use of atypical habitats such as saturated roadside ditches posing potential risks to bog turtles.

In summary, the results of my field studies suggest that hydrology should always be considered a dominant factor in the ecology of bog turtle habitat. Changes to the hydrologic regime of bog turtle wetlands, whether a result of periodic drought, climate change, or anthropogenic activities such as draining and ditching, can have impacts to bog turtle habitat use and movement.

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Appendix A: Characteristics at the 12 wetlands investigated in Chapter 1 and the Group A wetlands in Chapter 2

Table A.1. Site characteristics at the 12 wetlands investigated in Chapter 1 and Group A wetlands in Chapter 2. Wetland size calculated using ArcMap 9.2, aerial photography, and first-hand knowledge of existing landmarks from site visits such as fence lines, tree lines, and farm structures. Wetland slopes calculated using 10 x 10 m DEMs and the Spatial Analyst tool in ArcMap 9.2. Dominant soil series determined using the Soil Survey Geographic Database (SSURGO) displayed on ArcMap 9.2. Dominant vegetation types determined based on qualitative observations during numerous site visits.

Wetland Group	VDGIF site #	Size (ha)	Slope (%)	Dominant soil series	Soil status	Dominant vegetation types (common names)
Breeding wetlands	1	0.48	5.3	Hatboro sandy loam	Hydric	green ash, alder, sedges, rushes, bulrush
1-6 (top to bottom)	3	0.58	3.9	Hatboro sandy loam	Hydric	bulrush, rushes, water smartweed, willow
Also referred to as	28	1.27	3.4	Hatboro sandy loam	Hydric	alder, bulrush, rush, sedge, sphagnum moss
Wetland 1-6 or	18, 2	0.50	3.4	Hatboro sandy loam	Hydric	alder, bulrush, swamp rose, rhododendron
Wetlands used by	19	0.44	6.0	Myersville loam	Non-hydric	alder, spirea, poison ivy, bulrush, agrimony
multiple bog turtles	84	0.27	2.7	Hatboro sandy loam	Hydric	bulrush, sedge, sphagnum moss
Transiently	48	0.12	8.8	Nikwasi-Dellwood complex	Hydric	alder, rhododendron, sphagnum moss, red maple
Used 1-2	100	0.22	4.1	Hatboro sandy loam	Hydric	bulrush, sedge, rush
No turtle	49	0.32	12.6	Edneytown-Ashe complex	Non-hydric	bulrush, sedge, rush, blackberry
encounters 1-4	98	0.58	2.1	Hatboro sandy loam	Hydric	alder, bulrush, agrimony, goldenrod, rice cut grass
	52	0.31	3.1	Hatboro sandy loam	Hydric	alder, bulrush, agrimony, goldenrod
	97	0.62	4.3	Delanco-Kinkora complex	Hydric	bulrush, rush, ironweed, sweetflag

Appendix B: Analytical results for composite surface soil samples

Table B.1. Mean soil properties in 24 wetlands in Virginia grouped by bog turtle use status and identified by its unique Virginia Department of Game and Inland Fisheries (VDGIF) database number. Wetlands were placed into three different groups based on turtle use status. Wetlands used by multiple bog turtles (n=12) were the same as the *a priori* used wetlands in Table 2.4. Wetlands that were transiently used (n=2) are wetlands where a single turtle was encountered during the study. Wetlands with no turtle encounters (n=10) are wetlands where no turtles were encountered throughout the study, and comprised the *post hoc* unused wetlands in Table 2.4. Together, the "transiently used" and "wetlands with no turtle encounters" groups comprised the *a priori* unused wetlands in Table 2.4.

Wetland Group	VDGIF site # (when available)	pH	Organic carbon (%)	Sand (%)	Silt (%)	Clay (%)
		-----------------from 0 – 18 cm depth-------------				
Used by multiple bog turtles	CC0106	5.8	8.7	48.1	38.4	13.4
	99	5.7	10.8	35.6	55.6	8.8
	CC0010	5.8	6.0	35.1	60.5	4.4
	CC0014	6.0	6.9	37.7	54.1	8.3
	23	6.4	8.7	22.9	70.9	6.2
	8	6.4	11.7	31.2	47.3	21.5
	1	6.6	9.5	35.4	58.8	5.8
	3	6.6	11.4	42.3	50.2	7.6
	28	6.7	11.0	27.4	63.0	9.7
	18 and 2	6.3	9.7	41.1	51.6	7.3
	19	6.5	4.9	51.2	42.0	6.8
	84	6.7	6.6	57.2	34.3	8.5
Transiently used	48	NA	15.7	48.7	41.1	10.2
	100	6.3	8.1	57.3	35.8	6.8
No turtle encounters	49	6.1	7.1	49.3	41.1	9.5
	98	6.2	9.1	44.7	48.7	6.6
	52	6.1	8.3	21.0	72.1	6.9
	97	6.2	7.2	41.1	53.0	5.9
	N/A random wetland	5.8	5.6	38.7	55.0	6.2
	N/A random wetland	6.2	4.2	29.9	64.6	5.5
	N/A random wetland	7.2	3.0	48.8	47.8	3.4
	N/A random wetland	6.4	5.0	31.0	64.5	4.5
	N/A random wetland	6.5	3.1	51.7	44.1	4.1
	N/A random wetland	5.8	4.1	53.0	43.5	3.6

Table B.2. Mean soil properties in 12 wetlands used by bog turtles in North Carolina. Sampling was completed in May 2009 in multiple counties located in the vicinity of the Blue Ridge Parkway. Multiple turtles were known to be present in each of the wetlands. Wetland names and locations are withheld to prevent illegal collection of turtles; however, the unique database number given by the North Carolina Wildlife Resources Commission is provided. Note: This data is not discussed within the dissertation.

North Carolina site #	pH	Organic carbon	Sand	Silt	Clay
		--------- % from 0 – 18 cm depth-------			
55	6.0	7.5	44.8	44.1	11.1
144	6.2	3.7	18.9	68.4	12.7
140	6.4	3.7	27.1	64.4	8.5
111	5.6	10.2	54.1	29.6	16.3
109	4.6	18.3	29.5	59.9	10.5
110	5.3	7.7	20.9	67.9	11.2
17	6.0	4.7	51.8	41.6	6.6
5	5.5	12.6	52.5	35.1	12.3
24	5.9	9.9	36.5	53.3	10.1
138	6.3	7.0	44.0	47.7	8.2
37	5.7	14.9	37.4	47.7	14.9
124	6.3	4.4	69.2	17.2	13.6