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PERSISTENCE OF A VULNERABLE SEMI-AQUATIC TURTLE IN AN INTENSIVELY-MANAGED FOREST LANDSCAPE

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PERSISTENCE OF A VULNERABLE SEMI-AQUATIC TURTLE IN AN INTENSIVELY-MANAGED FOREST LANDSCAPE

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the Graduate School of
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Master of Science
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by
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Accepted by:
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ABSTRACT

Understanding spatial and population ecology of organisms allows land managers to predict how changes in distribution and composition of landscape features influence persistence. Our goal was to investigate body size, sex ratios, survival, individual movements, and habitat selection of a vulnerable freshwater turtle species, the spotted turtle (*Clemmys guttata*), in an intensively-managed forest landscape in eastern North Carolina, USA. Spotted turtles naturally occur in wetland-dominated landscapes, but this system is heavily-altered, with >222,000 hectares of pine plantations and >10,000 km of ditches managed by Weyerhaeuser Company. During 2012-2013, we captured and individually marked 280 turtles, and used radio-telemetry ($n = 31$) to investigate movements and habitat selection at multiple scales. Spotted turtle monthly survival estimates were high with an annual population growth rate >1. According to a stage-based population matrix, adult and juvenile survival were the most sensitive vital rates in the population. Turtle movements and habitat selection were focused on ditch networks, which appeared to provide travel corridors between upland and aquatic sites as well as access to potential mates. At the local scale, turtles selected for greater understory closure, more pine needle substrate cover, and greater substrate temperature, suggesting scale-dependent behaviors (i.e. thermoregulation) and the importance of pine forest cover around the ditches. At the landscape scale, ditch features and middle-old aged stands were important predictors of turtle locations, which may provide important habitat for imperiled species in highly-managed forest ecosystems. Also, the persistence of spotted turtles, a vulnerable, wetland-dwelling species, in an intensively-managed upland and aquatic landscape may suggest credibility of certain management regimes given the decline of the species in more natural ecosystems.

DEDICATION

I would like to dedicate this thesis to my family. Their patience and support was invaluable through the many hours, weeks, and months of field work, analyses, and writing.

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INTRODUCTION

Burgeoning human population and per capita consumption have resulted in an increased demand for wood products throughout the USA (Wernick et al. 1996) which subsequently has resulted in an increase in high-yield production forestry. High-yield production forestry is based on single-aged, single-species forest stands managed on short rotations to produce high volumes of wood fiber (Smith et al. 1997). Since 1952 there has been a 16-fold increase in the area of pine plantations in the southern United States (Fox et al. 2007). With over 74 million ha of commercial forest lands (Schultz 1997), the Southern Gulf Coast and Atlantic states are considered the wood basket of the United States, providing approximately 15% of the world's wood fiber (Siry et al., 2006). Loblolly pine (*Pinus taeda*), a dominant planted species, occupies nearly 14 million ha of land in the southeastern US, provides large yields per hectare, is fast-growing, and is marketable at a relatively early age (Schultz 1997; Prestemon and Abt 2002; Jokela et al. 2004), making it a valuable wood fiber resource.

To produce high yields of wood fiber, commercial forest landowners manage pine plantations with genetically improved seedlings, mechanical and chemical site preparation and maintenance, and/or fertilization (Schultz 1997; Jokela et al. 2004; Fox et al. 2007; Jones et al. 2010a). In addition to chemical and mechanical management of forest stands, soil moisture is managed through dredging and maintenance of historical water control structures (Allen et al. 1990) where the water table is continuously high (Schultz 1997). The Middle Atlantic Coastal Plain of the United States had extensive pocosin wetland surface hydrology in the 19th Century (Richardson 1983), with longleaf pines (*Pinus palustris*) (Brinson and Rheinhardt 1996). Prior to the “Swampbuster” Provisions of the Food Security Act of 1985, much of the Coastal Plain of North Carolina was heavily drained by a network of ditches for agriculture, forestry, and peat mining (Richardson 1983; Cashin et al. 1992). Although further draining of wetlands cannot be created after the Act, current ditches can be maintained via mechanical dredging to original configurations. In such areas there are extensive ditch networks to lower the water tables for the growth and survival of planted pines. As a consequence of intensive management of the upland and aquatic matrix, the structure, composition, and hydrological regimes of high-yield production landscapes differ from more natural forests (Miller and Miller 2004). Although a monoculture, intensively-managed forestlands are comprised of patches of stand ages, with varying successional stages (Smith et al. 1997). Also, forests that are certified under programs such as the Sustainable Forestry Initiative are required to support and incorporate research into management for forest sustainability, and include significant set-asides of forest for streamside and wetland buffers, cultural sites, and other areas of ecological importance (Jones et al. 2010).

Understanding the impacts of silvicultural regimes is important for proper management of species and affects economic and ecological stability (Homyack and Haas 2008). Hence, the impacts of intensive forest management have been the subject of numerous studies, with species-specific effects (Wigley and Roberts 1997; Hocking et al. 2013). Commercial forestry has been documented in some cases to negatively impact wildlife populations, at least in the short term (Petranka et al. 1993; Barber et al. 2001;

Homyack and Haas 2009; Hanberry et al. 2013; Hocking et al. 2013). However, landscape-level heterogeneity of habitat types has been shown to be an important factor in maintaining species richness (Nogués-Bravo and Martínez-Rica 2004; MacKay et al. 2014). Unlike urbanized landscapes which have been the cause of the greatest forest loss in the southeast (Wear and Greis 2013), intensively-managed forests are spatially and temporally dynamic, which can be beneficial to populations at the landscape scale (Wigley and Roberts 1997; Thompson et al. 2003). The Shifting Mosaic Steady State (SMSS) concept, developed by Bormann and Likens (1979), describes that patches of forests are at different successional stages, with varying biomass, species richness, and abundance, but can remain relatively constant at the landscape scale over time (Foushee and Wright 2009). Therefore, maintaining stand diversity, structure, and spatial connectivity may result in sustainable management of wildlife populations and promote biodiversity (Baskent and Jordan 1996; Wigley and Roberts 1997; Loehle et al. 2005), with minimal to no negative effects on landscape scale population structure (Chazal and Niewiarowski 1998; Renken et al. 2004).

There is limited information on responses of long-lived ectotherms to forest management (Jones and Dorr 2004; Diemer Berish et al. 2012; Currylow et al. 2012), especially turtles. Semi-aquatic turtles are ideal study organisms for understanding effects of intensively-managed forests because they require aquatic habitats to meet many life history needs, but also make frequent movements upland for nesting and thermoregulation. Because southern pine forest management involves manipulation of both terrestrial and aquatic systems, studies of impacts of those regimes on semi-aquatic wildlife may illuminate synergistic effects of the terrestrial and aquatic matrices. However, not all managed forest lands have manipulated aquatic habitats in the southeast, and ditch systems are not universal. Our study species, the spotted turtle (*Clemmys guttata*; Figure 1), ranges from northern Florida to Maine along the Atlantic Coastal Plain and Piedmont, westward through Ontario, New York, Pennsylvania, central Ohio, Indiana, and Michigan to northeastern Illinois (Ernst and Lovich 2009). Across their range, spotted turtles use shallow wetland habitats including ephemeral pools, swamps, bogs, fens, marshes, and small woodland streams (Lovich 1990; Joyal et al. 2001; Milam and Melvin 2001; Litzgus and Mousseau 2004; Beaudry et al. 2009).

Globally, turtles are a highly-imperiled taxa (Gibbons et al. 2000), and the spotted turtle is no exception. Spotted turtles are listed as endangered under the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, because the species has experienced an overall population reduction of 50% given a generation time of 25 years or more (van Dijk 2011), and international trade is regulated by recent inclusion on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES; Commission Regulation (EU) No 750/2013). The state provincial status of spotted turtles in the southeast is primarily “vulnerable” (Florida, Georgia, and North Carolina), but is considered “secure” in the state of South Carolina. Vulnerable is defined as being at moderate risk of extirpation due to a restricted range, relatively few populations (21-80), recent widespread declines, etc. (Bailey et al. 2006). Being a K-selected organisms with low fecundity (Litzgus and Mousseau 2006) and low egg survival (Ernst 1976), spotted turtle populations rely on survival of adults for population persistence (Enneson and Litzgus 2008). Spotted turtles, like most semi-aquatic turtles, have been declining due to loss of wetland habitat, poaching for the pet trade, and vehicle-related mortality (Ernst and Lovich 2009), all which negatively impact adults. Vehicle-related mortality is of particular concern and occurs during inter-wetland movements (Joyal et al. 2001) that often require crossing roads (Beaudry et al. 2008; Shepard et al. 2008; Patrick and Gibbs 2010). Ultimately, death by vehicle collision is reported mostly for gravid females who move upland to seek nest sites (Aresco 2005).

Monitoring spatial ecology and demography provides insight regarding an organism's susceptibility to management practices (Garshelis 2000; Fahrig 2007). Presumably, animals have higher fecundity and survival in habitats they prefer (Garshelis 2000), and the structure of a population hinges on the balance between recruitment and mortality. Therefore, understanding habitat selection and survival of a population is paramount for proper management and conservation (Lebreton et al. 1993). Spatial ecology integrated with information on population structure and multi-scale habitat selection can give a comprehensive picture of the aforementioned impacts, in that they are ecologically important by influencing species interactions, speciation, fitness, and population and community responses (Morris 2003; Borger et al. 2008). Few spotted turtle populations have been studied in highly reconfigured landscapes (Bottini 2005; Kaye et al. 2006; Yagi and Litzgus 2012); thus, we studied spotted turtles in an intensively-managed forest. If spotted turtles, classified as vulnerable, threatened, or endangered due to anthropogenic causes associated with development, can persist in a landscape that is managed for timber production, we can confidently give insight as to how to restore turtle populations in other areas. We investigated spotted turtles on loblolly pine plantations with extensive ditch networks in the Atlantic Coastal Plain of North Carolina. The objective of this study was to investigate three components of spotted turtle response to intensively managed landscapes: 1) population and life-history characteristics including population structure, nesting ecology, survival, and growth rate; 2) movement patterns and home ranges; and 3) habitat selection at the local-scale and landscape-scale. We hypothesized that our study population of spotted turtles in this intensively-managed forest landscape was sustained due to the ditch network, which may provide adequate movement corridors between essential aquatic and terrestrial sites, such as wetland areas, hibernacula, and estivation habitat. We predicted that movements and home range size would be different between males and females in this highly-ditched landscape, and that male movements would be considerably greater in the pre-nesting season compared to other seasons, because they are known to actively seek out females for courtship (Ernst 1970).

Figure 1. Spotted turtles (*Clemmys guttata*) are semi-aquatic, freshwater turtles that reside in a variety of wetland ecosystems. The species is declining due to habitat destruction and alteration, poaching for the pet trade, and vehicle mortality.

METHODS AND MATERIALS

Study site

We conducted this study on privately-owned timberlands in the Middle Atlantic Coastal Plain Ecoregion in Beaufort and Craven Counties of eastern North Carolina (Figure 2). The exact study location remains confidential due to the threat of poaching on spotted turtles for the pet trade. We conducted this study on an intensively managed pine landscape owned and managed by Weyerhaeuser Company for loblolly pine sawtimber.

Weyerhaeuser Company manages >10,000 km of ditches by dredging each ditch approximately every 20-25 years. They also manage >222,577 hectares of pine plantations with extensive, gated gravel roads in the Coastal Plain of North Carolina.

From this landscape, we selected 16 roadside ditch segments that varied in the length of time since maintenance had occurred. Prior to the start of the study, we used an approximate chronosequence approach and selected ditch segments that were last maintained 3 years (n=4), 6-8 years (n=4), 10-12 years (n=4), and 15-17 years (n=4) prior to the start of the study. Each site had ≥ 500 m segment maintained to avoid confounding effects of varying stand age. Of the ditch segments, we surveyed 25% of each site with a random starting point. We relied on hard copies of engineering reports from the landowner, which described the extent and timing of ditch maintenance, to compile a list of potential study sites. We visited sites and visually confirmed that the recorded maintenance history was consistent with vegetation structure and ditch configuration. Although available information regarding ditches prevented us from randomly selecting sites from the study area, the ditch segments we studied spanned 3-17 year post maintenance, were adjacent to plantations 1-33 years old, and thus were representative of those available on the landscape.

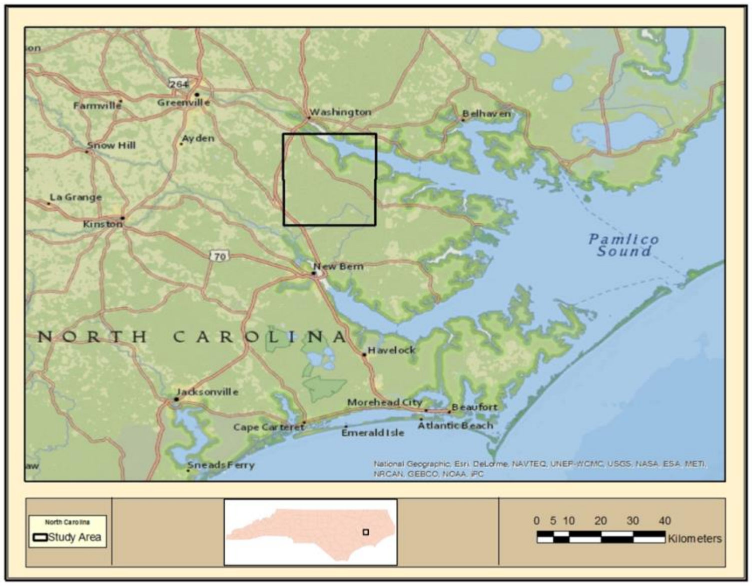

Figure 2. The study site and its setting in the Middle Atlantic Coastal Plain of North Carolina, USA.

Capture and radiotelemetry

We captured adult spotted turtles between January 2012 and April 2013 opportunistically, during visual encounter surveys, or from hoop traps for radiotelemetry and tracked turtles until July 2013. We captured turtles across 16 ditch sites with varying years since they were maintained. Upon capture, we uniquely marked all individuals by shell notching on the carapace and plastron with a battery-powered rotary tool using a modification of Cagle's method (1939). We measured plastron length (mm), carapace length (mm), mass (g), and significant abnormalities and injuries (see "Population Structure" methods). We attached Holohil RI-2B very high frequency (VHF) transmitters (Holohil Systems Ltd., Carp, Ontario, Canada) to 31 animals (15 females; 16 males) with high strength 5-minute epoxy (ITW Devcon, Danvars, MA, USA) on the anterior portion of the carapace to avoid interference with courtship and mating and to reduce drag from the antenna. Transmitter models weighed 10 g or 15 g, amounting to 8% of the body mass of the animal on average (range = 5-14%). We handled, marked, and released animals within an hour of capture. Transmitters were removed at the end of the study.

We located radio-tagged individuals approximately 1-2 times per week with at least 48 hours between locations to avoid serial autocorrelation. We located turtles using an R-1000 VHF receiver (Communication Specialists, Inc., Orange, CA, USA) handheld unit and a “rubber ducky” (RA-23K VHF) antenna (Telonics, Inc., Mesa, AZ, USA). We recorded locations between 0600 and 2000 (>90% of locations between 0800 and 1700), and we estimated GPS coordinates using a Trimble Juno handheld GPS unit (Trimble Navigation Ltd., Sunnyvale, CA, USA). We converted coordinates to decimal degrees on the 1983 North American Datum and processed as a point layer in a geographic information system (GIS) using ArcMap (ArcGIS Desktop v. 10.0, ESRI Inc., Redlands, CA, USA). When possible, we recorded GPS coordinates at the visual location of the animal. When animals could not be visually located (18% of locations), we used local triangulation and took GPS coordinates within 1 m of the estimated location.

Population structure

Upon initial capture and subsequent recaptures of an individual spotted turtle, we recorded the location and whether an individual was new or a recapture. We also recorded shell lengths (carapace and plastron) to the nearest 0.1 mm using a straight-line ruler or calipers. We recorded body mass of individuals with a spring scale (1000 g, Pesola, Kapuskasing, Ontario, Canada). We documented plastron length for the entirety of the study, and straight-line carapace length during 2013. Thus, we used plastron length for body-size frequency distributions. We compared our sex ratios and biometrics with those of other spotted turtle studies. We constructed body size frequency distributions by site, season, and month of capture, separated by gender and age stages for all captured turtles. We used three biologically-relevant seasons: pre-nesting, nesting, and post-nesting. We defined pre-nesting season as the period between emergence from hibernation and the first detection of a gravid female; nesting season as the period from which the first gravid female was detected and the last day of known oviposition; and post-nesting season as the period after the last day of oviposition and the last day of hibernation. We determined whether a female oviposited by direct observation or by recording no eggs via palpation from a known gravid female. Because female and male spotted turtles mature at similar sizes and ages (Litzgus and Brooks 1998), we determined size at sexual maturity (in plastron length) of males to be greater than or equal to the smallest individual showing secondary sex characteristics (concave plastron, dark chin morphology, and cloaca protruding past the posterior margin of the carapace; 71 mm). We determined size at sexual maturity of females to be ≥ the smallest gravid individual documented during the study (81 mm), because sexually immature females could exhibit female secondary sex characteristics (Ernst 1975; Ernst and Lovich 2009)

During the nesting season, we frequently monitored gravid, radio-marked females. We determined whether females were gravid by palpating between their hind legs and the edge of the plastron bridge, feeling the abdomen for eggs. Spotted turtles lay 1-4 eggs per nest at night, and (Ernst and Lovich 2009), making nests difficult to find (Beaudry et al. 2010). We employed two methods to determine nest locations: 1) we attached a thread-bobbin to the posterior margin of the carapace to track real-time movements of gravid turtles (Beaudry et al. 2010), and 2) we manually monitored gravid females at night using a high-beam red filter spotlight approximately 15 m away in order to avoid disturbing the turtles. We conducted nightly surveys of gravid females during nesting seasons from sunset to approximately 0300 hours depending on female behavior.

Using our mark-recapture data, we calculated survival and detection probabilities for our population with a Cormack-Jolly-Seber (CJS) live capture-mark-recapture analysis for open populations (Cormack 1964; Jolly 1965; Seber 1965). CJS provides an apparent survival estimate, which does not discriminate between death and emigration. We limited our model selection approach to a set of eight parsimonious candidate models that described apparent survival and detection probabilities as a function of time. We compared different subsets of models from our data: survival ($\Phi(.)$) or recapture ($p(.)$) (or both) constant with respect to time, models where either survival ($\Phi(t)$) or recapture ($p(t)$) (or both) varies with time, or models where either survival or recapture (or both) are constant over time for males and females ($\Phi(g)$ and $p(g)$, respectively (Lebreton et al. 1992). After conducting a sensitivity analysis on the time frame for survivability and detection, we chose to use monthly time increments, because our capture effort was roughly equal across the study area per month. We conducted the CJS analysis using Program MARK, which uses numerical maximum likelihood techniques to produce model parameters (White and Burnham 1999), and we compared models using Akaike's Information Criterion (Akaike 1974) adjusted for small sample sizes (AIC_c; further described under "Local Scale Habitat Selection").

We investigated the projected intrinsic population growth rate (λ) of this population using adult annual survival estimated by our CJS analysis and vital rates from Enneson and Litzgus (2008). We converted monthly survivorship (by sex if possible) to annual value by raising it to the power of 12. We constructed a pre-hatching pulse female-based, Lefkovitch three-stage population matrix (Lefkovitch 1965; Crouse et al. 1987) with life stages separated by size: 1) pre-hatching (eggs), 2) juveniles (sexually-immature), and 3) adults. We considered sexually-mature females to have plastron lengths ≥81 mm, the size of the smallest gravid female documented on our study area. This size is similar to other populations, which have been reported from 72-88 mm in plastron length (Litzgus and Brooks 1998).

We assumed a 1:1 sex ratio of hatchlings and estimated eggs laid/female (F_i) from the observed gravid females. However, we observed courtship activity during the post-nesting period (Sept-Oct), strongly suggesting bimodal reproduction in the population.

Bimodal reproduction has been observed in southern populations of spotted turtles (Enneson and Litzgus 2008; Ernst and Lovich 2009), which may be attributed to warmer climates. Given the observed behavior we assumed two nesting seasons and we doubled our estimate of eggs produced per year per female. We adopted egg and juvenile survivorship estimates Enneson and Litzgus (2008), who conducted a long-term study on spotted turtle demographics. Also, we had too small of a nest sample size to confidently determine egg survival.

Using our stage-based population matrix, we constructed analytical sensitivity and elasticity simulations (Caswell 2001) to predict how changes in vitals rates affect the population growth rate. We also constructed a population projection from the aforementioned population matrix to illustrate growth over 10 time steps for eggs, juveniles, and adults. Population matrices, sensitivity, elasticity, and projections were calculated with the PopTools 3.2.5 (G.M Hood, CSIRO Corporation) add-in to Microsoft Excel 2011 (Microsoft Corporation).

Movements

We estimated movement metrics for each individual radio-tagged turtle (*n*=31) by calculating the distance between two locations in a time series (Nieuwolt 1996). We calculated individual average daily distance by summing Euclidean straight-line movements during a season and dividing by the number of days in that season. We used a two-way analysis of variance (ANOVA) to test for differences in average daily distance between spotted turtle with sex and seasons as factors. Prior to analyses, we examined normality of data using a Shapiro-Wilk test and homogeneity of variances using a Bartlett's test. For a significant ANOVA, we used Tukey's honest significant difference (HSD) multiple comparison of means test to examine for differences in average daily distance between seasons. We calculated the distance between turtle locations using the adehabitatLT package in R (R Development Core Team 2012) and the ANOVA and HSD tests using R statistical software v.3.0.2 with alpha set to 0.05.

Home Range and Utilization Distribution

We employed two methods for home range and utilization distribution estimation for radio-marked animals. Burt (1943) defined the home range as the area traversed by the animal during its normal activities of foraging, mating and caring for young. First, we constructed 95% minimum convex polygons (MCP 95%; Mohr 1947) to compare the current study with prior ones (Burgman and Fox 2003). The MCP is the smallest polygon in which no internal angle exceeds 180 degrees and which contains all or most of the locations (Burgman and Fox 2003). By omitting 5% of the points, 95% MCP controls for outliers, and is commonly used for constructing utilization distributions (Getz et al. 2007). The MCP method is useful for defining an inclusive area, yet overestimates area and provides little information as to patterns of space-use, especially in linear aquatic systems like ours (Figure 3), and does not incorporate space-time relationships in the data (Lyons et al. 2013).

In addition to the MCP method, we used the time local convex hull method (T-LoCoH; Lyons et al. 2013), which is a better method for contouring to linear landscape features. The LoCoH approach is a non-parametric, bounded home range analysis that incorporates spatio-temporal patterns, constructs home ranges from movements influenced by boundaries such as streams and ditches, and applies the MCP construction to a subset of data (Lyons et al. 2013; Getz et al. 2007). The LoCoH method has been employed in numerous studies (Ryan et al. 2006; Temple-Miller et al. 2008; Loveridge et al. 2009; Beest et al. 2011; Bombi et al. 2011; Scull et al. 2012; Leuchtenberger et al. 2013). Further, the LoCoH approach creates convex hulls and density isopleths (i.e. utilization distributions) for each individual, by combining local MCPs constructed around each point (Getz and Wilmers 2004). The algorithm for the home range requires identification of a set of nearest neighboring points, and there are three options: fixed radius, adaptive, or fixed-*k* (Lyons et al. 2013). The fixed radius takes all points within a fixed radius; adaptive method selects the points whose cumulative distance is less than or equal to *a*; while the fixed-*k* method selects the k^{th} nearest neighbors around each point, a value selected by the researcher (Lyons et al. 2013). Further, local convex hulls are sorted by density which is proxied by hull area for the fixed-*k* method, and merged together creating an isopleth for a given percentage of points (i.e. 95% isopleths; Lyons et al. 2013). We chose to use the fixed-*k* method for our study animals, because it best represented their space use by contouring the home range to the extensive use of linear ditches. Due to the requirement of regularity between relocations of the LoCoH method, we used one location per week per individual for this analysis. In cases when there were multiple locations in a week, the first location was used for the home range analysis. We calculated home range and UDs using the T-LoCoH package for R statistical software v.3.0.2 (Lyons et al. 2013; R Development Core Team 2012). We compared home range sizes across gender, year, and method using a two-way ANOVA as described in "Movements".

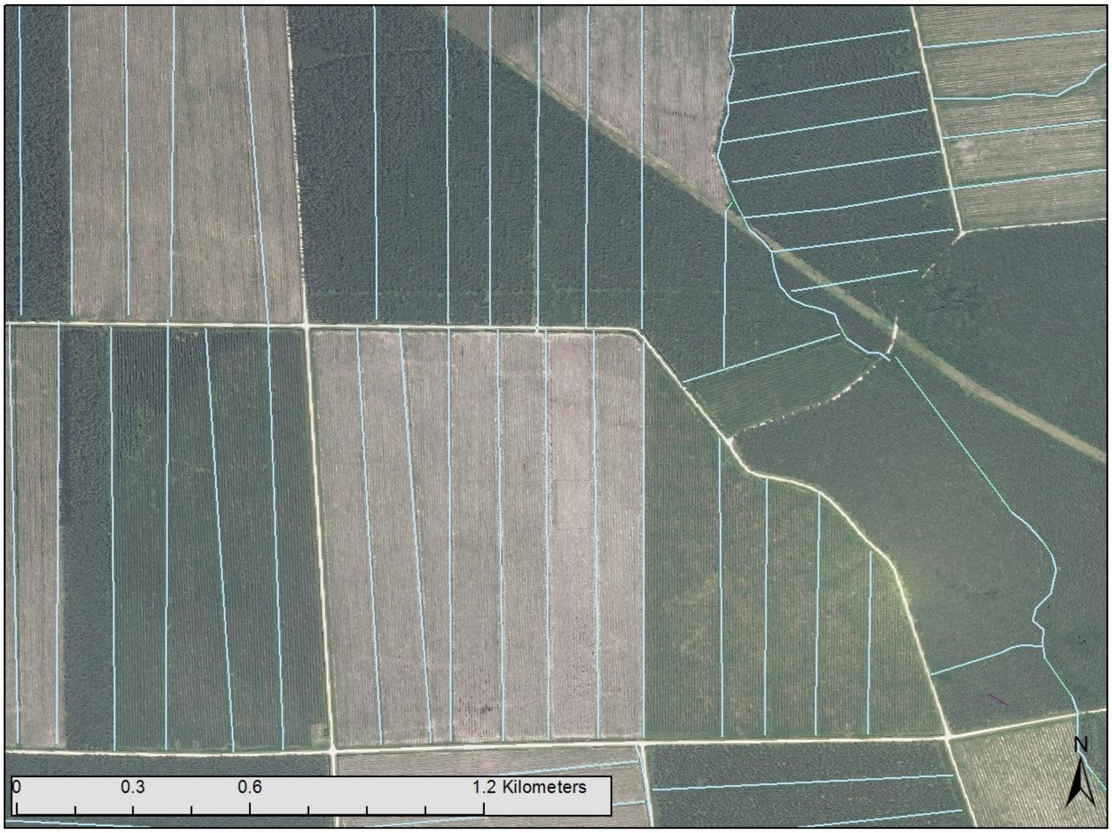

Figure 3. Linear ditch systems are maintained to regulate the water table for loblolly pine sawtimber production by Weyerhaeuser Company in the Atlantic Coastal Plain of NC. The blue linear features are the ditches and the white linear features are roads. Ditches typically border both sides of the roads in addition to inner-stand ditches. The landscape is a shifting mosaic of stand structure with dark green pine plantations and gray, young/harvested patches.

Local-level habitat selection

Habitat selection occurs when an organism uses habitats or habitat features disproportionate to available habitats (Johnson 1980). We adopted Garshelis' (2000) definition of a "habitat" to be a set of specific environmental features often equated to plant physiognomy, vegetative association, or cover type. We investigated local-scale habitat selection following a case-control (Keating and Cherry 2004), paired logistic regression design for radio-marked individuals under an information theoretic framework with a priori model selection (North and Reynolds 1996; Burnham and Anderson 2002; Compton et al. 2002). We estimated habitat metrics in square-meter plots centered on turtle locations (case plots) and at two additional locations (random/control plots) 2 m and 20 m away along a random compass azimuth. This design assumes that the habitat associated with the "control" plot is habitat that could be used by the animal. We considered the 2 m and 20 m scales to provide an accurate estimate of micro-habitat selection at biologically-relevant distances from the individuals. For example, the 2 m scale may provide inference as to the habitat selection of turtles in ditch systems, but the 20 m scale might provide insight to the influence of upland stands and other habitats that neighbor the ditch system. We visually estimated percent cover of deciduous leaf, pine needles, grasses/sedges, moss, bare soil, water, coarse woody debris (CWD), sticks/branches, woody shrubs, and herbaceous vegetation in the plot and followed a modified version described by Daubenmire (1959) to convert to cover classes (1= 0%, 2=1-5%, 3=6-25%, 4=26-50%, 5=51-75%, 6= >75%). Additionally, we measured substrate temperature (either soil or water), air temperature, and relative humidity with a soil thermometer or thermo-psychrometer (Optimum Energy Products Ltd., Alberta, Canada), and understory openness from the turtle's perspective at ground-level using a spherical convex densitometer. Further, we estimated forest stand structure by measuring basal area with a 10-BAF cruising prism. We described animal locations (e.g. road, upland, wetland, or ditch) and distance from CWD and standing water when known. When an individual was completely or partially covered by substrate, we considered that a "form" and recorded the form type (depression, leaf cover, woody cover, etc.), wetness (damp, saturated, or dry) and height/depth of the form. Forms are structures used for thermoregulation and protective cover (Baldwin et al. 2006) especially in ectothermic organisms like turtles.

To ensure stability of coefficients, we ran a Spearman's non-parametric rank-correlation coefficient matrix on our 40 habitat variables across all location plots (case plots; see Appendix A for data-sheet). We removed inter-correlated ($r \geq 0.4$) variables and variables with limited readings across plots. We chose the correlation cutoff of 0.4, because it represented a natural break in the data. We constructed eight biologically-meaningful, *a priori* candidate models (Hosmer and Lemeshow 1989; Tables 1) with 10 habitat variables (Table 2). We assessed model goodness-of-fit using a global chi-square test, which tests whether the model is different from the null model ($\beta = 0$; Allison 1999), and adjusted models as necessary. We ran paired logistic regressions for each individual with ≥30 location and paired random plots ($n = 27$) at the 2 m and 20 m scale. Paired logistic regression has been used in multiple habitat selection studies (Compton et al. 2002; Harden et al. 2009; Gorman and Haas 2011; Foley et al. 2012), and does not require multivariate normality or covariance equality of independent variables, thus allowing categorical variables in the analyses (North and Reynolds 1996). Additionally, paired logistic regression compares the location and paired random plots at the same time and location (Compton et al. 2002).

We conducted paired logistic regressions across the eight candidate models for each individual. Pooling locations leads to bias associated with individuals with more locations (Garshelis 2000). Conducting analyses separately by individuals allows the turtles to be the experimental unit, and inferences can be made of the larger population (Millspaugh and Marzluff 2001). We used an information theoretic approach (Burnham and Anderson 2002) and Akaike's Information Criterion to examine *a priori* models for parsimony and fit (AIC; Akaike 1974). However, AIC does not account for a small sample size, so we used corrected AIC (AICc; Hurvich and Tsai 1989), which is ideal for small sample sizes or models with many parameters (Burnham and Anderson 2002). Because AIC_c values are conditional for the data-set (i.e. the individual; Burnham and Anderson 2002), they cannot be compared across individuals. We used two approaches to examine the relative strength of models across individuals and separately by scale (i.e., 2 m or 20 m): 1) cumulative ranks, and 2) summed model weights (w_i). First, we adapted cumulative ranks from the low point scoring system used in sailboat regattas for comparing individual boat race results across races to produce a "winner" for the series (http://raceadmin.ussailing.org). Here, we ranked models from 1-8 based on ΔAIC_c values ranked (1-8) with "1" being the model where $\Delta AIC_c = 0$. Next, model ranks were summed across individuals to produce a cumulative rank for the model set. The most supported model across individuals had the lowest cumulative rank. Because the mathematical relationships within the cumulative rank approach are ordinal, we also summed across model weights, which are interpreted as the probability that a given model is the actual expected best model for the sampling situation considered (Hosmer and Lemeshow 1989). Together, we used a weight of evidence approach that combined information from the cumulative rank and summed model weights to summarize model selection results across individuals.

Table 1. Eight candidate models and their justification used to quantify local-level habitat selection of spotted turtles at the 2 m and 20 m scale in an intensively-managed forest landscape of eastern North Carolina, USA.

Model Name	**Model Variables**	**k**	***A Priori* Justification**	**Supporting Papers**
Pine stand protective cover	*under.open + lob.trees*	2	Have been documented to estivate under relatively closed canopies	Milam and Melvin 2001; Beaudry et al. 2009
Aquatic form protective cover	*under.open + water + decid.leaf + pine needles*	4	Known to bury under leaf cover in the water while hibernating, resting, or avoiding predators	Litzgus and Brooks 2000
Vegetation and woody debris cover	*under.open + grass + herb + stick*	4	Documented to bury under branches and vegetation while estivating, resting, or avoiding predators	Litzgus et al. 1999; Litzgus and Brooks 2000
Woody debris foraging and thermoregulatory conditions	*sub.temp + water + stick*	3	Feed mostly in the water with substrate temperatures above 15°C	Ernst 1976
Deciduous leaf foraging and thermoregulatory conditions	*sub.temp + water + decid.leaf*	3	Feed mostly in the water with substrate temperatures above 15°C	Ernst 1976
Pine needle foraging and thermoregulatory conditions	*sub.temp + water + pine needles*	3	Feed mostly in the water with substrate temperatures above 15°C	Ernst 1976
Soil foraging and thermoregulatory conditions	*sub.temp + water + soil*	3	Feed mostly in the water with substrate temperatures above 15°C	Ernst 1976
Global	*sub.temp + under.open + lob.trees + ALL COVER VARIABLES*	10	Model with all parameters. This model is used to assess goodness of fit.	Burnham and Anderson 1998

Table 2. Variables included in the local-scale analyses of spotted turtle habitat selection in an intensively-managed forest landscape of eastern North Carolina, USA.

Variable	Description	Method of measurement
decid.leaf	Categorical percent deciduous leaf surface cover estimated visually	0% (1), 1-5% (2), 6-25% (3), 26-50% (4), 51-75% (5), ≥ 75% (6)
grass	Categorical percent grass and/or sedge surface cover estimated visually	0% (1), 1-5% (2), 6-25% (3), 26-50% (4), 51-75% (5), ≥ 75% (6)
herb	Categorical percent herbaceous plant surface cover estimated visually	0% (1), 1-5% (2), 6-25% (3), 26-50% (4), 51-75% (5), ≥ 75% (6)
lob.trees	Pine basal area of loblolly pine trees surrounding plot	Estimated with a 10 BAF cruising prism
pine needles	Categorical percent loblolly pine needle surface cover estimated visually	0% (1), 1-5% (2), 6-25% (3), 26-50% (4), 51-75% (5), ≥ 75% (6)
soil	Categorical percent bare soil surface cover estimated visually	0% (1), 1-5% (2), 6-25% (3), 26-50% (4), 51-75% (5), ≥ 75% (6)
stick	Categorical percent woody debris (< 10 cm in diameter) surface cover estimated visually	0% (1), 1-5% (2), 6-25% (3), 26-50% (4), 51-75% (5), ≥ 75% (6)
sub.temp	Substrate temperature (°C) of soil or water, depending on the plot location	Estimated with a pocket case thermometer (water) or soil thermometer
under.open	Understory openness from a turtle's perspective (i.e. openness above 10 cm)	Estimated with a densiometer
water	Categorical percent water surface cover estimated visually	0% (1), 1-5% (2), 6-25% (3), 26-50% (4), 51-75% (5), ≥ 75% (6)

Landscape-level habitat selection

Studies of landscape-level patterns of forest disturbance have emphasized the importance of understanding species-specific responses in varying locales (Guerry and Hunter 2002; Russell et al. 2004; Loehle et al. 2005; Semlitsch et al. 2009; Currylow et al. 2012) . To assess selection of landscape features by spotted turtles, we compared individual turtle activity areas (*n* = 32) with random areas (*n* = 32) across the study site. Activity areas were defined for each turtle as those areas encompassing the 10% density isopleth constructed from the T-LoCoH home range estimate. We conducted an examination of isopleth size and chose 10% because it contained areas used intensively by each individual (Getz et al. 2007). Secondly, we constructed centroids for each of the resultant activity area polygons, and generated an equal number of random points for each activity area (Figure 4). We constrained random points to the ditch network and isolated wetlands within the outermost boundaries of all animal locations (100% MCP), because these were the expected and observed areas of our radio-tagged individuals. Although the landscape contains a network of ditches, it still has surface hydrology including abundant ephemeral wetlands (Leonard et al. 2012), which turtles often used. To reduce spatial autocorrelation, we removed random points within 300 m from any activity area. To maintain independence of activity areas, we averaged parameter values for those individuals with multiple activity areas (*n* = 3). Next, we constructed biologically-relevant buffers (Bodie 2001) around activity area centroids and random points with three radial distances: 30 m, 175 m, and 300 m. We chose the 30 m because it equaled the average daily distance moved by our radio-marked individuals, the 175 m because it represented average weekly distance moved and the 300 m because Semlitsch and Bodie (2003) recommended nearly 300 m as buffers for terrestrial habitat use in reptiles. Within these scales, we compared landscape features from GIS. These included: percent of the buffer in forest stand age classes (young: 0-5 years old; mid-late: 6-20 years old; late: 20-30 years old, and natural: 30+ years old), total length of ditches (both inner-stand and roadside ditches), length of roads, distance to nearest wetland, and area of wetland within the buffer (Table 3). We obtained wetland GIS layers originating from Leonard et al. (2012) of which mapped isolated wetlands using LiDAR technology in Beaufort and Craven Counties of NC. Stand ages and ditches were validated by visual confirmation or using 2012 orthoimagery from the United States Department of Agriculture (USDA) Natural Resources Conservation Service (NRCS) Geospatial Data Gateway.

After quantifying landscape-feature data, we ran a Spearman's non-parametric rank-correlation coefficient matrix on our set of eight habitat variables across all 32 activity areas. We removed highly correlated ($r \geq 0.6$) variables and discarded "Area.Wetland", which was highly correlated with "Dist.Wetland" ($r = -0.82$) and "Ditch.Length" ($r = -0.61$). We used a backward elimination procedure to produce a set of top candidate models for habitat selection. Since stepwise model selection can produce a false reliance on a single best model (Wittingham et al. 2006), we chose to include all competing models within two AIC_c values of each other (Burnham and Anderson 2002). Logistic regressions were conducted in program R (R Development Core Team 2012).

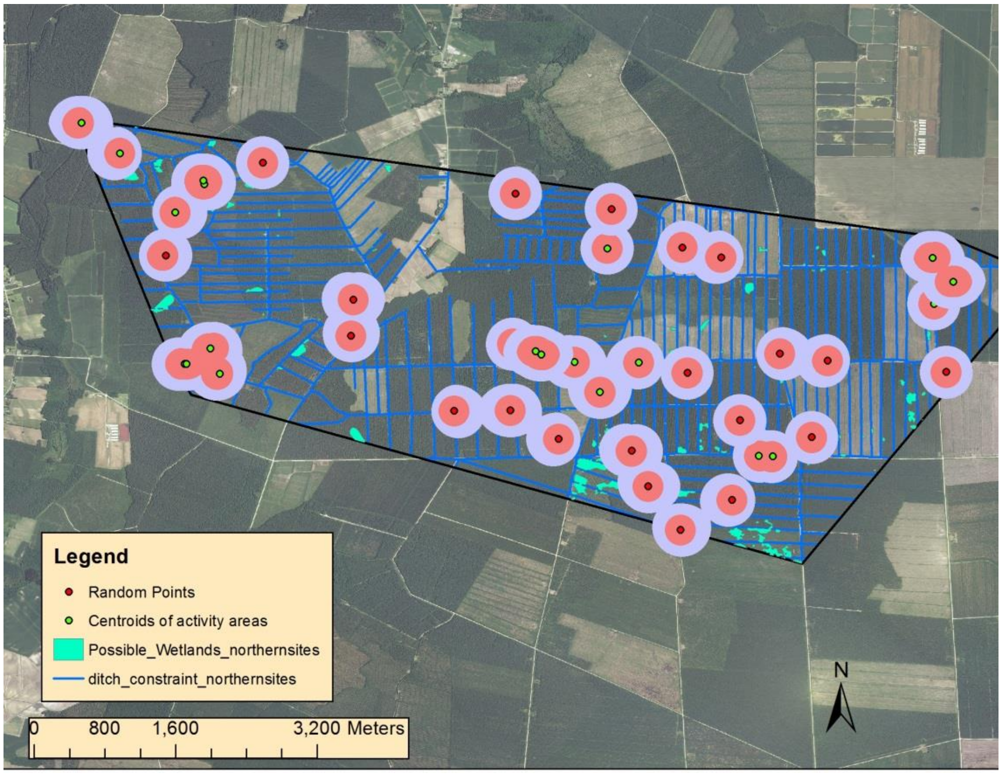

Figure 4. An example of activity area centroids (green dots) with an equal number of random points (red dots) buffered by multiple scales (30 m, 175 m, 300 m) to assess landscape-level habitat selection of spotted turtles in an intensively-managed forest landscape in eastern North Carolina, USA. Both activity area centroids and random points were constrained to the ditch network and isolated wetlands.

Table 3. Variables used to quantify landscape-level habitat selection of spotted turtles at the 30 m, 175 m, and 300 m scales in an intensively-managed forest landscape in eastern North Carolina, USA.

Variable	Description	Method of measurement	Supporting papers
Young.Stand	Area of forest stands (in square meters) that have no tree cover, or are < 5 years old	Stand polygons were clipped and area measurements calculated for each buffer scale in GIS, using the "clip" tool	Russell et al. 2002a Renken et al. 2004 Currylow et al. 2012
Mid-Late.Stand	Area of forest stands (in square meters) between 6-20 years old	Stand polygons were clipped and area measurements calculated for each buffer scale in GIS, using the "clip" tool	Renken et al. 2004
Old.Stand	Area of forest stands (in square meters) between 20-30 years old, and near the end of the rotation	Stand polygons were clipped and area measurements calculated for each buffer scale in GIS, using the "clip" tool	Renken et al. 2004
Stand.Natural	Area of forest stands (in square meters) > 30 years old and/or are restricted from commercial harvest	Stand polygons were clipped and area measurements calculated for each buffer scale in GIS, using the "clip" tool	Renken et al. 2004
Ditch.Length	Length of ditches (in meters). This includes both 3rd stage and roadside ditches	Ditches were clipped and measured for each buffer scale in GIS, using the "clip" tool	Yagi and Litzgus 2012
Road.Length	Length of roads (in meters)	Roads were clipped and measured for each buffer scale in GIS, using the "clip" tool	Patrick and Gibbs 2010 Langen et al. 2012
Dist.Wetland	Distance to the nearest wetland (in meters)	Distance was calculated for each buffer scale in GIS, using the "near" tool	Joyal et al. 2001 Russell et al. 2002b Beaudry et al. 2009
Area.Wetland	Area of wetland (in square meters)	Wetland polygons were clipped and area measurements calculated for each buffer scale in GIS, using the "clip" tool	Gibbs 1993 Joyal et al. 2001 Russell et al. 2002b Beaudry et al. 2009

RESULTS

Population structure

We captured 280 spotted turtles and marked 276. Three of the unmarked turtles were too small to be marked and one was an adult that escaped before marking. Most turtles were adults (94.6%); males (n = 177) were twice as common as females (n = 86), and juveniles (n = 15) and adults of unknown gender (n = 2) were least detected (Figure 5). We captured 73% of spotted turtles during the pre-nesting season, 21% during the nesting season, and 6% during the post-nesting season (Figure 6). February (21%) and March (25%) accounted for the most captures. Most individuals captured (56%) were between 81-90 mm in plastron length. Twelve gravid females were monitored during the 2012 field season, and 10 females were monitored in 2013. We identified five nests during the study (2012: n = 1; 2013: n = 4). All five nests failed during incubation periods from predation (n = 1) or flooding (n = 4). Four of five nests were constructed on ditch banks and eggs were exposed or under water following heavy rains. We documented 16 eggs ($\bar{x} = 2.7$ eggs/nest).

We ran CJS models with 226 individuals (159 males and 67 females) from our mark-recapture individuals after omitting radio-marked animals, juveniles, and adults with unknown gender. The most parsimonious model included constant apparent survival and time varying detection probabilities ($\Phi(.)\ p(t)$) ($w_i = 0.72$). Additionally, the model with constant survival and time-dependent detection probabilities ($\Phi(g)\ p(t)$; Table 4) also received substantial support ($w_i = 0.28$), but other models were not within two AIC_c

values of the minimum. For the first model, monthly survival was estimated to be 1.00. For the second model, monthly survival was similar between males (0.98) and females (1.00). The monthly detection probability averaged 12% for model 1 and 9% for model 2 (Table 4). We estimated annual survival by raising our monthly survival value to the power of 12. Our gender-based model indicated that males have a 78% probability and females a 100% probability of yearly apparent survival in our population.

In addition to the apparent survival estimates from the complete mark-recapture data-set, we conducted a post-hoc known-fate model from our 31 radio-tracked animals in Program Mark. The results indicated high weekly apparent survival (0.996), with annual apparent survival of 0.81. Two males died from predation and no female deaths were documented. Using our estimated apparent survival from the known-fate model (0.81), we conducted 400 simulations of population projection matrices in program R, with a range of egg (0.30 – 0.70) and juvenile annual survival values (0.45 – 0.85) from the literature (Enneson and Litzgus 2008) to examine uncertainties of these parameters (Figure 7). The results of the simulations show that greater juvenile and egg annual survival increases the population growth rate.

Our stage-based population projection matrix indicated probability of surviving and remaining a juvenile was 0.797 and the probability of surviving and remaining an adult was 1.00. Further, we estimated $\lambda = 1.06$, indicating the population was growing at an annual rate of 6%. We projected our population matrix over 10 time steps (in years) using the number of eggs, juveniles, and adults captured during the study as a baseline vector. The resultant time projection reveals a sharp increase in juveniles in slightly over a year, with a steady increase in number of eggs, but a slower rate of increase for adults (Figure 8).

Sensitivity and elasticity analyses indicated that the population growth rate was sensitive to a small change in adult survival and juvenile survival. The probability of surviving from being a juvenile to an adult was the most sensitive vital rate (2.55) in regards to the sensitivity analysis. Elasticity of the adult survival value (0.73) was >2× other elements of the population matrix (Figure 9).

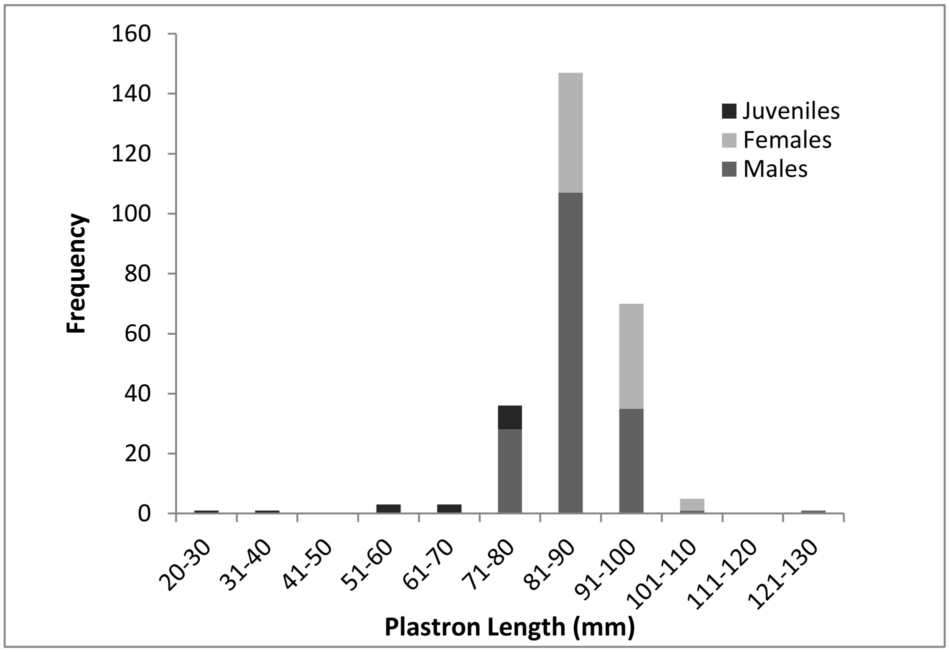

Figure 5. Body size frequency distributions of juveniles (*n* = 15), adult female (*n* = 79), and adult male (*n* = 172) spotted turtles in an intensively-managed forest landscape in eastern North Carolina, USA.

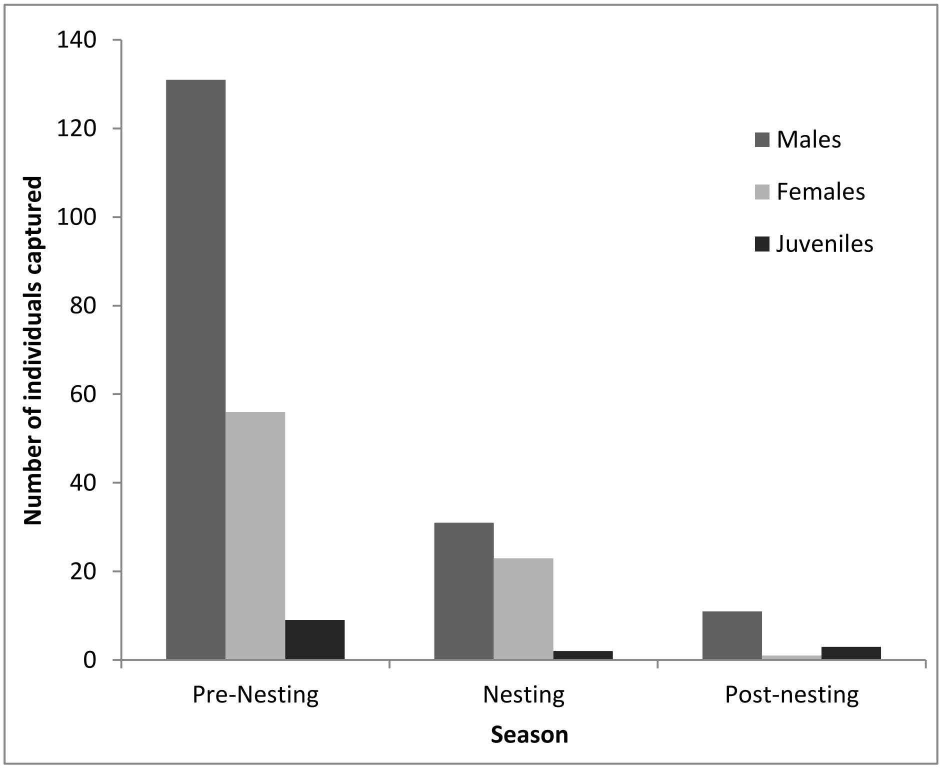

Figure 6. Number of individual spotted turtles captured across seasons in an intensively-managed forest landscape in eastern North Carolina, USA.

Table 4. Monthly apparent survival and detection probabilities for the top two selected CJS models along with yearly apparent survival estimates of spotted turtles in an intensively-managed forest landscape in eastern North Carolina, USA.

Model #	**Model**	**k**	**AIC_c**	**Delta AIC_c**	***wi***	***Monthly Φ* (± SE)**	***Mean Monthly p* (± SE)**	***Yearly Φ***
1	***Φ(.) p(t)***	12	915.76	0	0.72	1.00 (± <0.001)	0.12 (± 0.12)	1.00
2	***Φ(g) p(t)***	13	917.67	1.92	0.28	M: 0.98 (± 0.049) F: 1.00 (± <0.001)	0.091 (± 0.091)	M: 0.78 F: 1.00

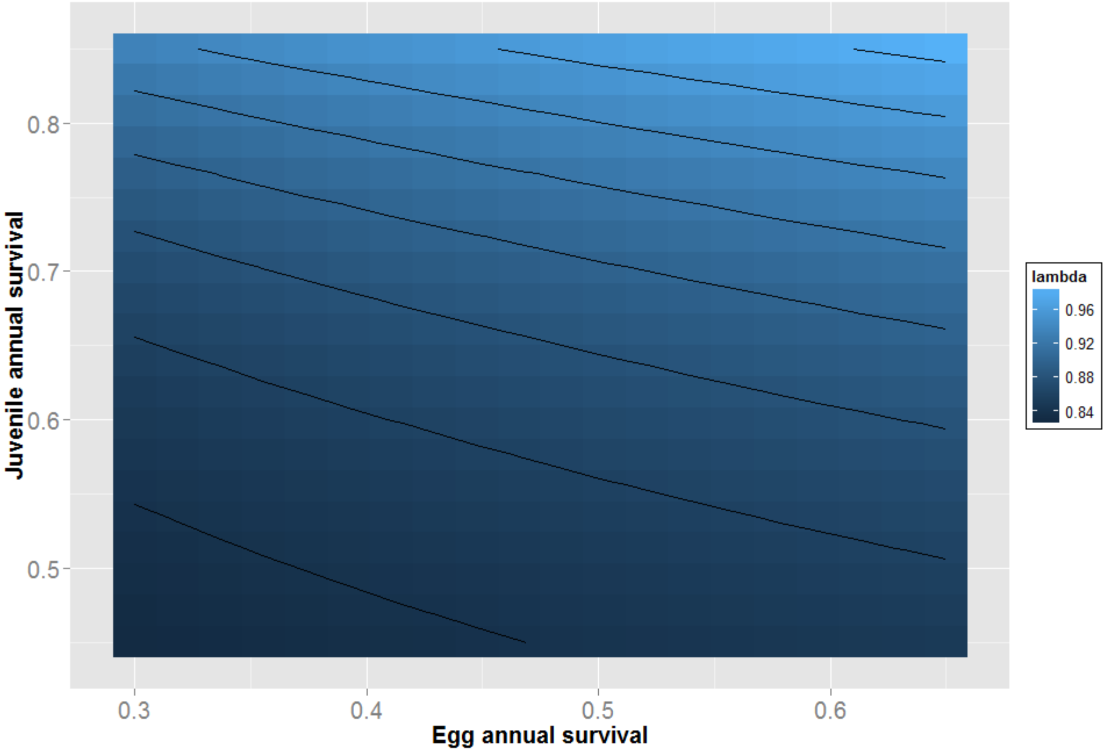

Figure 7. Surface contour plot of population growth rates (black lines and color scheme) as an effect of various juvenile and egg annual survival values reveals that increasing egg and juveniles survival rates will increase population growth rate. This is a result of 400 population projection matrix simulations of spotted turtles in an intensively-managed forest landscape in eastern North Carolina, USA.

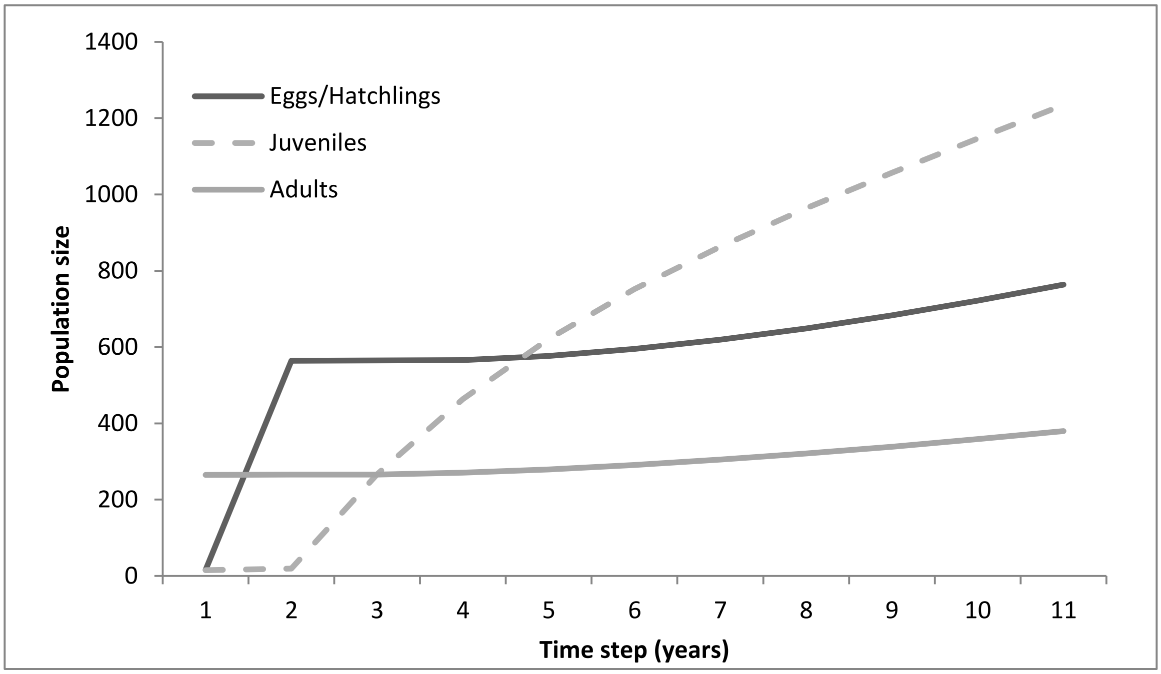

Figure 8. Number of individuals from a stage-based population matrix of spotted turtles with egg/hatchling, juvenile, and adult life-stages projected to 10 years in an intensively-managed forest landscape in eastern North Carolina, USA. We used the number of eggs, juveniles and adults observed during our study as the baseline vector for this projection.

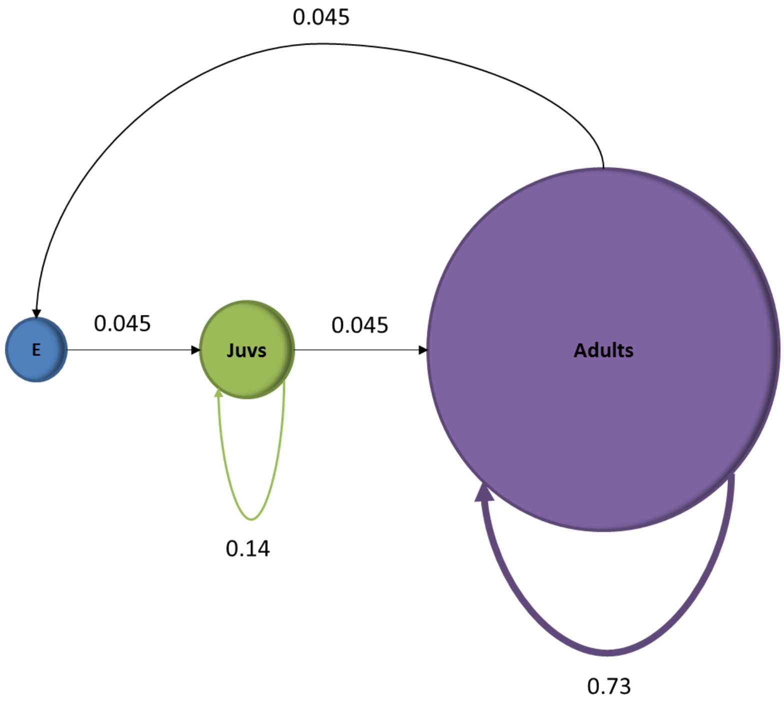

Figure 9. Life table diagram based off a stage-based population matrix of spotted turtles with arrows for each vital rate's elasticity value in an intensively-managed forest landscape in eastern North Carolina, USA. Adult survival had the greatest influence on the population growth rate. The size of the bubbles indicates reproductive value, which is the importance of different age classes to future reproduction –the larger the bubble, the more reproductive value.

Movements

We radio-tracked turtles 1-2 times/week. However, the emergence/courtship period had the most telemetry locations for both years, amounting to 45% of locations (Table 5). Data were normally distributed for males ($W = 0.956$, $P = 0.127$) and females ($W = 0.939$, $P = 0.035$), and variances were homogenous across genders ($k^2 = 0.399$, df =

1, *P* = 0.528). Average distance moved between relocations was 173.4 m (± 73.1 SE). Mean average daily distance was 29.7 m (± 16.6 SE) across all turtles (Table 6), and differed among seasons (*F* = 11.9, df = 2, *P* < 0.05) and between sexes (*F* = 8.87, df = 1, *P* < 0.05) but there was not a significant interaction (*F* = 2.89, df = 2, *P* = 0.062; Table 7). Mean average daily distance for the pre-nesting season was 39.1 m (± 24.6 SE), 43.4 m (± 22.5 SE) for the nesting season, and 26.4 m (± 21.7 SE) for the post-nesting season. More specifically, males differed from females significantly during the pre-nesting season (Table 8) and showed considerably longer movements (average daily distance = 43.5 m, ± 11.7 SE) than females (28.2 m, ± 14.7 SE) during this time, but were similar during other seasons (Figure 10).

Table 5**.** Individual radio-tagged spotted turtle (*n*=31) average number of relocations per week and number of locations for males and females by season in an intensively-managed forest landscape in eastern North Carolina, USA.

Season	Average # of locations per week per individual	Males total locations	Females total locations	Total
Pre-nesting	2	466	430	896
Nesting	1	193	211	404
Post-nesting	1	345	327	672
	Total	1004	968	1972

Table 6**.** (*n*=31) Mean average daily distances of individual radio-tagged spotted turtles compared across sex and season in an intensively-managed forest landscape in eastern North Carolina, USA.

Season	Average Daily Distance Males (SE)	Average Daily Distance Females (SE)	Average Daily Distance Total (SE)
Pre-nesting	50.1 (± 13.7)	28.2 (± 14.7)	39.1 (± 24.6)
Nesting	44.5 (± 24.6)	42.4 (± 21.1)	43.4 (± 22.5)
Post-nesting	25.3 (±12.7)	27.4 (± 28.2)	26.4 (± 21.7)
Total (all seasons)	32.6 (±13.7)	26.9 (± 18.9)	29.7 (± 16.6)

Table 7**.** Two-way ANOVA test of season, gender, and interaction of season and gender for average daily distance of spotted turtle individuals (*n*=26) in an intensively-managed forest landscape in eastern North Carolina, USA.

	DF	**Sum of Squares**	**Mean Squares**	**F value**	**P-value (>F)**
Season	2	4450	2220	11.9	<0.001
Gender	1	1660	1660	8.87	0.004
Season:Gender	2	1080	539	2.89	0.062
Residuals	72	13400	187		

Table 8. Tukey's HSD test of pairwise comparisons between seasons for average daily distance of spotted turtle individuals (*n*=26) in an intensively-managed forest landscape in eastern North Carolina, USA.

Season	**Difference in means**	**Lower 95% CI**	**Upper 95% CI**	**P-value (adjusted)**
Post-nesting-Nesting	-17.9	-27.0	-8.83	<0.001
Pre-nesting-Nesting	-4.91	-14.0	4.15	0.401
Pre-nesting-Post-nesting	13.0	3.92	22.1	<0.001

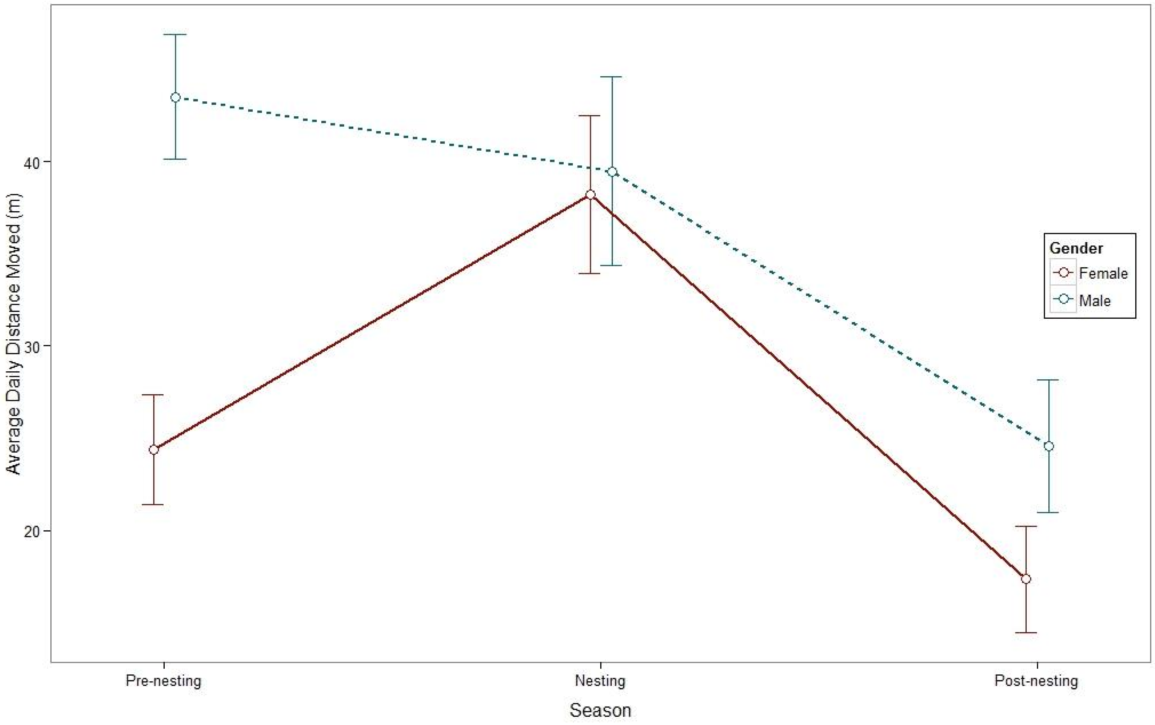

Figure 10. Average daily distance moved in meters and standard errors (SE) for spotted turtle individuals (*n*=26) across sex and season in an intensively-managed forest landscape in eastern North Carolina, USA.

Home Range and Utilization Distributions

We constructed home ranges for 28 of 31 radio-tracked spotted turtles with >40 locations. We tested for differences between years on 27 individuals, because one individual did not have enough locations for one of the years. Across all seasons, 95% MCP home ranges averaged 24.3 ha (± 6.73 SE), but averaged 12.3 ha (± 3.69 SE) during pre-nesting, 7.71 ha (± 2.89 SE) during nesting, and 11.8 ha (± 2.18 SE) during post-nesting seasons. There was a significant difference in MCP home range size between years (Wilcoxon signed rank: $z = 317$, $P < 0.05$; Figure 11), with home ranges in 2012 being 5.5 ha > than 2013 (2012: 15.9 ± 2.89 SE; 2013: 10.4 ± 1.86 SE). Male MCP home range sizes (mean 37.3 ± 50.3 ha) were significantly larger than females (12.2 ± 7.0 ha) ($F = 6.12$, df = 1, $P < 0.05$; Table 9). However, home range size did not differ across season ($F = 0.59$, df = 2, $P = 0.56$) and there was not a season × gender interaction ($F = 0.20$, df = 2, $P = 0.82$).

For the local convex hull approach, we used the 95% density isopleth as our home range metric. Individuals occupied home ranges that were on average 12.6 ha (± 2.54 SE) across all seasons of the project, 52% of average MCP home ranges. Further, sizes of turtle home ranges had less seasonal variation, amounting to 8.67 ha (± 2.16 SE) during pre-nesting, 8.96 ha (± 3.34 SE) during nesting, and 7.72 ha (± 1.49 SE) during post-nesting. There was a significant difference in LoCoH home range size between the years of the study (Wilcoxon signed rank: $z = 286$, $P < 0.05$), with 2012 home ranges on average 10.2 ha (± 2.22 SE) and 2013 home ranges on average 5.85 ha (± 1.04 SE). Conversely, home range size was not significantly different across season ($F = 0.30$, df = 2, $P = 0.74$), gender ($F = 1.96$, df = 1, $P = 0.17$), and season × gender interaction ($F = 0.77$, df = 2, $P = 0.47$) (Table 10). Although not significant, males have generally larger home ranges than females during the pre-nesting and post-nesting seasons (Figure 12).

Table 9. Two-way ANOVA test of season, gender, and interaction of season and gender for 95% minimum convex polygon (MCP) home range area (ha) of spotted turtle individuals (*n*=28) in a highly-managed landscape of Coastal North Carolina, USA.

	DF	**Sum of Squares**	**Mean Squares**	**F value**	**P-value (>F)**
Season	2	310	155	0.594	0.555
Gender	1	1596	1596	6.124	0.0155
Season:Gender	2	101	50.7	0.195	0.824
Residuals	77	20100	261		

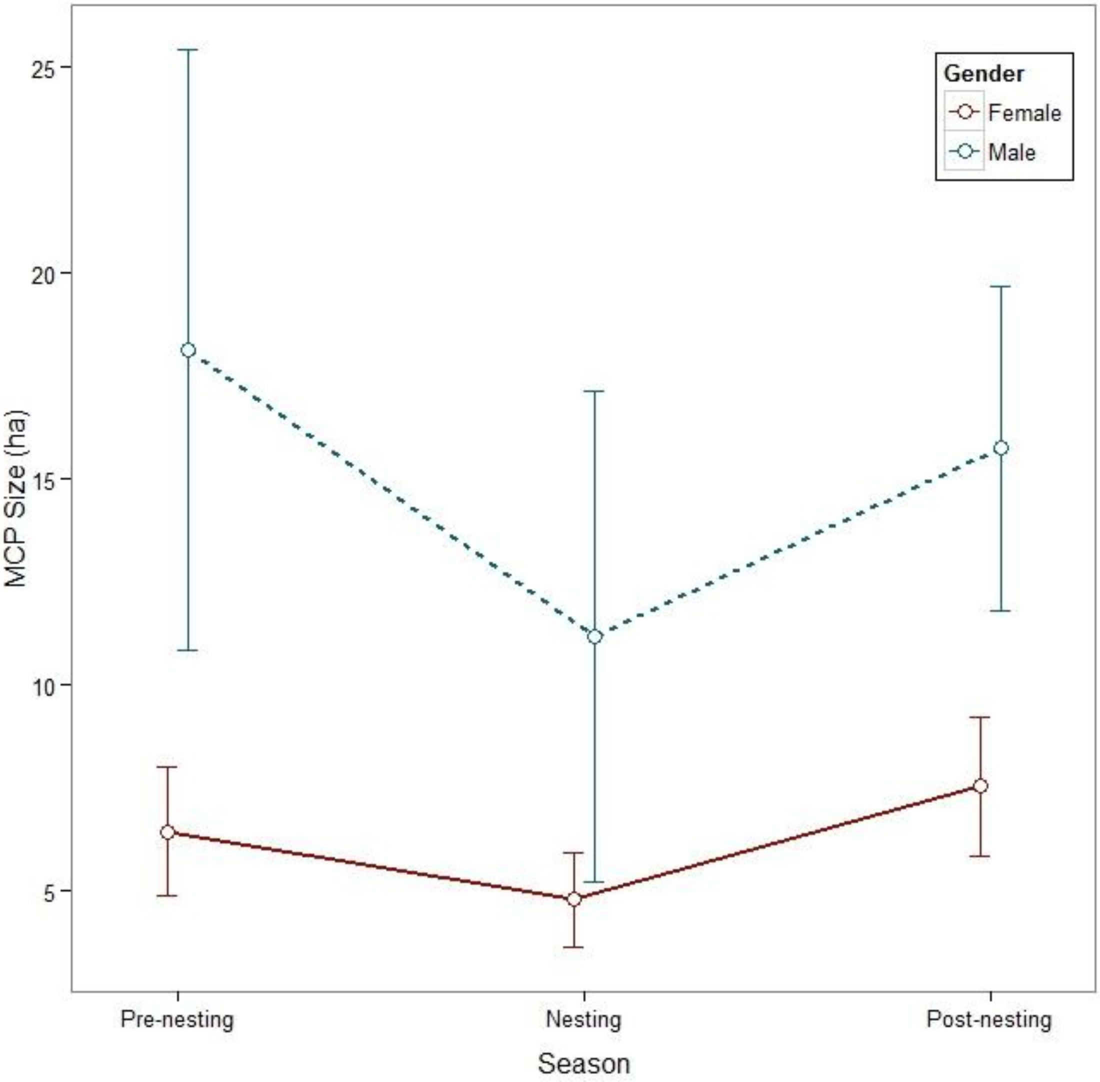

Figure 11. Ninety-five percent minimum convex polygon (MCP) home range area (ha) and standard errors of spotted turtle individuals (*n*=28) across sex and season in an intensively-managed forest landscape in eastern North Carolina, USA.

Table 10. Two-way ANOVA test of season, gender, and interaction of season and gender for time local convex hull (T-LoCoH) 95% isopleth home range area (ha) of spotted turtle individuals (*n*=28) in an intensively-managed forest landscape in eastern North Carolina, USA.

	DF	**Sum of Squares**	**Mean Squares**	**F value**	**P-value (>F)**
Season	2	43	21.63	0.299	0.743
Gender	1	142	141.58	1.96	0.169
Season:Gender	2	110	55.25	0.765	0.472
Residuals	44	3179	72.25		

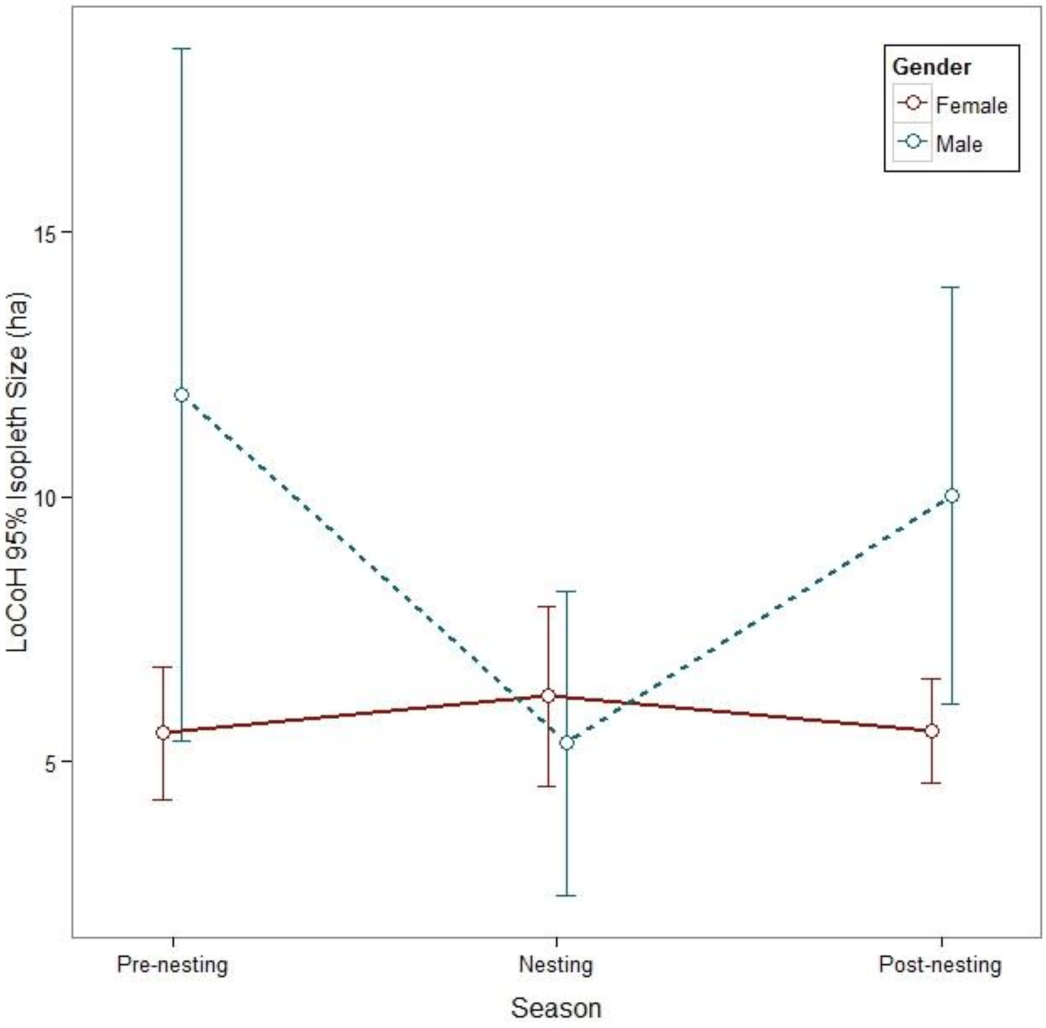

Figure 12. Time local convex hull (T-LoCoH) 95% isopleth home range area (ha) and standard errors of spotted turtle individuals (*n*=28) across sex and season in an intensively-managed forest landscape in eastern North Carolina, USA.

Local-level Habitat Selection

We collected habitat data for 31 individual turtles at 2256 location and paired random plots at the 2 m scale and 20 m scale. Turtle locations ranged from 9 – 106 per individual. Individuals were pared down by number of locations (at least 30 paired use and random plots) and presence of variables across plots, resulting in 1969 points for the 2 m scale analyses and 1974 locations at the 20 m scale analyses for 27 turtles. Nearly 85% of all locations were in the ditch system, with approximately 15% of locations in upland habitat (Figure 13). The remaining <1% of turtle locations were on roads. Turtles were in forms for >18% of locations with most forms consisting of leafy debris (deciduous and pine litter) or vegetation. We were confident in our placement of location plots for habitat selection analyses in that over 91% of locations had visual confirmation of radio-tracked individuals. Seventeen habitat variables were used for subsequent habitat analyses.

Both the cumulative rank and sum of weights approach indicated that the same models best described habitat selection at the 2 m scale. The model that described aquatic form protective cover was the highest ranked model ($\Delta AIC_c = 0$) for 23 of 27 turtles (total cumulative rank of 70), which also accounted for 30.7% of the total model weight (8.29 of 27; Table 11). The model that described soil cover foraging/thermoregulatory conditions was the second-highest ranked model for 20 of 27 turtles (total cumulative rank of 72), which also accounted for 25.9% of the total model weight (Table 11). Maximum likelihood coefficients of the highest-ranked model (*under.open* + *water* +

decid.leaf + *pine needles*; see Table 2 for detailed description of variables) indicated that turtles selected for habitats with increased closed canopy, percent water cover, slight presence of deciduous leaf cover, and a slight absence of pine needles. The median odds ratios (Table 12) suggested that water was the most important descriptor of selection (likelihood of selection increases over 600% with every one categorical unit increase of water cover). Further, for every 1% increase in understory openness, there was a 46% decrease in likelihood of selection, for every one categorical unit increase in percent deciduous leaf cover there is a 32% decrease in likelihood of selection, and for every one categorical unit increase in percent pine needle cover there is a 12% increase in likelihood of selection.

For the 20 m scale, the model describing deciduous leaf foraging/thermoregulatory conditions was the highest ranked ($\Delta AIC_c = 0$; total cumulative rank of 74), which also accounted for 20.8% of the total model weight (of 27; Table 13). The model that described aquatic form protective cover was the second-highest ranked model for 25 of 27 turtles (total cumulative rank of 72), which also accounted for 28.6% of the total model weight (Table 13). Maximum likelihood coefficients of the highest-ranked model (*sub.temp* + *water* + *decid.leaf*) indicated that turtles selected for habitats with increased percent water cover, deciduous leaves, and warmer temperatures. The median odds ratios (Table 14) suggest that water was the best predictor of selection. Further, for every 1°C increase in substrate temperature (either water or soil), there was a 12% increase in the likelihood of selection, and for every one-unit increase in percent deciduous leaf cover there was a 13% increase in the likelihood of selection.

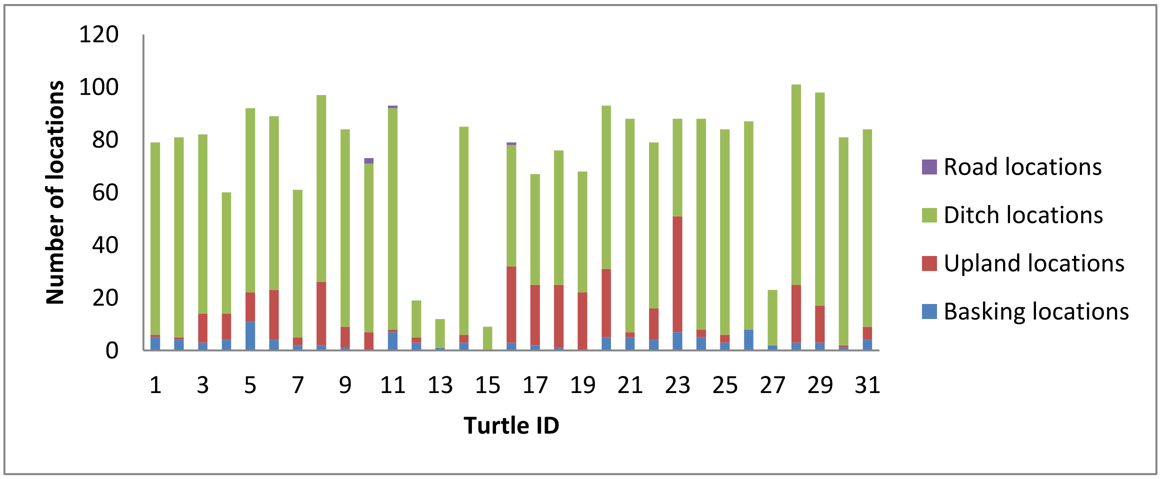

Figure 13. Number of road, ditch, upland, and basking locations of radio-tracked spotted turtles in an intensively-managed forest landscape in eastern North Carolina, USA.

Table 11. Comprehensive paired logistic regression models ($n = 8$) of habitat selection at the 2 m scale by spotted turtles in a highly-managed landscape of Coastal North Carolina, USA, supported by AIC_c ($n = 27$). *Models were ranked by level of AIC_c support and summed across individuals (maximum cumulative rank is 216). **AIC weights (w_i) were summed across individuals (maximum weight is 27) and converted to percentages to account for total model weight. ***AIC weights (w_i) were averaged across individuals (maximum weight is 1) and include standard deviation (SD) in parenthesis.

			Sum	**Sum**	**Mean**
Model Name	Model	k	Cumulative Rank	w_i ** (%)	w_i *** (SD)
Aquatic form protective cover	*under.open + water + decid.leaf + pine needles*	4	70	8.29 (30.7)	0.307 (0.304)
Soil foraging conditions	*sub.temp + water + soil*	3	72	7.00 (25.9)	0.260 (0.287)
Woody debris foraging conditions	*sub.temp + water + stick*	3	91	3.50 (13.0)	0.130 (0.194)
Deciduous leaf foraging conditions	*sub.temp + water + decid.leaf*	3	96	2.43 (0.090)	0.090 (0.106)
Pine needle foraging conditions	*sub.temp + water + pine needles*	3	113	1.85 (0.069)	0.069 (0.077)
Global	*sub.temp + under.open + lob.trees + ALL COVER VARIABLES*	10	126	3.91 (14.5)	0.145 (0.212)
Vegetation and woody debris cover	*under.open + grass + herb + stick*	4	191	0.019 (0.070)	<0.001 (0.004)
Pine stand protective cover	*under.open + lob.trees*	2	213	<0.001 (<0.001)	<0.001 (<0.001)

Table 12. Paired logistic regression model that best explains habitat selection at the 2 m scale across all spotted turtles (n = 27) in an intensively-managed forest landscape in eastern North Carolina, USA.

Variable	**Coefficient (median)**	**Odds ratio (median)**	**Odds ratio (interquartile range)**
under.open	-0.617	0.54	(0.320, 0.692)
water	1.97	7.148	(5.39, 10.0)
decid.leaf	-0.383	0.682	(0.553, 0.863)
pine needles	0.112	1.118	(0.780, 1.62)

Table 13. Comprehensive paired logistic regression models ($n = 8$) of habitat selection at the 20 m scale by spotted turtles in a highly-managed landscape of Coastal North Carolina, USA, supported by AIC$_c$ ($n = 27$). *Models were ranked by level of AIC$_c$ support and summed across individuals (maximum cumulative rank is 216). **AIC weights (w_i) were summed across individuals (maximum weight is 27) and converted to percentages to account for total model weight. ***AIC weights (w_i) were averaged across individuals (maximum weight is 1) and include standard deviation (SD) in parenthesis.

Model Name	Model	k	**Sum** Cumulative Rank	**Sum** w_i** (%)	**Mean** w_i*** (SD)
Deciduous leaf foraging conditions	*sub.temp + water + decid.leaf*	3	74	5.63 (20.9)	0.208 (0.212)
Aquatic form protective cover	*under.open + water + decid.leaf + pine needles*	4	79	7.73 (28.6)	0.286 (0.289)
Pine needle foraging conditions	*sub.temp + water + pine needles*	3	84	3.82 (14.1)	0.141 (0.183)
Woody debris foraging conditions	*sub.temp + water + stick*	3	94	3.86 (14.3)	0.143 (0.188)
Soil foraging conditions	*sub.temp + water + soil*	3	101	3.58 (13.3)	0.133 (0.157)
Global	*sub.temp + under.open + lob.trees + ALL COVER VARIABLES*	10	146	2.39 (8.85)	0.0887 (0.231)
Vegetation and woody debris cover	*under.open + grass + herb + stick*	4	194	<0.001 (5.56)	<0.001 (<0.001)
Pine stand protective cover	*under.open + lob.trees*	2	200	<0.001 (<0.001)	<0.001 (<0.001)

Table 14. Paired logistic regression model that best explains habitat selection at the 20 m scale across all spotted turtles (*n* = 27) in an intensively-managed forest landscape in eastern North Carolina, USA.

Variable	Coefficient (median)	Odds ratio (median)	Odds ratio (interquartile range)
sub.temp	0.226	0.877	(0.572, 1.83)
water	3.12	22.659	(9.33, 37.6)
decid.leaf	0.213	1.127	(0.640, 2.23)

Landscape-level Habitat Selection

We conducted backwards elmination regression with AIC model selection to assess whether landscape characteristics in activity areas compared to available habitats. We conducted the analysis across 32 activity areas and 32 random points constrained to the ditch network and isolated wetlands. Regarding spatial independence of buffered activity areas, we determined that spatial independence decreases as buffer size increases, with the 300 m scale having >80% overlap with adjacent 300 m buffers (Figure 14). Also, 19% of the 10% density isopleth activity areas overlapped with adjacent activity areas. We expected to see some overlap in turtle activity areas, because spotted turtles spend a considerable amount of time in the ditch network, and often interact with other individuals, especially during courtship.

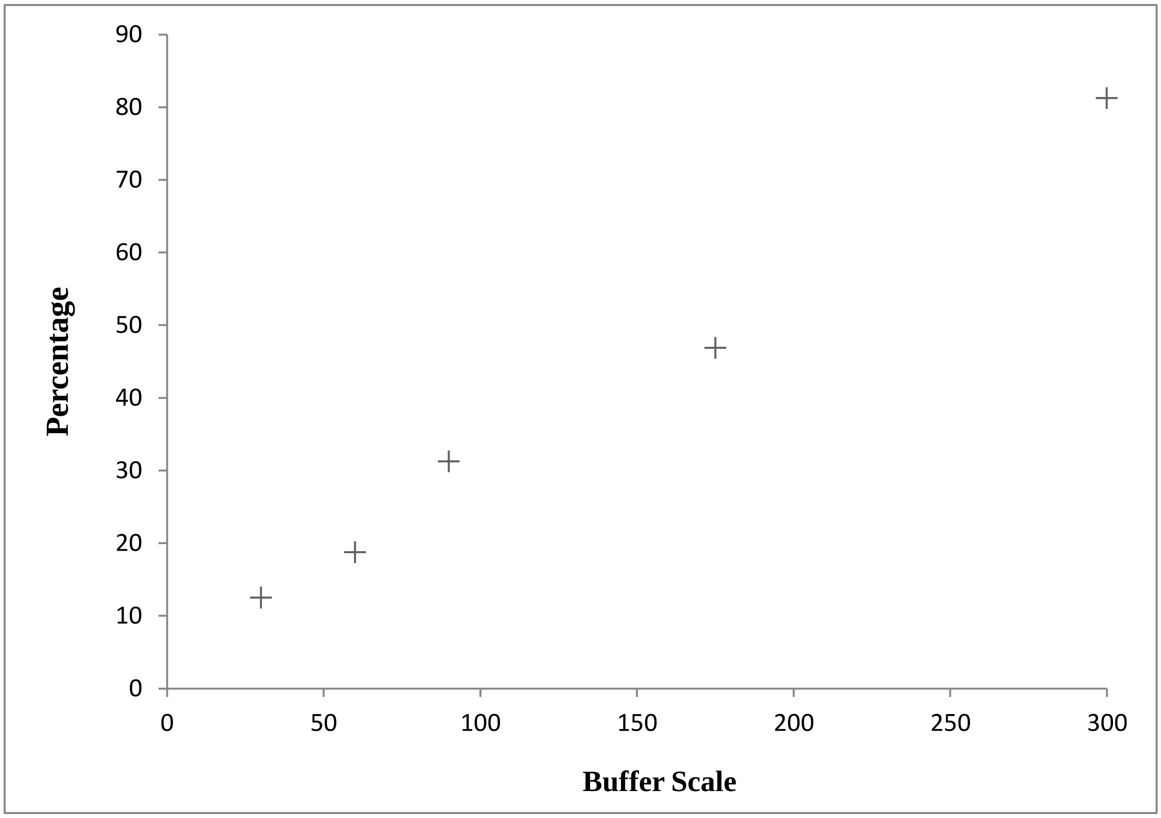

Figure 14. Percentage of overlap across spotted turtle activity area buffers indicating a decrease in spatial independence as buffer size increases. For example, about 13% of the 30 m buffers overlapped with each other.

For the 30 m scale analysis, turtles used road length disproportionate to the randomly available landscape features we examined ($\Delta AIC_c = 0$, $w_i = 0.58$). The second supported model revealed selection of middle-late aged forest stands in conjunction with road length ($\Delta AIC_c = 0.67$, $w_i = 0.42$). However, the independent variables odds ratios and corresponding confidence intervals were large (Table 15). At the 175 m scale, turtles were positively associated with forest stands >30 years old and natural stands and with ditch length and road length ($\Delta AIC_c = 0$, $w_i = 0.67$). The maximum likelihood estimates and odds ratios indicated that areas with a greater proportion of older forests were more likely to have a turtle activity area, while a greater length of roads and ditches within the buffer decreased likelihood of an activity area being present (Table 16). However, the second supported model indicated selection of middle-late aged forest stands along with forests older than 30 years, ditch length, and road length ($\Delta AIC_c = 1.39$, $w_i = 0.33$), and the maximum likelihood estimates and odds ratios revealed a similar pattern as the top model, but greater ditch length results in an increased likelihood of activity area selection.

The 300 m scale revealed turtle selection of all forest stand ages coupled with ditch length and road length ($\Delta AIC_c = 0$, $w_i = 0.68$). The second supported model revealed the same variables with an addition of distance to wetland ($\Delta AIC_c = 0.76$, $w_i = 0.41$), but both models did not converge (no upper confidence limit). A post-hoc sensitivity analysis of buffer scales between 30 m and 175 m (90 m) revealed that proximity to nearest wetland was an important factor in activity area selection ($\Delta AIC_c = 0$, $w_i = 0.59$). Also, the greater the road length resulted in an increase in likelihood of activity area selection, but was not the case for ditch length (Table 17). The competing model of the sensitivity analysis showed that middle-late aged stands were also important for activity area selection ($\Delta AIC_c = 0.76$, $w_i = 0.41$), with a greater proportion of middle-late aged stands resulting in an increased likelihood that an activity area will be present.

Table 15. Coefficients and odds ratios of top-supported models from a stepwise logistic regression of the 30 m scale for landscape-level habitat selection across all spotted turtle activity areas (*n* = 32) in an intensively-managed forest landscape in eastern North Carolina, USA.

Model #	**Variable**	**Coefficient (SE)**	**Odds Ratio**	**95% CI**
1	***Road.Length***	14.49 (3.77)	1971731	(1922, 6483217290)
2	***Mid-Late.Stand***	18.46 (15.84)	104086957	(0.0000016, 5.95e+21)
2	***Road.Length***	14.12 (3.82)	1355776	(1189, 4856973000)

Table 16. Coefficients and odds ratios of top-supported models from a stepwise logistic regression of the 175 m scale for landscape-level habitat selection across all spotted turtle activity areas (*n* = 32) in an intensively-managed forest landscape in eastern North Carolina, USA.

Model #	**Model variable(s)**	**Coefficient (SE)**	**Odds Ratio**	**95% CI**
1	***Natural.Stand***	2.38 (0.73)	0.38	(0.12, 1.00)
1	***Ditch.Length***	-4.08 (1.47)	0.017	(0.00065, 0.24)
1	***Road.Length***	-0.98 (0.54)	10.85	(3.00, 55.29)
2	***Mid-Late.Stand***	0.49 (0.62)	1.63	(0.48, 5.81)
2	***Stand.Natural***	-0.80 (0.58)	0.45	(0.13, 1.30)
2	***Ditch.Length***	-4.05 (1.49)	0.017	(0.00065, 0.25)
2	***Road.Length***	2.27 (0.74)	9.7	(2.60, 50.41)

Table 17. Coefficients and odds ratios of competing models from a post hoc logistic regression at the 90 m scale for landscape-level habitat selection across all spotted turtle activity areas (*n* = 32) in an intensively-managed forest landscape in eastern North Carolina, USA.

Model #	**Model variable(s)**	**Coefficient (SE)**	**Odds Ratio**	**95% CI**
1	***Ditch.Length***	-0.59 (0.37)	0.55	(0.25, 1.11)
1	***Road.Length***	1.14 (0.36)	3.11	(1.60, 6.76)
1	***Dist.Wetland***	-0.84 (0.42)	0.43	(0.16, 0.88)
2	***Ditch.Length***	-0.54 (0.37)	0.58	(0.26, 1.17)
2	***Road.Length***	1.05 (0.37)	2.86	(1.43, 6.29)
2	***Dist.Wetland***	-0.83 (0.42)	0.44	(0.16, 0.91)
2	***Mid-Late.Stand***	0.33 (0.30)	1.40	(0.77, 2.61)

DISCUSSION

Persistence in an intensively-managed landscape

Using multiple lines of evidence examining population demography, spatial ecology, and multi-scale habitat selection, we determined that spotted turtles are persisting in an intensively-managed forest landscape. This persistence is likely attributed to the extensive ditch network, a system with a high density of individual turtle locations, movements, and home ranges. Individuals also selected for ditches at the landscape scale. Although spotted turtles have been well-studied in wetland-dominated ecosystems, particularly at the northern extent of their range, few populations have been intensively studied in highly-reconfigured landscapes (Bottini 2005; Kaye et al. 2006; Yagi and Litzgus 2012), and none that we are aware of have been examined in intensively-managed forests. Moreover, this landscape was once dominated by pocosin-like wetlands, but now has been structurally changed. This study elucidates potential behavioral plasticity of a long-lived ectotherm to a highly-reconfigured aquatic and terrestrial landscape. We demonstrate that spatial ecology and multi-scale habitat selection indicates the quality of the ditch network and surrounding forest stand ages, and suggests the importance of a shifting mosaic in landscape features for sensitive, long-lived organisms.

Population structure

Our demographic data of spotted turtles, including survival and population growth rate, indicate a persisting population in this intensively-managed forest landscape of North Carolina, USA. Spotted turtles on our intensively managed study area were abundant, and were the most commonly detected reptile in roadside ditches (Appendix B). Spotted turtles were quite abundant, but only 5% of turtles we observed were hatchling and juvenile aquatic turtles. This stage class of turtles is notoriously difficult to find, presumably due to their smaller size which limits detection or differential habitat use compared to adults (Ernst 1976, Reeves and Litzgus 2008). Further, our methods were not designed to target juveniles. However, the proportion of juveniles we observed was smaller than other studies (Table 18) and may suggest low recruitment (Ernst 1976) or high mortality (Bodie and Semlitsch 2000), but one of our captured hatchlings was found in a roadside flooded depression, a feature rarely used by adults. Compared to other studies, our study population included the largest number of juveniles, males, and females (Table 19). Further, our sex ratio of males to females was opposite of what has been documented in other studies. The shell lengths and weights of the animals were comparable to other studies.

The male: female sex ratios were ca. 2:1. Skewed sex ratios may be evidence of intersexual differences in mortality (Aresco 2005) or maturation schedules (Gibbons and Lovich 1990), temperature dependent development, or detection bias. Here we discuss each in turn and present supporting evidence where available. Freshwater turtle populations that are skewed male have occurred near roadways, but not in populations without roadways, suggesting high female mortality due to vehicles (Steen and Gibbs 2004; Aresco 2005; Steen et al. 2006). However, our population is subject to little vehicle traffic, as roads are gated with limited access. Further, we radio-tracked turtles for two years and documented no road-related mortalities. Because this species, like many reptiles, exhibits temperature-dependent sex determination (TSD), skewed sex ratios may be caused by specific temperature regimes during egg developmental stages, with 1:1 sex ratio at 29°C, males being produced at temperatures <29°C and females being produced at >29°C (Ewert and Nelson 1991). To explore the possibility of TSD as a causal factor of overabundance of males, we consolidated all soil temperature collected from the location, 2 m, and 20 m habitat plots for the habitat selection analysis during an approximate nest incubation period (June-August, 2012-2013; Ernst 1970) and found that soil temperatures (n = 1092) averaged 23.7°C (range: 12.2-35.8°C, median: 23.9°C), supporting the hypothesis that the male bias we observed may be due to temperature effects during development. We did not, however, record soil temperatures of the incubation periods for when the observed adult spotted turtles were incubating (anywhere from 7-30+ years ago; Ernst 1970), which may have completely different temperature profiles. Instead we suggest that detectability may have influenced our observed sex ratio in that we used a combination of opportunistic and systematic surveys. Also, the pre-nesting season is when males seek out females for courtship (Ernst 1976), and males were often out in the open, oblivious to our presence. We caught 76% of males during the pre-nesting season (Figure 6), often capturing males that were courting females. After releasing the captured individuals, we frequently observed males immediately finding the female they were originally chasing. Although anecdotal, it suggests high-detectability and subsequent vulnerability to predation and poaching for spotted turtles during the courtship season.

Further, spotted turtles exhibited high apparent survival in this intensively-managed landscape. This high adult survival may be attributed to the fact that this project was short in duration relative to the lifespan of the organism, and no females died during the project. Our mark-recapture CJS models indicated apparent survival of females was higher than males, and thus less likely to emigrate and/or die. Other turtle studies have also revealed higher apparent survival estimates for females compared to males (Bowen et al. 2004; Converse et al. 2005), but the opposite has been documented (Dodd et al. 2006), of which may be a result of mortality or permanent emigration due to overland nesting movements by females. However, our observed nesting females oviposited on ditch banks, effectively reducing risk of overland movements. Males moved considerably longer distances (Table 6) and had larger home ranges than females (Figure 7) especially during the pre-nesting season, which may result in higher detection and predation risk. Apparent survival estimates were slightly lower in our known-fate model, but this could be attributed to the fact that an individual lost its transmitters during the first season of the project. Our CJS annual survival estimate for females is higher than what has been previously recorded in spotted turtle populations (1.00 compared to 0.97; Enneson and Litzgus 2008).

This population is experiencing a positive population growth rate according to our mark-recapture population projection matrix. Similarly, Enneson and Litzgus (2008) documented 2% annual growth in an Ontario, Canada spotted turtle population. Our elasticity and sensitivity analyses, along with Enneson and Litzgus (2008) indicate that changing adult survival vital rates in spotted turtles would have the greatest effects on the population growth rate. Although importance of adult survival is expected for long-lived, K-selected organisms with low annual fecundity and low juvenile survival, it further demonstrates the need for research and conservation of all age classes (Congdon et al. 1993).

Table 18. The percentage of juvenile spotted turtles captured during our study compared to other studies.

% Juveniles captured	Study
5.4	Current study
9.3	Litzgus and Brooks (1998)
11.7	Rowe and Gradel (2013)
13.6	Litzgus and Mousseau (2004)
15.6	Seburn (2003)
17.5	Graham (1995)
27.5	Reeves and Litzgus (2008)

Table 19. Table modified from Rowe and Gradel (2013) showing demographic (J = juveniles, including hatchlings, F = females, M = males), sex ratio, and body-size statistics across the distributions of spotted turtles. We include our study as a comparison.

Location of population	**N (J : M : F)**	**Sex ratio M : F**	**CL (mm) Mean Min-Max**	**PL (mm) Mean Min-Max**	**Mass (g) Mean Min-Max**	**Study**
Lancaster Co., PA	-	1 : 1.5	-	F:89.8 - M: 86.3 -	-	Ernst 1976 (as reported in Litzgus and Brooks 1998)
Cedar Bog, OH	-	-	F: 92.4 - 86.1	80.7	-	Lovich 1985 (as reported in Litzgus and Brooks 1998)
Lockport Prairie, IL	-	-	F: 106.4 - M: 104.8 -	F: 94.9 - M: 87.9	-	Mauger 1990 (as reported in Litzgus and Brooks 1998)
Cedar Swamp, MA	7 : 12 : 21	1 : 1.8	F:110.2 79-126 M:113.3 105-123	F: 101.5 72-116 M: 96.4 89-105	-	Graham 1995
Georgian Bay (inland), Ontario	11 : 49 : 58	1 : 1.2	F: 115.0 - M: 116.3 -	F: 101.1 - M: 94.9 -	-	Litzgus and Brooks 1998
Perry Nuclear Site, OH	-	-	F: 98.0 - M: 104.8 -	F: 87.3 - M: 87.6 -	-	Collins (as reported in Litzgus and Brooks 1998)
Mer Bleue Bog, Ontario	5 : 6 : 21	1 : 3.5	F: 106.4 - M: 108.5 -	F: 192 - M: 187 -	-	Seburn 2003
Francis Beidler Forest, SC	6 : 17	1 : 1.2	F: 103.8 - M: 105.2 -	F: 91.2 - M: 86.8 -	F: 190 - M: 168 -	Litzgus and Mousseau 2004
Georgian Bay (island), Ontario	11 : 6 : 23	1 : 3.8	F: 108.9 - M: 117.9 -	F: 96.8 - M: 97 -	F: 212.2 - M: 219.8 -	Reeves and Litzgus 2008
Southwestern Michigan	10 : 28 : 47	1 : 1.7	F: 88.2 66-114 M: 87.5 65-105	F: 80.3 53-105 M: 75.7 48-90	F: 105.9 45-200 M: 102.3 54-150	Rowe and Gradel 2013
Coastal North Carolina	15 : 177 : 86	2.1 : 1	F: 104.2 90-104.2 M: 107.9 99.5-120.8	F: 89.5 69-105 M: 86.5 71-130	F: 166.5 80-158 M: 156.9 97-183	Current Study

Spatial ecology

Spotted turtles extensively used the anthropogenic aquatic system, a ditch network designed to manipulate the water table for improved pine growth and survival, for movements, activity areas, and home ranges. Given heterogeneity in habitat structure, spotted turtles are known to stay in aquatic sites with permanent and ephemeral water sources (Seburn 2012; Yagi and Litzgus 2012), but frequently move upland in response to drought, temperature increases, or for nesting (Ernst and Lovich 2009). Average daily distance moved by males was nearly double that of females during the pre-nesting period (50.1 vs 28.2 ha; Figure 8). Large movements by males during courtship are indicative of mate-searching (Rasmussen and Litzgus 2010). More natural populations are subject to mortality when migrating between isolated wetlands and water bodies (e.g. road traffic; Langen et al. 2012), but the ditch network may allow for increased connectivity between individuals in this managed forest. Also, turtles often used the ditch network to access the upland matrix, which may also reduce potential risk of extensive overland movements.

Home ranges were often centered on ditches, and the T-LoCoH method appeared to better represent use of space in this highly-linear aquatic system compared to the standard MCP method, which is frequently used in home range studies. Home range size (T-LoCoH) was comparable to other studies, but was slightly greater (and the MCP greater still) than the largest average home range reported from a South Carolina population (Litzgus and Mousseau 2004). Home ranges did not differ by gender, season, or gender by season interaction for the T-LoCoH method (Figure 8) which did not support our hypothesis of gender differences in home range size. However, we did hypothesize that male movement patterns would be significantly different between males and females during the pre-nesting season, which was the case in our movement data (Figure 6). Space-use can elucidate the areas of a landscape that have higher fitness potential for an organism (Garshelis 2000), and both the MCP and T-LoCoH home range methods indicate a centralization of utilization distributions over the ditch network.

Multi-scale habitat selection

Using an individual-based cumulative ranks approach to habitat selection modeling, we found that spotted turtles selected for behaviorally-relevant habitats at the local-level. Also, turtle activity areas selected for old forest stands and proximity to wetlands at the landscape-level. Individual-based analyses of habitat selection allow for better understanding of individual contribution to variation, and stronger inference at the population level. To this end we average (or take the median of) model selection results across individuals (Compton et al. 2002). However, it is ill-advised to compare AIC values across data sets (Burnham and Anderson 2002), because their absolute values are contingent to the input data. We devised two new approaches to compare AIC-derived top models across individuals, and compared their efficacy in the context of this study. Summed/averaged model weights and cumulative ranks across individual models produced similar model selection results, indicating the promise of using a cumulative ranks and weights approach when comparing information theoretic models across data sets.

For local-level habitat selection, presence of water in a given plot was a good predictor of selection. Selection of percent water cover is well known for this species (Ernst and Lovich 2009). Over 80% of turtle locations were documented in the ditch network. Therefore, at the 2 m scale, most locations and paired random plots were within the ditch environments and around the ditch system or in adjacent stands at the 20 m scale. Specifically, spotted turtles selected for closed understory and thicker pine needle cover at the 2 m scale and for warmer substrate temperatures and deciduous leaf cover within and around the ditch system at the 20 m scale. Spotted turtles, along with most ectothermic organisms, often utilize substrate cover for forms, which provide protection and thermoregulatory opportunities (Litzgus and Brooks 2000; Baldwin et al. 2006). The fact that closed understory openness was selected for at the 2 m scale, and warmer temperatures were selected for at the 20 m scale may indicate a balance between thermoregulation, feeding, and/or form protective cover within the ditch environment. Additionally, behaviors at the 2 m scale are potentially different than the 20 m scale for this species. For example, we observed individuals seeking cover under substrate within 2-3 m of capture, suggesting use of habitat for protective cover from predators. We also documented turtles estivating under thick forest leaf cover closer to the 20 m scale. Other organisms are known to select for behaviorally-specific habitats at multiple scales. Multi-scale habitat selection studies are rare in the literature (du Toit 2010), but animal space use and habitat selection is often scale-dependent, warranting the need for multi-scale habitat selection research. Our local-level results suggest the importance of maintaining canopy closure near and around the ditch system, comprised of both deciduous trees and loblolly pines.

At the landscape-level, spotted turtle activity areas selected for the ditch system and road length consistently across scales. Wetland-dwelling species are often subject to road-related mortality, in that they make frequent movements within and among isolated wetlands and water features (Litzgus and Mousseau 2004; Beaudry et al. 2009), which increases the chances of crossing roadways. However, on Weyerhaeuser Company property, roadways are heavily gated with limited public access, resulting in little vehicle traffic. Consequently, we believe that vehicle mortality is of little concern for this population, and suggest that forest industry companies continue to keep their roads gated. This may also reduce poaching risk for the pet trade.

We found that turtles selected for older stands and/or stands that are restricted from harvest at the 175 m scale. Old stands in coniferous plantations have shown to be important features for other animals (MacKay et al. 2014), and indicate the importance of a shifting mosaic in landscape features. A post-hoc analysis at the 60-90 m scale indicated proximity to wetlands as an important landscape metric in addition to older stands. The analysis at the 30 m and 300 m scales indicated lack of fit, of which could be caused by poor model parameters. This documented selection of older stands and proximity to isolated wetlands may give insight as to how vulnerable, semi-aquatic organisms can persist in highly-modified landscapes.

CONCLUSION

Our study indicates short-term (i.e., 2-year) persistence of a declining, freshwater turtle species in an intensively-managed forest landscape. Our landscape-level habitat selection analysis suggested that spotted turtles select for old forest stands and proximity to wetlands, which may give insight as to how this population is able to persist. Therefore, managers can identify activity areas that form a landscape-level complex with nearby isolated wetlands and more mature forests. Our data also suggest that maintaining connectivity between the aquatic and terrestrial landscape features (i.e. ditch networks and forest congruity) would be important for the persistence of sensitive organisms like spotted turtles in highly-reconfigured systems. Further, the ditch network appears to be a vital landscape feature for spotted turtles in that over 85% of locations were documented there, and the landscape analysis indicated selection of activity areas to ditches. Before the intensive dredging of pocosin wetlands for agriculture, forestry, and development, we suspect that spotted turtle populations were abundant in the Atlantic Coastal Plain. This study indicates that spotted turtles, considered vulnerable or threatened throughout most of their range, are persisting in a highly-reconfigured aquatic and terrestrial landscape.

Organisms are often subject to anthropogenic habitat modification. Some species are able to persist, while others do not survive (e.g. relic populations). Moreover, organisms may not survive habitat modification if sensitive to a specific aspect of the reconfiguration in that a resource is removed or a key threat is enhanced (Baldwin 2010). The ability for a species to persist in the presence of habitat reconfiguration may be attributed to adaptation, whether genetically, or through a plastic response in behavior (Chevin et al. 2010). Consequently, more research is necessary, including comparing spatial ecology and habitat selection across pre- and post-harvest treatments (in the case of forest management) to determine the mechanisms behind persistence. Spotted turtles tended to focus their spatial ecology around the ditch network, indicating the importance of the network for this population's persistence. Currently, Weyerhaeuser Company mechanically manages their ditch networks by scouring accumulated sediment and vegetation with an excavator approximately every 20-25 years. We captured spotted turtles across a series of ages since ditch maintenance (Figure A-2). Also, given stand rotations around the ditch network, this species appears to be persisting in spite of the intensive management. This persistence is likely attributed to the shifting mosaic of landscape structure in this system. For example, turtles selected for closed canopy and warmer temperatures at the local-level, and for proximity to wetlands and older stands at the landscape-level, suggesting the importance of habitat heterogeneity for this species. However, additional study investigating the effects of space-use and habitat selection pre- and post-ditch management at varying frequencies may give insight as to the appropriate management regimes for this species. Although using population structure, spatial ecology, and habitat selection gives a robust picture of the status of a species and its response to landscape alteration, long-term projects are paramount to understanding the future status of a species (Bennett and Adams 2004; Jones et al. 2010b). However, our findings can aid forest managers in developing effective management regimes for this species in intensively-managed landscapes.

APPENDICES

APPENDIX A

Telemetry datasheet: local-scale habitat plots

TELEMETRY DATASHEET (Observer: ________________________; Site:______________)

Date: ____________ Time: ___________ Frequency (MHz): __________________ Serial #: ______________

GPS: ____ # satellites: ____

New capture: **Y N** New transmitter: **Y** (new transmitter freq:__________ serial #:_________________) **N**

Notch Code: __________________

Gender: **Male Female** Gravid: **Y N** Photo #s: ____

Mass (g): ___________ Plastron Length (mm): __________ Transmitter & glue mass (g):____________

Method found: **Hoop Trap VES Local triangulation Visual (w/ receiver)** Time to locate:__________

Inspection: **In hand On ground/water Not obs.** Tag injuries: **N/A None Abrasion Other**__________

Activity state: **Active Alert Inert/tucked Basking?**

Macrohabitat: **Upland Canal (main or 3rd stage) Road Other______________________**

Last location distance: _________________ Bearing: ________________

Weather: **Overcast Partly cloudy Clear Sunny Rain Mist Snow Frost Ice skim Other**________

Microhabitat: **In form Under log In water body In open Other ________________________________**

Approximate distance to water body (M): ____________________

Form class: **Lean-to Tent Sleeping bag Open cup Earthen cave Other _________________________**

Form cover: **Leaf** [Species:_____________________; Thickness (mm):__________; **Damp Saturated Dry**]

CWD [Diameter (cm): ________; Length (cm): ________ Decay class: _____; **Damp Saturated Dry**]

Other:____

Distance to nearest CWD (cm): __________ [Diameter (cm): ________; Length (cm): ______Decay class: ___]

Substrate characteristics: **Inundated (i.e., in standing water) Damp Saturated Dry**

Full Leaf/leaves [Species:_____________________; Thickness (mm):_______] **Leaf fragments Moss**

CWD [Diameter (cm): ________; Length (cm): ______Decay class: ______] **Other___________________**

Other vertebrate species present? **Y N** Species:

Notes:

Date: ____________ Frequency: ___________________

LOCATION PLOT

1 m: Macrosite slope:_________ aspect:__________; Microsite slope:_________ aspect:______

Microhabitat: RH: ________ Ambient Temp. (°C): ________; Water Temp. (°C): ________;

Air: RH: ________ Ambient Temp. (°C): ________;Soil Temp. (°C): ________; Water depth (cm):________;

Soil moisture (VWC): _____________ Light: _____________________________________lux

Canopy openness:______________ X 1.04 Understory openness:______________ X 1.04

Decid.	Sat. leaf	Tree/root	Fern	Grass/ sedge	Bryophyte(moss)	Lichen	Pine eedles	Gravel	Packed gravel
Soil	Water	CWD 1	CWD 2	CWD 3	CWD 4	Stick	Shrub	Herb	Other

CWD species							
Decay class							
Type							
Touching (Y/N)							
Diam. class							

Tree spp.	Loblolly								
#									

Illustration and Field Notes:

2=1-5%,

3=6-25%

4=26-50%

5=51-75%

6=>75%

Type: shard/bark, stump, log

Diam class:

1=1-5 cm

2=6-10cm

3=11-20cm

4=21-30cm

5=31-50cm

6=51-75cm

7=>75cm

Date: ____________ Frequency: ___________________ Direction of random plots: __________________

2M PLOT

1 m: Macrosite slope:_________ aspect:__________; Microsite slope:_________ aspect:______

Microhabitat: RH: ________ Ambient Temp. (^{o}C): ________; Water Temp. (^{o}C): ________;

Air: RH: ________ Ambient Temp. (^{o}C): ________;Soil Temp. (^{o}C): ________; Water depth (cm):________;

Soil moisture (VWC): _____________ Light: _____________________________________lux

Canopy openness:______________ X 1.04 Understory openness:______________ X 1.04

Decid.	Sat. leaf	Tree/root	Fern	Grass/ sedge	Bryophyte(moss)	Lichen	Pine eedles	Gravel	Packed gravel
Soil	Water	CWD 1	CWD 2	CWD 3	CWD 4	Stick	Shrub	Herb	Other

CWD species							
Decay class							
Type							
Touching (Y/N)							
Diam. class							

Tree spp.	Loblolly								
#									

Illustration and Field Notes:

2=1-5%,

3=6-25%

4=26-50%

5=51-75%

6=>75%

Type: shard/bark, stump, log

Diam class:

1=1-5 cm

2=6-10cm

3=11-20cm

4=21-30cm

5=31-50cm

6=51-75cm

7=>75cm

Date: ____________ Frequency: ___________________ Direction of random plots: __________________

20M PLOT

1 m: Macrosite slope:_________ aspect:__________; Microsite slope:_________ aspect:______

Microhabitat: RH: ________ Ambient Temp. (^oC): ________; Water Temp. (^oC): ________;

Air: RH: ________ Ambient Temp. (^oC): ________;Soil Temp. (^oC): ________; Water depth (cm):________;

Soil moisture (VWC): _____________ Light: _____________________________________lux

Canopy openness:______________ X 1.04 Understory openness:______________ X 1.04

Decid.	Sat. leaf	Tree/root	Fern	Grass/ sedge	Bryophyte(moss)	Lichen	Pine eedles	Gravel	Packed gravel
Soil	Water	CWD 1	CWD 2	CWD 3	CWD 4	Stick	Shrub	Herb	Other

CWD species							
Decay class							
Type							
Touching (Y/N)							
Diam. class							

Tree spp.	Loblolly								
#									

Illustration and Field Notes:

2=1-5%,

3=6-25%

4=26-50%

5=51-75%

6=>75%

Type: shard/bark, stump, log

Diam class:

1=1-5 cm

2=6-10cm

3=11-20cm

4=21-30cm

5=31-50cm

6=51-75cm

7=>75cm

APPENDIX B

Reptile and amphibian surveys

We conducted visual encounter surveys for reptiles and amphibians and aural surveys for amphibians across 16 roadside ditch sites intermittently during the project. We also recorded all haphazard/opportunistic captures that occurred during the study. The goal of this project was to examine assemblages of herpetofauna across a choronosequence of time since ditch maintenance on detection, richness, occupancy, and species composition in an intensively-managed forest landscape. The 16 ditch sites were stratified by the time since they were maintained, with sites aging from 3 years (n=4), 6-8 years (n=4), 10-12 years (n=4), and 15-17 years (n=4), and each site had ≥500 m segment maintained to avoid confounding effects of varying stand age. Of the ditch segments, we surveyed 25% of each site with a random starting point. We relied on hard copies of engineering reports from the landowner, which described the extent and timing of ditch maintenance, to compile a list of potential study sites. We visited sites and visually confirmed that the recorded maintenance history was consistent with vegetation structure and ditch configuration. Although available information regarding ditches prevented us from randomly selecting sites from the study area, the ditch segments we studied spanned 3-17 year post maintenance, were adjacent to plantations 1-33 years old, and thus were representative of those available on the landscape.

Visual encounter surveys and opportunistic captures

We conducted visual encounter surveys at ditch sites from January – May 2012 and March – July 2013. Opportunistic captures were made from January 2012 – July 2013. We conducted the visual encounter surveys by walking the length of a site and recording all reptile and amphibian species observed. We would visually scan the embankments, the water surface, and the bottom of the ditches if possible for herpetofauna. Opportunistic captures included incidences when a reptile or amphibian was captured haphazardly or via hoop trap at a site, but not during a formal visual encounter survey. For this descriptive analysis, we include the opportunistic captures with the visual encounter survey data across the ditch sites. When an observed/captured individual could not be identified to species (i.e. escaped prior to identification), we recorded genus or family level if possible. When animals were captured, we recorded snout-vent or plastron lengths (mm) and weight (g). Additionally, we documented abnormalities such as lost limbs, scars, bite marks, and contusions. If an individual could not be captured, we recorded the sighting as “visual only”. Prior to surveys, we documented ambient and water temperature of the ditch site with a thermo-psychrometer (Optimum Energy Products Ltd., Alberta, Canada) and pocket-thermometer, respectively. We also visually estimated cloud cover and precipitation.

Across 2012-2013, we completed 22 visual encounter surveys for each of the 16 sites. We documented 12 amphibian and 19 reptile species (Table A-1). For amphibians, Southern leopard frogs (*Lithobates sphenocephalus*; 90 detections) and Southern cricket frogs (*Acris gryllus*; 48 detections; Figure A-1) were most commonly documented. For reptiles, the most encountered was the spotted turtle (*Clemmys guttata*; 203 detections), followed by the green anole (*Anolis carolinensis*; 108 detections; Figure A-2). Amphibian species within genus *Lithobates* were the most common across ditch ages comprising 79% of detections (Figure A-1). The American bullfrog (*L. catesbeianus*) was observed at the "5-year" (21 detections) and "10-year" sites (11 detections) considerably more than the "0-year" (four detections) and "15-year" sites (five detections), and the Southern leopard frog (*L. sphenocephalus*) was detected more at "0-year" (26 detections) and "5-year" sites (29 detections) than the "10-year" (16 detections) and "15-year" sites (19 detections). Also noteworthy were the large number of detections of Southern cricket frogs (*Acris gryllus*) at the "0-year" sites (32 detections) amounting to 67% of detections. In contrast, Oak toads (*Anaxyrus quercicus*) were only detected at "15-year" sites (one detection). Pine woods treefrogs (*Hyla femoralis*; two detections) along with carpenter frogs (*L. virgatipes*; one detection) were detected only at "0-year" sites. Similarly, a greater siren (*Siren lacertina*) was captured using a minnow trap at a "10-year" site, but was not captured at any other age since ditch maintenance. However, trapping was limited to January – April, 2012 due to logistical restraints. Further, Cope's gray treefrogs (*H. chrysoscelis*) and squirrel treefrogs (*H. squirella*) were found in less than five surveys. On the other hand, green treefrogs (*H. cinerea*) were found across all ditch ages, but with minimal observations (<5).

For reptiles, green anoles (*Anolis carolinensis*) were observed across all ditch ages, but were most detected at the "10-year" sites, nearly twice as much (42 vs at the most 23 detections; Figure A-2). Further, spotted turtles were detected at all ditch ages, but were detected half as much in the “0-year” sites compared to the other ages since maintenance (31 vs at least 52 detections). Additionally, the cottonmouth (*Agkistrodon piscivorous*; $\bar{x}$ = 5.8 detections), black racer (*Coluber constrictor*; $\bar{x}$ = 3.5 detections), redbelly watersnake (*Nerodia erythrogaster*; $\bar{x}$ = 3.8 detections), and mud turtle (*Kinosternon subrubrum*; $\bar{x}$ = 6.5 detections) were observed across all ages since maintenance. *A. piscivorous* was also detected more at the “10-year” sites (12 vs at the most five detections. Corn snakes (*Elaphe guttata*; four detections) and rough green snakes (*Opheodrys aestivus*; two detections) were recorded only at the “10-year” sites. Further, black rat snakes (*E. obsolete*; one detection) and Eastern glass lizard (*Ophisaurus ventralis;* one detection*)* were documented at only the “5-year” sites. Yellowbelly sliders (*Trachemys scripta*) were not observed at “15-year” sites, but cottonmouths (*A. contortrix*) were documented only at “15-year” sites with one detection.

Table A-1. Reptiles and amphibians captured or observed during the visual encounter surveys or opportunistic captures across 16 sites with varying years since maintenance in an intensively-managed forest landscape in eastern North Carolina, USA.

Reptiles	**Amphibians**
Agkistrodon contortrix	*Acris gryllus*
Agkistrodon piscivorous	*Anaxyrus quercicus*
Anolis carolinensis	*Hyla chrysoscelis*
Chyrsemys picta	*Hyla cinerea*
Chelydra serpentina	*Hyla femoralis*
Clemmys guttata	*Hyla squirella*
Coluber constrictor	*Lithobates catesbeianus*
Crotalus horridus	*Lithobates clamitans*
Elaphe guttata	*Lithobates sphenocephalus*
Elaphe obsoleta	*Lithobates virgatipes*
Eumeces fasciatus	*Unknown Lithobates*
Kinosternon subrubrum	*Siren lacertina*
Lampropeltis getula	
Nerodia erythrogaster	
Nerodia fasciata	
Opheodrys aestivus	
Terrepene carolina	
Trachemys scripta	
Ophisaurus ventralis	

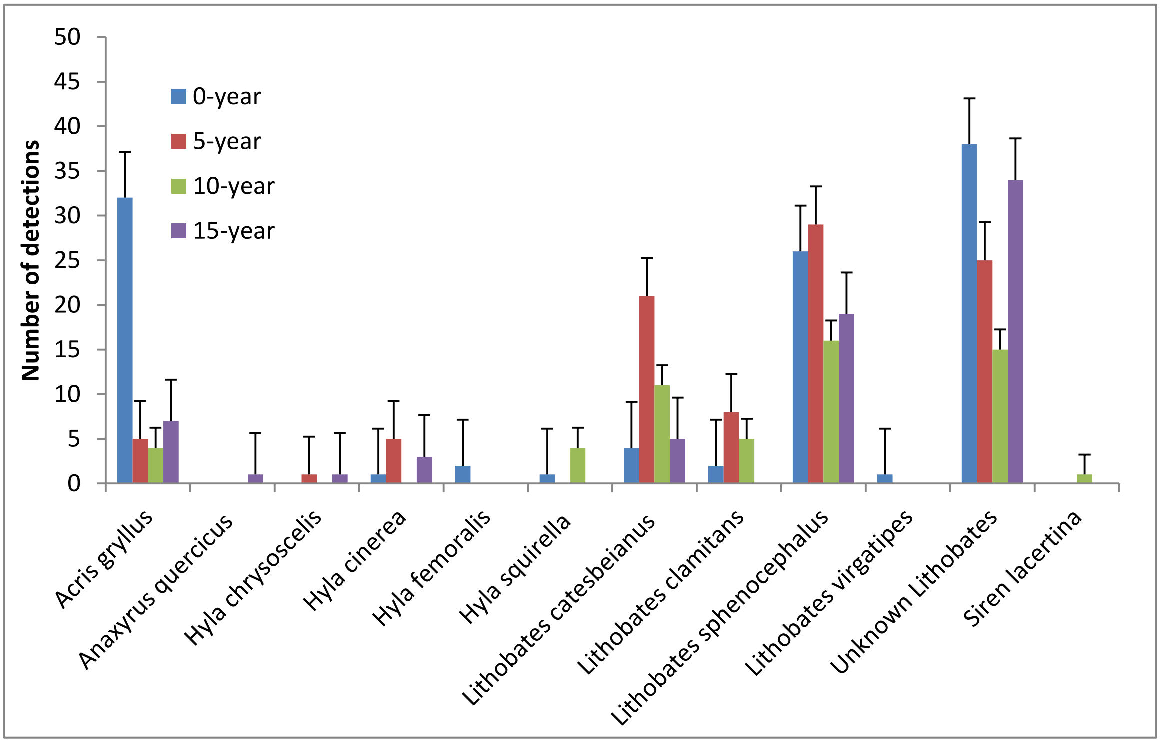

Figure A-1. Number of amphibian species detections (with standard errors) during visual encounter surveys or opportunistic captures across 16 sites with varying years since maintenance in an intensively-managed forest landscape in eastern North Carolina, USA.

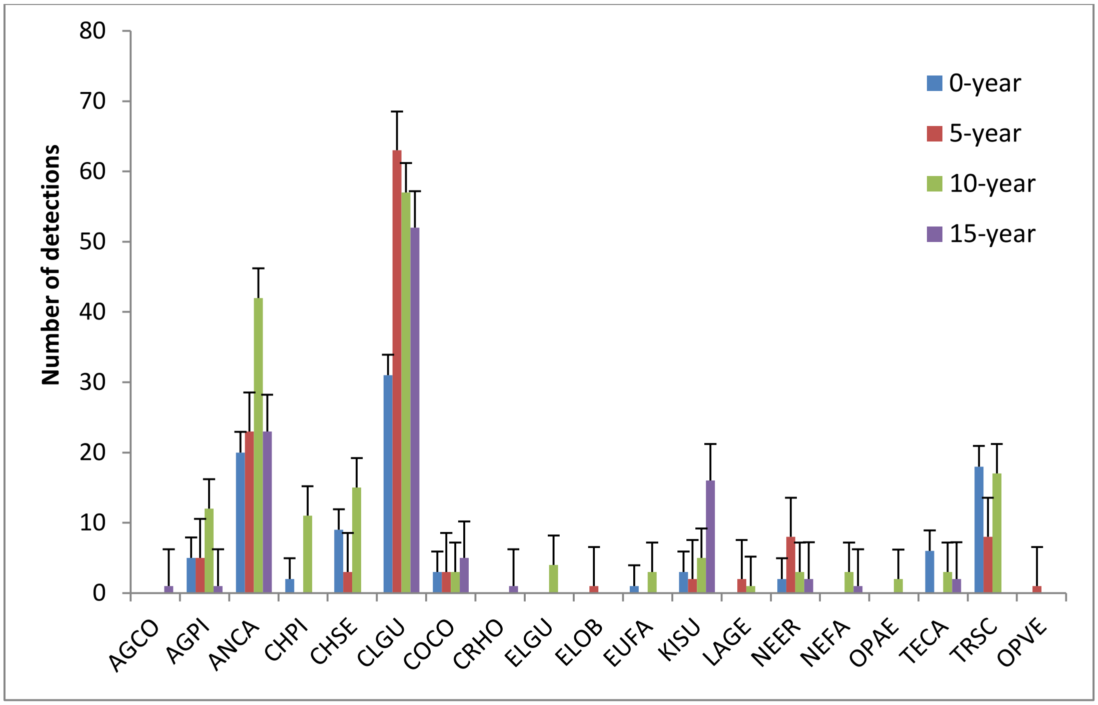

Figure A-2. Number of reptile species detections (with standard errors) during visual encounter surveys or opportunistic captures across 16 sites with varying years since maintenance in an intensively-managed forest landscape in eastern North Carolina, USA.

Amphibian aural surveys

Amphibian call surveys were conducted February, May, June, and July of 2012 and April – July, 2013, for 14 survey nights in order to cover the phenologies of all known species in the region. Call surveys were structured similar to the North American Amphibian Monitoring Program guidelines (NAAMP; https://www.pwrc.usgs.gov/naamp/index.cfm?fuseaction=app.description), in that surveys were conducted approximately 30 minutes after sunset and ended by 0100 hours.

We did not conduct surveys with temperatures below 5.6°C or if there was a moderate to heavy breeze (13-18 mph) or heavy rain as that would impair our ability to hear calls. Each survey was conducted by a single, consistent observer. All amphibian species heard within a five-minute period were documented. The observer was stationed at the center of the ditch site, which was marked at the beginning of the study to be the half-way point between the start and end of the ditch site.

We documented 15 amphibian species (Table A-2). The most detected species of amphibian was Southern leopard frogs (*L. sphenocephalus*; 81 detections) and green frogs (*L. clamitans*; 77 detections; Figure A-4). Similar to the visual encounter and opportunistic survey data, the Southern cricket frog (*Acris gryllus*) was detected considerably more at the "0-year" sites (31 vs at most 15 detections). Further, both toad species, oak toads (*Anaxyrus quercicus*) and southern toads (*Anaxyrus terrestris*), were found at all ditch ages, but oak toads were more commonly detected at more recently maintained sites, while southern toads were found more at the "0-year" and "5-year" sites. For *Hyla,* no considerable trends were observed across sites, but they were detected at all ditch ages since maintenance. However, the squirrel treefrog (*H. squirella*) was found considerably less at "0-year" sites than the other ages (two vs at least six detections). Green frogs had only six detections at "15-year" sites, but >20 detections at the other ages since maintenance. Also, American bullfrogs (*L. catesbeianus*) were not detected at "15-year" sites. Carpenter frogs (*L. virgatipes*) and little grass frogs (*Pseudacris ocularis*) were only found at "0-year" and "10-year" sites, respectively.

Further, Brimley's chorus frogs (*P. brimleyi*) were not detected at "5-year" sites, and had the majority of detections at "15-year" sites (seven vs two detections).

Table A-2. Amphibian species documented during the anuran call surveys across 16 sites with varying years since maintenance in an intensively-managed forest landscape in eastern North Carolina, USA.

Amphibians
Acris gryllus
Anaxyrus quercicus
Anaxyrus terrestris
Gastrophryne carolinensis
Hyla chrysoscelis
Hyla cinerea
Hyla femoralis
Hyla squirella
Lithobates catesbeianus
Lithobates clamitans
Lithobates sphenocephalus
Lithobates virgatipes
Pseudacris brimleyi
Pseudacris crucifer
Pseudacris ocularis

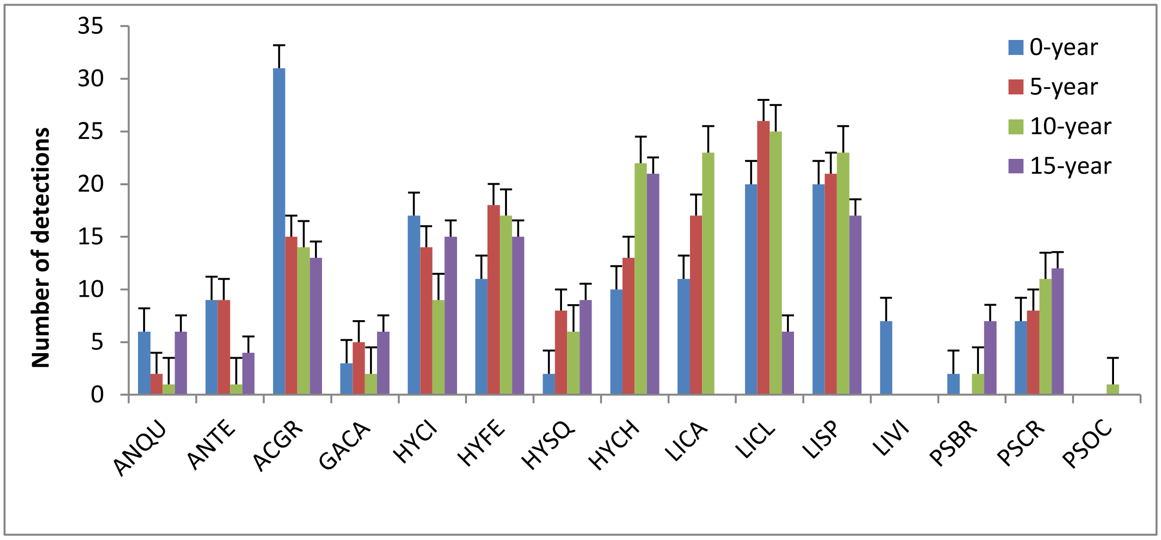

Figure A-3. Number of amphibian species detections (with standard errors) during anuran call surveys across 16 sites with varying years since maintenance in an intensively-managed forest landscape in eastern North Carolina, USA.

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