
INTER- AND INTRA-POPULATION VARIATION IN HABITAT SELECTION FOR A FOREST-DWELLING TERRESTRIAL TURTLE, *TERRAPENE CAROLINA CAROLINA*

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Abstract.—Habitat selection, where observed use of a resource is disproportionate to availability, is an important behavior allowing individuals to position themselves spatially relative to critical resources in heterogeneous environments. For species that experience variable environments across broad geographic ranges, we expect resource selection templates to vary among populations accordingly. Using radiotelemetry, we examined habitat selection for populations of Eastern Box Turtles, *Terrapene carolina*, in fire-maintained forests of the sandhills compared to nearby unburned coastal plain forests in south-central North Carolina. Turtles at the fire-maintained sandhills site preferred bottomland habitats and areas near streams, whereas turtles in the unburned coastal plain environment preferred uplands and used streams randomly. In addition, turtles in the fire-maintained sandhills avoided Longleaf Pine and more strongly preferred hardwood and non-Longleaf Pine forests compared to turtles at the unburned coastal plain site. Body size, but not sex, was also an important source of variation in habitat selection within populations, with smaller turtles more strongly preferring areas near water. Selection of habitat structural components in the immediate area of locations did not differ between sites, sexes, or body sizes. These results highlight the variety of resource selection templates in *T. carolina*, underscoring a potential need for population- or region-specific conservation and management strategies.

Key Words.—Eastern Box Turtle; habitat preference; forest management; Longleaf Pine; prescribed fire; sandhills

INTRODUCTION

In heterogeneous environments, individuals typically position themselves spatially and temporally relative to critical resources through the process of habitat selection, where the observed use of a resource is disproportionate to its availability (Johnson 1980). Habitat selection templates can vary within a population according to intrinsic differences among individuals including sex (Hillen et al. 2011), body size, age, and life stage (Wilbur 1980; Mittelbach 1981; Stamps 1983), dominance position (Petit and Petit 1996), reproductive status (Harvey and Weatherhead 2006), or in response to habitats already selected by others (i.e., frequency- or density-dependence; Fretwell and Lucas 1970). Habitat selection can also vary spatially among populations of the same species owing to extrinsic variation in resource quality and distribution (Morellet et al. 2011), climate (Carfagno and Weatherhead 2006), interspecific interactions (Hoare et al. 2007), anthropogenic influences (Rees et al. 2009), and other environmental factors. Assessment of the occurrence and mechanisms responsible for maintaining both inter- and intra-population variation in habitat selection over multiple spatiotemporal scales is critical for advancing our understanding of evolutionary ecology, population regulation, and biodiversity conservation (Morris 2003).

Terrestrial and semi-aquatic turtles are useful organisms for the study of individual interactions with their environment for several reasons. Logistically, the shell offers a minimally invasive location for external attachment of a transmitter for the frequent and repeated monitoring of individual behavior (Doody et al. 2009). Their slow movement rates and relatively small home range sizes (Slavenko et al. 2016) both facilitate observations of habitat use and detailed quantifications of habitat availability on manageable spatial scales. Their long lifespans and high annual survivorship can extend the period of study to cover both seasonal cycles and inter-annual variability to better understand behavior (Currylow et al. 2012; Anthonysamy et al. 2013). As ectotherms, turtles are especially sensitive to external environmental factors that influence their body temperatures, which in turn governs nearly every aspect of their physiology and performance including locomotion speed (Adams et al. 1989), feeding and digestion (Gatten 1974; Dubois et al. 2008), and energy and water balance (Foley and Spotila 1978; Penick et al. 2002). The thermal and hydric characteristics of habitat are often variable over space and time depending on season, vegetative structure, topography, and many other extrinsic environmental variables that factor into the habitat selection process. Moreover, the heavy protective shell and unique shoulder-girdle morphology



FIGURE 1. Woodland Box Turtle (*Terrapene c. carolina*) in a fire-maintained sandhills Longleaf Pine (*Pinus palustris*) forest in Moore County, North Carolina, USA. (Photographed by John Roe).

of a turtle constrain their movement rate compared to other vertebrates (Zani and Kram 2008), limiting their ability to move in response to changes in environmental conditions and making their positioning in close proximity to critical resources especially important. The selection of appropriate habitat is thus of critical and immediate importance to individual fitness in turtles (Dubois et al. 2009; Lagarde et al. 2012).

Studies that directly examine variation in habitat selection (i.e., comparing use to availability) between turtle populations of the same species and among individuals in the same population are rare (but see Rittenhouse et al. 2008; Paterson et al. 2012). This bias in part results from a focus of most studies on single populations of specialist species of conservation concern, with the intention of applying such knowledge to improve management strategies (Carter et al. 1999; Edge et al. 2010; Rasmussen and Litzgus 2010). Comparisons among studies of the same species are often complicated by differences in study objectives, design, data collection and analysis methods, as well as the different times at which the studies were conducted. However, for species with broad geographic ranges, we expect populations to experience environments that vary in several extrinsic factors such as the spatial distribution and availability of resources, climate, and

the frequency and intensity of disturbances (e.g., storms, floods, and fire). Moreover, intrinsic asymmetries among individuals such as sex and body size could interact with extrinsic factors to influence motivations and environmental tolerances that in turn influence resource selection templates.

The Eastern Box Turtle (*Terrapene carolina*, Fig. 1) is widespread in the eastern United States and occupies temperate forests and early successional mosaics throughout its range (Dodd 2001; Keister and Willey 2015). While the many subspecies of *T. carolina* have been the subject of numerous independent investigations into habitat associations and selection (Dodd 2001; Keister and Willey 2015), studies specifically designed to elucidate inter- and intra-population variation in habitat selection within a subspecies are lacking (but see Rittenhouse et al. 2008). Here, we compare habitat selection at different spatiotemporal scales between nearby populations for a subspecies of *T. carolina*, the Woodland Box Turtle (*T. carolina carolina*), in natural areas of the sandhills and upper Atlantic Coastal Plain Ecoregions of south-central North Carolina. The sandhills have deep, coarse-textured sandy soils, rolling topography, and xeric uplands, while the coastal plain has flatter terrain, loamy and poorly drained soils, and extensive bottomlands (Frost 1998; Griffith et al. 2002). Such contrasting conditions influence forest communities, hydrology, fire regime, and other environmental variables to which turtles likely respond. We predict that the selection of mesic forest types, aquatic resources, and habitat structural features that provide refuge from thermal and hydric stress will be stronger in sandhills than in coastal plain environments given the scarcity of such resources in the sandhills. *Terrapene carolina* is a species of conservation concern in many states with well-documented declines throughout their range (Keister and Willey 2015), and it may serve valuable ecological roles such as seed and spore dispersal in areas where it is still common (Liu et al., 2004; Dodd 2006; Jones et al. 2007). Thus, it is important to understand variation in *T. carolina* resource selection and apply this knowledge to improve conservation and management efforts for this species.

MATERIALS AND METHODS

Study sites.—We conducted the study at two North Carolina state parks, including Weymouth Woods Sandhills Nature Preserve (hereafter Weymouth Woods), a 202-ha section of park in the Sandhills Level IV Ecoregion (Griffith et al. 2002) of south-central North Carolina near Southern Pines, North Carolina, USA. The habitat is a mosaic of mixed pine and hardwood forests (Fig. 2). Pine species are primarily Longleaf Pine (*Pinus palustris*) and Loblolly Pine (*P. taeda*),

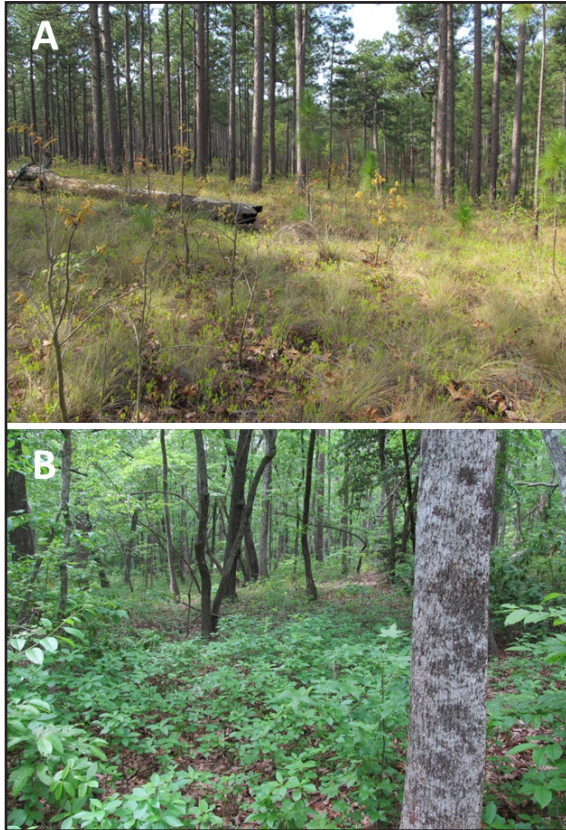


FIGURE 2. Examples of (A) fire-maintained xeric Longleaf Pine savannah habitats characteristic of the Weymouth Woods sandhills site and (B) unburned mesic hardwood forest habitats characteristic of the Lumber River coastal plain site and streamside habitats at Weymouth Woods, Moore County, North Carolina, USA. (Photographs by John Roe).

along with several species of hardwood, including mixed oak (*Quercus* spp.), hickory (*Carya* spp.), Red Maple (*Acer rubrum*), Sweetgum (*Liquidambar styraciflua*), American Holly (*Ilex opacum*), Sassafras (*Sassafras albidum*), and Tuliptree (*Liriodendron tulipifera*). The majority of the site is xeric uplands with a small stream network (James Creek, part of the Cape Fear Watershed) and associated bottomlands running through the center of the park. The topography is rolling hills ranging in elevation from 102–154 m. Prescribed fire has been used regularly to manage the Longleaf Pine ecosystem since 1974, with 76% of the area being managed using low-intensity, small-scale controlled burns. Areas targeted for controlled burns range in size from 0.9–23.9 ha, with a mean burn frequency of every 5.9 y (range 1.5–17 y) from 2000–2016 (Weymouth Woods Sandhills Nature Preserve, unpubl. data).

The other site, 24 km south, was the Lumber River State Park (hereafter Lumber River), a 225-ha reserve in the Atlantic Southern Loamy Plains and Southeastern Floodplains and Low Terraces Level IV Ecoregions adjacent to the Lumber River (Griffith et al. 2002) near

Wagram, North Carolina, USA. The habitat of Lumber River includes bottomland forest adjacent to the river and several small tributaries and swamps. Upland forests are comprised of mixed pine and hardwood species (Fig. 2) including Loblolly and Longleaf Pine, mixed oaks, and hickory, while bottomlands also include Bald Cypress (*Taxodium distichum*), tupelo (*Nyssa* spp.), Tulip Tree, Sweetgum, Red Maple, and Atlantic White Cedar (*Chamaecyparis thyoides*). The elevation ranges from 65–70 m. A prescribed burn program was initiated in 2017, but prior to this and for the entirety of this study, fire had not been used in management since it was designated as a state park in 2001. We cannot be certain of its previous fire history, but the vegetative communities, depth of litter, and accumulation of woody debris suggest that fire disturbance had not been a regular part of this system for at least several decades.

Habitat mapping.—We restricted mapping of habitat and landscape features to within the park borders. To facilitate mapping, we established a grid dividing each study site into 50 × 50 m cells using ArcMap 10.1 (Esri, Redlands, California, USA). At the center of each grid cell, we assessed the relative composition of tree types in the surrounding area using a CRUZ-ALL angle gauge (Forestry Suppliers, Inc., Jackson, Mississippi, USA). This method involved rotating 360° while holding the angle gauge at head height at a standard length (about 64 cm) from the eye of the observer and counting the number of tree trunks that completely filled (or more than filled) the 10-factor gauge opening. We counted trees in three categories, including (1) Longleaf Pine, (2) non-Longleaf Pines, and (3) hardwoods. We calculated the relative proportion of each category and used this to classify each grid cell based on its forest habitat composition. We included tree types in the forest classification if their relative proportion was ≥ 0.25. We classified grid cells with no trees as open.

We also classified each grid cell as either upland or bottomland first by examining National Wetland Inventory (NWI) maps (<http://www.fws.gov/wetlands/>). We then ground-truthed each grid cell and assessed several field indicators, including surface water presence, signs of recent flooding (watermarks, debris and substrate scouring), plant communities, and animal sign (e.g., crayfish burrows) to more accurately reflect the spatial extent of bottomland areas. The locations of NWI wetland boundaries generally agreed with field indicators of wetland conditions, though the exact distribution did not always align with on-site indicators, perhaps owing to different spatial scales of sampling and local landscape modifications (e.g., ditching, road construction, and landfill) associated with recent site land management practices or natural diversions of floodwaters (e.g., American Beavers,

TABLE 1. Sample size (n), mean, standard deviation (SD), and range of body sizes of male and female Woodland Box Turtles (*Terrapene c. carolina*) studied by radiotelemetry in fire-maintained sandhills forests (Weymouth Woods) and unburned coastal plain forests (Lumber River), North Carolina, USA.

Site	Sex	n	Carapace length (mm)		Mass (g)	
			Mean \pm SD	Range	Mean \pm SD	Range
Weymouth Woods	Male	18	131.7 \pm 7.9	121.3–149.6	401 \pm 66	305–575
	Female	18	128.4 \pm 9.4	109.3–140.0	435 \pm 86	260–615
Lumber River	Male	15	138.7 \pm 10.0	124.1–151.7	435 \pm 78	330–577
	Female	14	131.6 \pm 7.8	122.1–149.1	462 \pm 64	385–615

Castor canadensis). In such cases, we reclassified grid cells to reflect field indicators. We classified grid cells as wetland if $\geq 50\%$ of its area was wetland.

Finally, we mapped stream networks by walking each watercourse following heavy rainfall. We collected coordinate positions of each stream channel using handheld GPS units (GPS 72H, Garmin, Olathe, Kansas, USA) and digitized the network as polylines using ArcMap 10.1. By mapping streams during high water, we were able to include areas where surface water was present on a temporary basis.

Turtle tracking.—To encompass variation resulting from environmental heterogeneity in habitats, we captured individuals from a variety of forest types spread out across each site, including from burn units and areas where fire has been historically excluded at the fire-maintained site (Weymouth Woods). We equipped turtles with radiotransmitters (RI-2B, 10–15 g, Holohil Systems Ltd., Carp, Ontario, Canada) using five-minute epoxy gel (Devcon, Solon, Ohio, USA). From April 2012 to December 2016, we tracked 65 individual turtles for 1–56 mo (Table 1). Transmitter mass did not exceed 4.5% of turtle body mass in any case. Upon initial capture, we measured midline carapace length (CL) to the nearest 0.1 mm using vernier calipers and mass to the nearest gram using a spring scale. We determined sex based on several sexually dimorphic features, with males typically having a concave posterior plastron, stouter and longer curved claws on hind feet, a red iris, and thicker and longer tails compared to females (Palmer and Braswell 1995).

We located telemetered turtles using a Communication Specialists R-1000 receiver (Orange, California, USA) and Yagi antenna. We located individuals once per week during the active season (May–September), every two weeks around the times of winter ingress (October–November) and spring egress (March–April), and once per month for the remainder of the overwintering period (December–February). At each location, we determined the coordinate position using GPS units. We then plotted turtle location coordinates on habitat maps using ArcMap 10.1.

We collected additional data on habitat structural components in the areas immediately surrounding a

subset of locations for 10 individuals at Lumber River (five males and five females) and 13 at Weymouth Woods (six females and seven males). Measurements included litter depth at the turtle location and distances from the turtle to the nearest tree (diameter at breast height [DBH] ≥ 10 cm), shrub or sapling (DBH < 10 cm), and log. We also positioned a 1×1 m square on the ground (with turtle at the center) and counted the number of woody stems and visually estimated coverage of coarse woody debris, leaf litter, vine, fern, Wiregrass (*Aristida stricta*), herbaceous vegetation (not including Wiregrass), water, and bare ground. We estimated canopy coverage using a spherical densiometer facing the four cardinal directions and we averaged scores for a single estimate at each location. For each turtle location where habitat structure was assessed, we measured the same variables (on the same day as turtle habitat measures) at a nearby random location selected by following a bearing (1–360°) for 1–25 m, with both distance and bearing selected from a random number table (Rossel et al. 2006).

Fire intensity.—One week following a prescribed fire at Weymouth Woods, we measured the height of burn scars (as a proxy of fire intensity) along an elevation gradient near a stream. We made measurements every 50 m along five 200–350 m long transects centered on a streambed. At each sample location, we measured the height of blackened burn scars from the recent fire using a meter tape for the five nearest trees. When burn scars were beyond our reach, we tied orange flagging around the tree at a height of 1 m and photographed trees from a 5 m distance. We later measured the height of burn scars in ImageJ (National Institutes of Health) software using the straight-line tool, using the flagging to calibrate for the scale on each image. We also measured the straight-line distance from each sample location to the stream, and estimated elevation from topographic contour maps using ArcMap 10.1.

Data analyses.—We performed statistical analyses with SPSS v. 23.0 (SPSS Inc., Chicago, Illinois, USA). Where appropriate, we examined the assumptions of homogeneity of variances and normality; when data failed to meet assumptions, we transformed data to approximate normal distributions or equal variances. If

transformations did not rectify parametric assumptions, we used appropriate non-parametric tests. We accepted statistical significance at $\alpha < 0.05$ unless otherwise noted. To constrain the experiment-wide Type I error to 0.05, we used multivariate tests where possible and further investigated individual response variables using univariate tests only when multivariate tests were significant. When non-parametric tests were required, we applied the Bonferroni method (Sokal and Rohlf 2012) for groups of related tests to adjust the α level of statistical significance. Values are reported as mean \pm 1 SE unless otherwise stated.

We examined variation in turtle size between sample groups using multivariate analysis of variance (MANOVA; Morrison 2005), with log-transformed carapace length and mass as the dependent variables and site, sex, and site \times sex as independent variables. We then used Euclidian distance analysis to assess whether turtles used a non-random set of available habitats. Distance-based approaches offer many advantages over traditional multinomial or classification-based approaches (e.g., compositional analysis), including lower sensitivity to locational errors and thus no need for explicit error modeling, improved ability to identify important nearby habitat patches of various sizes and shapes and their edges, and the capacity to combine linear, point, and aerial data into a single analysis framework (Conner and Plowman 2001; Conner et al. 2003). We adopt the terminology of Conner et al. (2003) when interpreting habitat analyses: Selection is when the observed use of a habitat is disproportionate to the availability of that habitat; Preference is when observed use of a habitat is higher than expected given its availability; and Avoidance is when observed use of a habitat is lower than expected based on its availability. For each habitat variable, we calculated a habitat selection index that quantified the difference between observed use and availability. We first compared habitat selection indices to a null model to identify whether habitat characteristics were preferred (use $>$ availability), avoided (use $<$ availability), or used randomly (use = availability) at each site. We then compared habitat selection indices among groups (site, sex, and sex \times site) and body sizes (carapace length) to determine if the strength of selection (i.e., magnitude of difference between use and availability) differed between populations. We only used individuals in analyses that were tracked for an entire year, resulting in 50 individual turtles (14 male and 13 female from Weymouth Woods, 12 male and 11 female from Lumber River).

For each turtle location, we measured the nearest distance to each forest class, bottomland and upland habitat, and stream (permanent or temporary). We also generated an equivalent number of random points

within the study area, defined as the minimum convex polygon encompassing locations for turtles within the borders of each site. We selected random points using the create random points tool in ArcMap 10.1 and measured nearest distances to each habitat class and landscape feature as described above. For each turtle, we calculated the mean distances to each habitat class or landscape feature (u_i) using all active season locations (April–November) and one overwintering location per year per individual to avoid pseudoreplication of locations when turtles were sedentary from December–March. We then divided mean distances from turtles to each habitat class by mean distances from random points (r_i) to calculate a habitat selection index, or distance ratio (u_i / r_i). To assess habitat selection within each site, we compared distance ratios to a matrix of the value one to assess if habitats were preferred ($u_i / r_i < 1$), avoided ($u_i / r_i > 1$), or used randomly ($u_i / r_i = 1$; Conner et al. 2003) using MANOVAs; one examining variation in forest composition and another examining variation in hydrology (upland/bottomland and stream) at each site. To assess variation in the strength of habitat selection between sites, sexes, and body sizes, we used MANOVAs with distance ratios (u_i / r_i) as the dependent variables, site, sex, and site \times sex as independent variables, and carapace length as the covariate. We ran separate MANOVAs for the forest composition and hydrological variables. All distance ratios and carapace length were \log_{10} -transformed prior to analyses. For variables that did not meet assumptions for parametric tests following transformations, we compared variation in distance ratios among groups using Mann-Whitney U tests (Sokal and Rohlf 2012).

To investigate selection of habitat structural components in the immediate area (i.e., within 25 m from the turtle location), we calculated a selection index by subtracting the values (distances to habitat features [tree, shrub/sapling, log], litter depth, percentage coverages [canopy, coarse woody debris, litter, vine, fern, herbaceous vegetation, wiregrass, water, bare ground], and counts [woody stem density]) for random locations from the values for accompanying turtle locations. We then calculated a mean selection index for each variable for each turtle. Given that random and turtle locations were paired in calculating this selection index, we could not calculate a distance ratio (as we did for forest composition and hydrology) comparing use to availability owing to the number of zero values in many measurements. To assess variation in strength of habitat selection between sites, sexes, and body sizes we used MANOVA with selection indices as the dependent variables, site, sex, and site \times sex as independent variables, and \log_{10} carapace length as the covariate. We then compared selection indices to a matrix of the value zero using MANOVAs to assess whether habitat

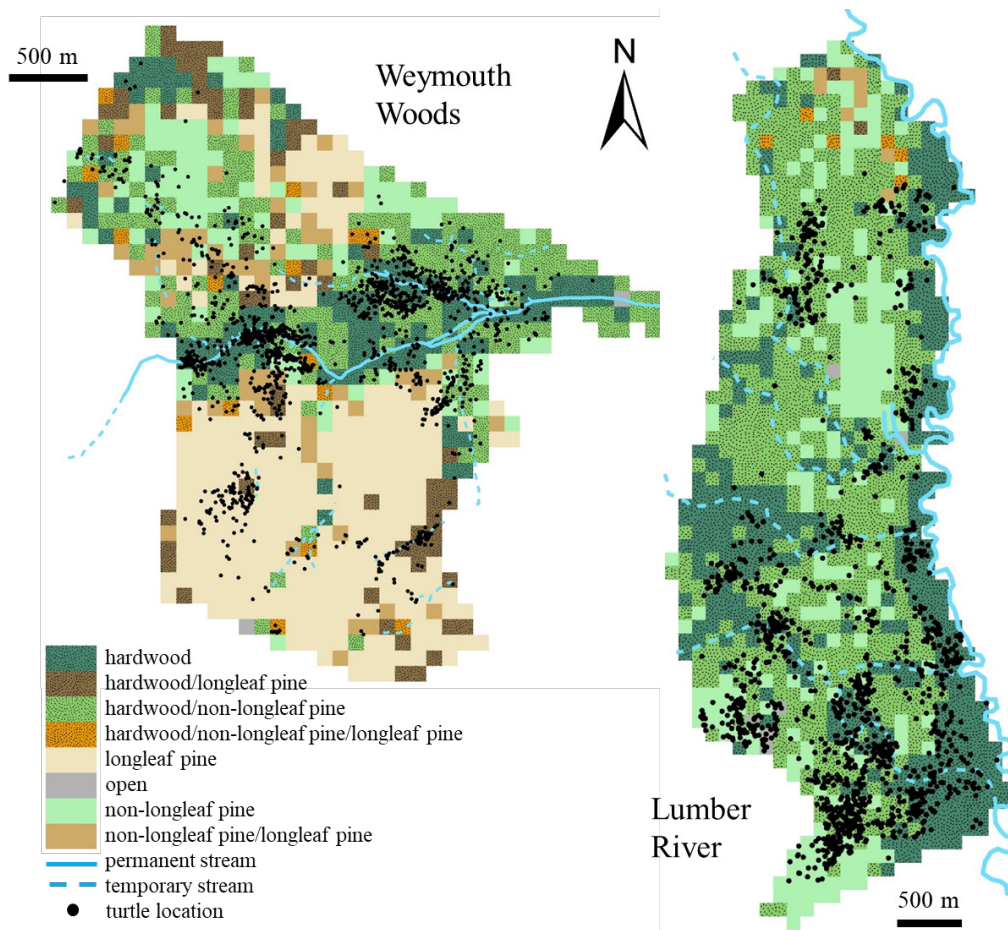


FIGURE 3. Maps of Woodland Box Turtle (*Terrapene c. carolina*) radiolocations relative to forest composition and watercourses at the fire-maintained Weymouth Woods (Moore County, North Carolina, USA) sandhills site and the unburned Lumber River (Scotland County, North Carolina, USA) coastal plain site. Forest habitat classes including hardwoods are stippled. Grid cells are 50 × 50 m.

features were preferred, avoided, or used in accordance with availability. For variables that did not meet assumptions for parametric tests, we compared variation in selection indices using Mann-Whitney U tests. We examined how fire intensity varied across the landscape using multiple regression analysis, with elevation and distance from stream as independent variables, and height of burn scarring as the dependent variable.

RESULTS

Study site habitats.—Weymouth Woods was comprised of habitat forest classes including Longleaf Pine (35.0%), hardwood and non-Longleaf Pine (20.7%), hardwood (15.0%), non-Longleaf Pine (11.3%), hardwood and Longleaf Pine (7.9%), non-Longleaf Pine and Longleaf Pine (7.8%), hardwood, non-Longleaf Pine, and Longleaf Pine (2.0%), and open (0.2%; Fig. 3). The majority of the landscape at Weymouth Woods was upland (91.8%), with bottomlands accounting for only 8.2% of the study area. The forest habitat classes

at Lumber River included hardwood and non-Longleaf Pine (44.9%), hardwood (32.9%), non-Longleaf Pine (19.9%), non-Longleaf Pine and Longleaf Pine (0.9%), hardwood, non-Longleaf Pine, and Longleaf Pine (0.6%), open (0.6%), and hardwood and Longleaf Pine (0.2%; Fig. 3). Uplands accounted for 64.6% of the landscape at the Lumber River study area, while bottomlands covered 34.5% of the site.

Turtle morphometrics.—Body size did not differ significantly between sites ($F_{2,60} = 2.64, P = 0.080$) nor the interaction between site and sex ($F_{2,60} = 0.629, P = 0.537$), but males were significantly larger than females at both sites ($F_{2,60} = 22.39, P < 0.001$; Table 1). Males had significantly longer carapace lengths than females ($F_{1,61} = 5.52, P = 0.022$) but both sexes were of similar body mass ($F_{1,61} = 2.68, P = 0.107$).

Habitat selection.—We obtained 55.3 ± 37.2 (mean \pm standard deviation) and 67.3 ± 34.0 locations for female and male turtles, respectively, at Weymouth Woods, and

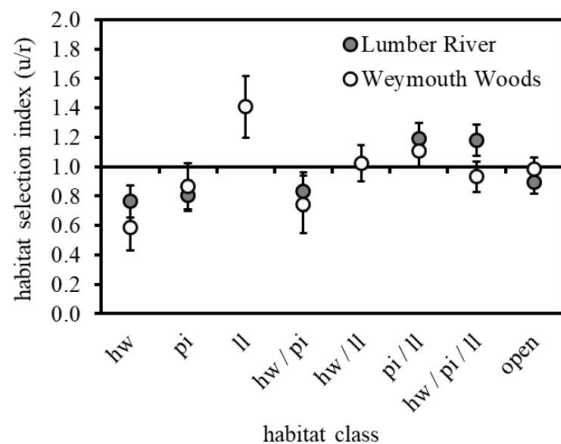


FIGURE 4. Forest class habitat selection indices for Woodland Box Turtles (*Terrapene c. carolina*) at the fire-maintained Weymouth Woods sandhills site compared to the unburned Lumber River coastal plain site (Moore and Scotland counties, North Carolina, USA). Note that indices (u/r) < 1 indicate preference, (u/r) > 1 indicate avoidance, and (u/r) = 1 indicate random use of habitats. Values are mean \pm 1 SE. Forest habitat classes are hardwood (hw), Longleaf Pine (ll), non-Longleaf Pine (pi), and mixtures of these tree types.

64.8 \pm 36.0 and 62.1 \pm 30.0 locations for female and male individuals, respectively, at Lumber River. Turtles at Weymouth Woods preferred hardwood ($U = 135.0$, $P < 0.001$), non-Longleaf Pine ($U = 189.0$, $P = 0.001$), and mixed hardwood and Longleaf Pine ($U = 135.0$, $P < 0.001$), while all other forest habitats were used in accordance with availability ($F_{5,48} = 2.46$, $P = 0.046$; Figs. 3 and 4). Avoidance of Longleaf Pine forests approached significance ($F_{1,52} = 3.19$, $P = 0.056$). In the above analyses for forest composition at Weymouth Woods, the Bonferroni adjusted α level of statistical significance was 0.013. At Lumber River, forest habitats were also used non-randomly ($F_{5,40} = 4.92$, $P = 0.001$; Figs. 3 and 4). Turtles preferred hardwood forests ($F_{1,44} = 4.57$, $P = 0.038$) and used all other forest habitats in accordance with their availability ($U = 184.0$, $P = 0.059$ for non-parametric tests, $F_{1,44} \leq 3.594$, $P \geq 0.065$ in all cases for parametric tests). In the above analyses for forest composition at Lumber River, the Bonferroni adjusted α level of statistical significance for univariate tests was 0.025.

Comparison of selection indices indicated that strength of selection for forest habitats differed between sites. Turtles at Weymouth Woods more strongly preferred hardwood forests ($U = 181.5$, $P = 0.012$) compared to the Lumber River (Figs. 3 and 4). There were no differences between sites in the selection indices for any other forest habitat class ($U = 211.0$, $P \geq 0.053$ in all cases for non-parametric tests, $F_{1,46} \leq 2.686$, $P \geq 0.108$ in all cases for parametric tests). We could not compare Longleaf Pine and mixed hardwood and Longleaf Pine forests between sites, as these classes were either too rare or not present at Lumber River at

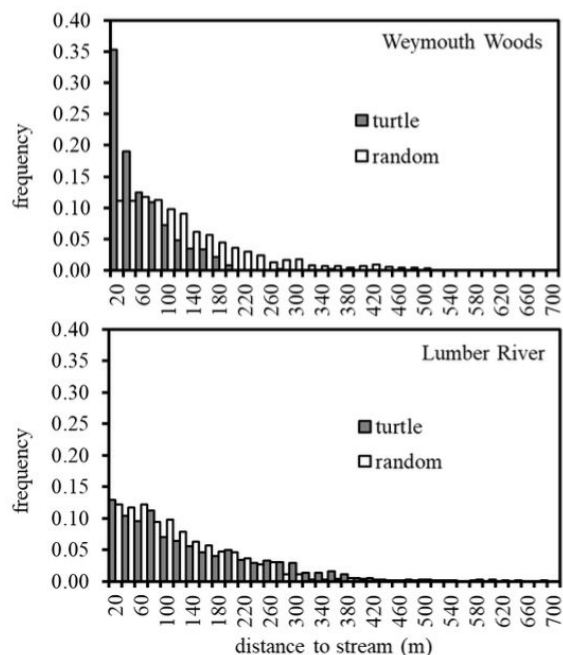


FIGURE 5. Frequency distributions of distances from Woodland Box Turtle (*Terrapene c. carolina*) radio-locations and randomly-selected locations to the nearest stream for turtles at the fire-maintained Weymouth Woods sandhills site compared to the unburned Lumber River coastal plain site (Moore and Scotland counties, North Carolina, USA).

the spatial scales of our sampling. Selection of forest habitat classes did not vary by sex ($F_{1,46} \leq 0.300$, $P \geq 0.108$ in all cases for parametric tests, $U = 368.5$, $P \geq 0.277$ in all cases for non-parametric tests).

The selection of habitat hydrological components differed within and between sites. The strength of selection for stream habitats differed between sites ($F_{1,45} = 17.10$, $P < 0.001$) and body sizes ($F_{1,45} = 12.62$, $P = 0.001$), but not between sexes ($F_{1,45} = 1.91$, $P = 0.174$) or the interaction of site and sex ($F_{1,45} = 1.16$, $P = 0.288$). We found no interaction between site and carapace length ($F_{1,46} = 1.77$, $P = 0.190$), so this term was dropped from the analysis. Turtles at Weymouth Woods preferred areas near streams ($F_{1,52} = 172.3$, $P < 0.001$), while turtles at the Lumber River used streams randomly ($F_{1,44} = 0.718$, $P = 0.402$; Fig. 5). Turtle locations at Weymouth Woods were an average of 50.5 \pm 5.0 m from streams compared to 127.2 \pm 16.4 m at Lumber River. Smaller turtles selected areas in closer proximity to streams compared to larger turtles at both sites, with distance to stream accounting for 20–21% of the variation in selection indices (Weymouth Woods: $r^2 = 0.202$, Lumber River: $r^2 = 0.213$; Fig. 6). Strength of selection of bottomland habitats differed between sites ($U = 148.0$, $P = 0.002$), while differences between selection of uplands approached significance ($U = 416.0$, $P = 0.039$). Turtles at Weymouth Woods preferred bottomlands ($U = 189.0$, $P = 0.001$) and used

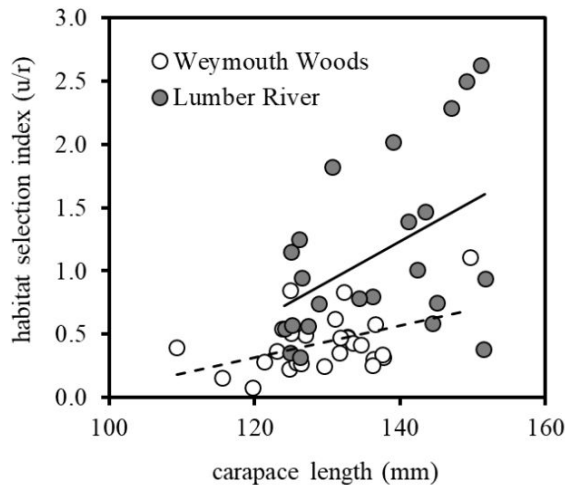


FIGURE 6. Relationships between stream selection indices and body size for Woodland Box Turtles (*Terrapene c. carolina*) at the fire-maintained Weymouth Woods sandhills site (dashed line) and the unburned Lumber River coastal plain site (solid line) (Moore and Scotland counties, North Carolina, USA). Note that lower values of selection indices reflect stronger selection of stream habitats, while higher values reflect weaker selection.

uplands randomly ($U = 432.0$, $P = 0.212$; Fig. 6). In contrast, turtles at Lumber River preferred uplands ($F_{1,44} = 7.87$, $P = 0.007$) and used bottomlands randomly ($F_{1,44} = 1.95$, $P = 0.170$; Fig. 7). Sex was not an important factor in selection of bottomland or upland habitats ($U \geq 236.5$, $P > 0.140$ in both cases). In the above analyses of habitat hydrological components, the Bonferroni adjusted α levels of statistical significance was 0.017 for both between- and within-site comparisons.

Habitat structural components.—We obtained 24.8 ± 8.2 (mean \pm standard deviation) and 22.1 ± 8.8 locations for female and male turtles, respectively, at Weymouth Woods, and 23.0 ± 4.2 and 22.2 ± 3.8 locations for female and male individuals, respectively, at Lumber River for use in analysis of selection of habitat structural components in the immediate surrounding area. Selection of habitat structural features was independent of site ($F_{12,7} = 0.540$, $P = 0.834$), sex ($F_{12,7} = 0.495$, $P = 0.864$), body size ($F_{12,7} = 0.801$, $P = 0.650$), and the interaction of site and sex ($F_{12,7} = 0.721$, $P = 0.705$). We thus combined turtles from both sites in all further analyses of habitat structural components. Turtles used several habitat structural components non-randomly, preferring sites in closer proximity to logs, with deeper litter, more coverage of leaf litter, coarse woody debris, vine, and fern ($F_{11,34} = 10.98$, $P < 0.001$; Table 2), and higher woody stem density (Mann-Whitney $U = 460.0$, $P < 0.001$). Turtles used all other habitat structural components randomly (Mann-Whitney $U = 218.5$, $P \geq 0.191$ for all non-parametric tests, $F_{1,44} = 2.301$, $P \geq 0.136$ in all cases for parametric tests; Table 2).

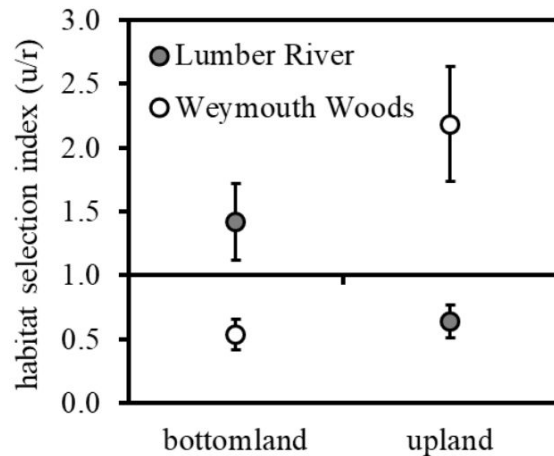


FIGURE 7. Upland and bottomland habitat selection indices for Woodland Box Turtles (*Terrapene c. carolina*) at the fire-maintained Weymouth Woods sandhills site compared to the unburned Lumber River coastal plain site (Moore and Scotland counties, North Carolina, USA). Note that indices (u/r) < 1 indicate preference, (u/r) > 1 indicate avoidance, and (u/r) = 1 indicate random use of habitats. Values are mean \pm 1 SE.

Fire intensity.—Fire intensity varied over the landscape gradient ($F_{2,31} = 12.19$, $P < 0.001$, $r^2 = 0.44$), primarily in response to elevation ($t = 2.614$, $df = 233$, $P = 0.014$), with fire intensity increasing at higher elevations. Fire intensity also increased with increasing distance from water, but this relationship was largely indirect, as distance from water increased with elevation ($F_{1,32} = 31.64$, $P < 0.001$, $r^2 = 0.50$). After accounting for variation due to elevation in the multiple regression analysis, distance from water was not a strong predictor of fire intensity ($t = 1.139$, $df = 233$, $P = 0.264$).

DISCUSSION

While primarily an inhabitant of forests and forest edges (Dodd 2001; Keister and Willey 2015), *T. carolina* exhibits variation in habitat use across its range. However, much of this variation is a result of regional differences among subspecies (Dodd 2001; Keister and Willey 2015). By studying turtles along an environmental gradient and in reserves with different forest management practices, we detected considerable differences in habitat selection templates between populations of the same subspecies, *T. c. carolina*. The close proximity of sites coupled with their simultaneity of study minimized methodological, climactic, seasonal, and genetic factors that could make such comparisons difficult to interpret, while also allowing for direct quantitative comparisons. Turtles at both sites preferred forests with more hardwood and non-Longleaf Pine trees, but strength of selection for forest habitats differed between sandhills and coastal plain populations. Populations also differed in selection of various

TABLE 2. Summary of habitat use, availability, and selection behavior in Woodland Box Turtles, *Terrapene c. carolina*, from fire-maintained sandhills forests (Weymouth Woods) and unburned coastal plain forests (Lumber River), North Carolina, USA. For selection behavior, habitat selection indices did not differ between sites, so individuals from both sites were combined to compare overall use to availability. See methods for description of selection behavior.

Variable	Weymouth Woods		Lumber River		Selection behavior
	Turtle	Random	Turtle	Random	
Distance to log (m)	3.6 ± 0.4	4.6 ± 0.5	6.5 ± 0.4	6.6 ± 0.4	preference
Distance to tree (m)	3.1 ± 0.3	2.7 ± 0.2	2.4 ± 0.1	2.4 ± 0.2	random
Distance to shrub/sapling (m)	0.3 ± 0.1	0.5 ± 0.1	0.4 ± 0.1	0.7 ± 0.1	random
Litter depth (cm)	6.5 ± 0.8	4.4 ± 0.6	8.9 ± 0.8	6.1 ± 0.6	preference
Woody stem density (n)	17.6 ± 1.7	12.0 ± 1.4	12.9 ± 2.2	8.2 ± 1.3	preference
Canopy openness (%)	24.4 ± 3.7	23.5 ± 2.8	16.2 ± 1.9	16.3 ± 2.0	random
Litter (%)	88.5 ± 1.8	84.7 ± 2.0	92.6 ± 1.4	89.8 ± 2.0	preference
Coarse woody debris (%)	13.0 ± 1.9	6.2 ± 0.7	16.7 ± 2.3	6.9 ± 0.8	preference
Herbaceous (%)	12.4 ± 2.6	13.7 ± 2.1	6.5 ± 1.8	6.4 ± 1.4	random
Wiregrass (%)	1.7 ± 0.9	2.5 ± 1.0	0.3 ± 0.3	0.0 ± 0.0	random
Water (%)	2.5 ± 1.3	2.8 ± 1.0	6.7 ± 1.5	7.8 ± 1.3	random
Vine (%)	8.4 ± 1.6	5.4 ± 0.9	7.4 ± 3.1	2.9 ± 1.0	preference
Fern (%)	6.0 ± 1.7	3.3 ± 0.9	2.2 ± 0.7	1.6 ± 0.6	preference
Bare (%)	2.8 ± 1.1	4.4 ± 1.1	3.0 ± 1.4	4.0 ± 1.1	random

hydrological characteristics of the environment. Habitat selection did not differ between sexes, but body size was an important source of intrinsic variation in habitat selection among individuals in both populations. These results, together with those of Rittenhouse et al. (2008), demonstrate a variety of resource selection templates in *T. carolina* that allow this wide-ranging species to adjust to diverse local environmental conditions. Such behavioral variation also underscores a potential need for flexible conservation and management strategies for wide-ranging species.

Habitat selection typically operates on multiple spatiotemporal scales in animals (Mayor et al. 2009), but identifying which scales are most important requires clear definitions of spatial and temporal resolutions of sampling that are of relevance for the species in question (Heisler et al. 2017). Our sampling and analyses were designed to capture two levels of resource selection. At the broader scale, we compared use to availability of forest composition and hydrology variables sampled at 50 × 50 m resolutions across the study sites, representing larger areas (i.e., several hectares) over which individual *T. c. carolina* could traverse in visiting locations used on a seasonal basis for reproduction, foraging, overwintering, and other critical behaviors within the multi-year home range (Currylow et al. 2012; unpubl. data). At the finer scale, we examined selection of habitat structural components within 1–25 m of locations, which is consistent with typical daily movements for *T. c. carolina* as individuals respond to local-scale and shorter-term temporal variation in conditions of the immediate surrounding environment

(Penick et al. 2002; Currylow et al. 2012; Parlin et al. 2017). These spatiotemporal scales represent only two of potentially many points along a continuum of scale-dependent habitat selection behaviors of relevance for inter- and intra-population comparisons. However, these scales are consistent with other studies of terrestrial and semi-aquatic turtles, including *T. c. carolina*, that generally align with the macrohabitat and microhabitat (or landscape and local) levels of inquiry (Edge et al. 2010; Rasmussen and Litzgus 2010; Kapfer et al. 2013; Greenspan et al. 2015). In our study, we found considerable inter- and intra-population variation in habitat selection templates at the broader spatiotemporal scale, but consistency of selection at the finer scale of habitat structural components.

The sandhills and coastal plain ecoregions offer contrasting environments in topography, soils, hydrology, and plant communities that could influence *T. c. carolina* resource selection in many ways. The close proximity of the sites (< 25 km) would have likely minimized variation in temperature and rainfall. However, the rolling topography and well-drained soils of the sandhills creates predominantly xeric surface conditions, while the flat terrain and poorly drained soils of the coastal plain creates vast bottomlands of more mesic conditions. While *T. carolina* is a nominally terrestrial species, populations often maintain close associations with aquatic habitats (Rossel et al. 2006; Rittenhouse et al. 2008), especially during hot and dry periods (Donaldson and Echternacht 2005). As expected, the sandhills population preferred mesic environments in closer proximity to streams and bottomlands than did

the coastal plain population. Preference for these more limited mesic environments would allow individuals to more easily maintain positive water balance by soaking in or drinking surface water or burying in forms in the moist substrate. That smaller (and presumably younger) turtles more strongly preferred areas in closer proximity to streams supports this contention, as we expect smaller turtles to be in greater water stress given their high evaporative water loss rates and lower total body water (Foley and Spotila 1978; Finkler 2001). Consistent with our findings, juvenile *T. carolina bauri* (Florida Box Turtle) were found more frequently in moist substrates than were adults (Jennings 2007), and our results suggest that habitat selection gradients for moisture and aquatic resources also extend to influence subadults and adults of different body sizes. Other species of terrestrial and semi-aquatic turtles that occur along dry to wet environmental gradients demonstrate considerable inter-population variation in behavior and physiology to meet challenges of energy and water balance (Peterson 1996; Ligon and Peterson 2002; Roe and Georges 2008). Preferred food items for *T. carolina* such as mushrooms, litter and soil invertebrates, and fruits (Dodd 2001) may also be in greater abundance near streams and bottomlands, though we did not assess food preferences or availability.

Preference for predominantly hardwood or mixed pine and hardwood forests is consistent with habitat selection in *T. carolina* populations across their range (Rittenhouse et al. 2008; Kapfer et al. 2013; Greenspan et al. 2015; Keister and Willey 2015). The dense canopy of such forests likely provides favorable moisture conditions as well as cooler and less variable temperatures along with canopy gaps and edges for basking (Reagan 1974; Dodd 2001; Parlin et al. 2017; Roe et al. 2017). However, the stronger preference for hardwood and hardwood forest mixtures in the sandhills population may be in part a consequence of their stronger preference for mesic environments, as hardwood forests primarily occur near streams and in bottomland habitats at both sites. It is thus difficult to decouple these correlated variables to infer mechanisms driving habitat selection. Mesic hardwood forests may also offer the habitat structures that *T. c. carolina* prefers including deep leaf litter, logs and other coarse woody debris, and complex under- and mid-story vegetation such as vines, ferns, and small woody plants (e.g., shrubs, saplings). Interestingly, the selection of structural habitat components in the immediate vicinity of turtle locations did not vary by site, sex, or body sizes, suggesting that resource selection templates at this level are more conservative and that availability of suitable microsites is a necessary component of broader-scale selection of forest community types. We caution that our measures of finer-scale habitat structural variables were

not stratified by different behaviors (e.g., subsurface inactive vs. surface active), seasons, or time of day, all of which can influence selection of such resources in *Terrapene* (Converse and Savidge 2003; Rossel et al. 2006).

Another factor that could influence differences in habitat selection between populations is the frequency, type, and magnitude of disturbances. *Terrapene carolina* responds to natural and anthropogenic disturbances by altering resource allocation and growth (Dodd and Dreslik 2008) and modifying activity, movements, and dispersal (Dodd et al. 2006; Currylow et al. 2012). We expect turtles to prefer habitats that minimize exposure to threats that could injure, kill, or disrupt important behaviors. One such factor is flooding, particularly in coastal plain habitats, which are subject to increased flood depth, duration, and frequency given their low and gently sloping elevation, especially adjacent to large rivers. Indeed, the Lumber River and tributaries frequently flooded with high volume flows covering much of the park at times during the study. Stickel (1978) suggested that severe floods may have been an important source of mortality in a declining population of *T. c. carolina* in a bottomland habitat, and Dodd et al. (2006) found *T. c. bauri* to abandon areas flooded by a series of severe tropical storms. In our study, turtles in the riverine floodplain were occasionally flushed nearly 1 km downstream and took several days or weeks to return to core areas of their home range, and turtles in bottomlands were regularly displaced from overwintering refuges by floodwaters and forced to relocate to nearby uplands. Such displacements were likely costly in exposure to predators and cold temperatures, as well as in time and energy expenditure to return to core areas in the active season (Hester et al. 2008). Stronger preference for upland habitats may be favored in coastal plain environments to minimize exposure to such threats, as was observed in the Lumber River population.

Another possibility is that fire could influence inter-population variation in habitat selection. Historically, natural wildfires were an important disturbance in both the sandhills and coastal plain regions (Frost 1998), though fires would have been less frequent in the lowland terraces near extensive riverine floodplains in the coastal plain, likely only penetrating during periods of drought. More recently, fire has been excluded from the Lumber River site for at least several decades, while Weymouth Woods has applied prescribed fire in forest management for the past 42 y. Fire removes or reduces understory vegetation and structure in ways that could affect habitat quality for *T. c. carolina* by altering thermal and hydric conditions and distribution of critical habitat structural resources on finer spatial scales (York 1999; Iverson and Hutchinson 2002; Greenberg and Waldrop

2008; Hossack et al. 2009). Forest composition may influence fire dynamics and behavior in ways that may affect habitat selection on broader spatial scales in *T. c. carolina* as well. For instance, Longleaf Pine forests have a suite of species that promote more frequent and intense fires, with fires burning hottest under Longleaf Pine canopies owing to the dry, aerated, fine, and resinous litter compared to oak forests (Williamson and Black 1981; Mitchell et al. 2009). The trend for *T. c. carolina* to avoid predominantly Longleaf Pine forests at Weymouth Woods (albeit non-significantly) and in other pyrogenic systems (Greenspan et al. 2015), along with stronger preference for mesic hardwood sites could reduce risks of exposure to fire. Indeed, fire intensity was highest in the xeric uplands and lowest in the lower elevations near streams. Proximity to streams and other mesic environments not only affects fire behavior and intensity, but turtles could more easily escape to aquatic refuges as fire approaches. We observed several instances of turtles moving away from approaching fire fronts, with those surviving uninjured often escaping into nearby streams. Similar escape behavior was documented in *T. c. bauri* that moved into nearby wetlands during fire (Platt et al. 2010), suggesting selection of sites in close proximity to water is critical in fire-maintained systems. In the few studies of *T. carolina* responses to fire, prescribed fire was estimated to have killed 10–22% of the population (Platt et al. 2010), with high incidence of injury and reduction of body condition of surviving turtles (Howey and Roosenburg 2013) but minimal impacts to habitat thermal quality (Roe et al. 2017). In our study system, turtle mortality varied spatially depending on the frequency and extent of fire, with annual adult mortality as high as 54.1% in the most frequently burned areas (Roe et al. 2019). However, more detailed information from replicated study sites examining links between habitat quality, habitat selection, and fitness consequences in *T. c. carolina* and other subspecies in fire-managed and other systems is needed before broader generalizations can be made.

The inter- and intra-population variation in habitat selection with respect to several environmental variables in *T. c. carolina* highlights the flexibility of resource selection templates of this wide-ranging species. Variable habitat selection phenotypes between populations of the same species could be a result of behavioral plasticity and/or genetic differences (Wiens 1970; Davis and Stamps 2004; Stamps and Swaisgood 2007). Interestingly, *T. carolina triunguis* (Three-toed Box Turtle) translocated to a site differing in the type and distribution of habitats exhibited fidelity to resource selection templates consistent with their original capture site, suggesting that habitat selection behavior was inherent and shaped by either genetic predispositions or early experiences with particular resource cues

(Rittenhouse et al. 2008). In our study, however, the proximity of sites is well within the distance over which *T. c. carolina* populations vary genetically (300–500 km; Kimble et al. 2014), with no major barriers to dispersal and historic gene flow between sites that could contribute to genetic divergence. Our study is limited in that we only examined turtle responses to habitat heterogeneity at two sites, but despite this limitation and regardless of the mechanisms responsible for maintaining the variation, the existence of variable habitat selection behaviors between populations in neighboring but distinct physiographic regions identified here suggests such variation is likely to exist elsewhere. Further comparative studies using standardized methods to examine population responses to variation in environmental conditions, resource distribution and availability, anthropogenic disturbances, and other factors across the range of *T. carolina* would allow for more accurate generalizations.

The existence of variable resource selection templates among populations of *T. c. carolina* also suggests caution when extrapolating results from particular locations to other sites across the geographic range of a species for use in conservation and management. Many conservation strategies assume that the same actions applied across a species range will have similar results, but several aspects of imperiled species management including reserve design, habitat restoration, forest management practices, and translocation should ideally be flexible enough to account for variable phenotypes among populations. It is unlikely that resource managers would ever have population or site-specific information of sufficient detail across a species entire geographic range, but identifying broader regional variation in behavior, life history, physiology, or other traits that could inform management decisions is a realistic goal. For instance, important regional management units have been identified for species of marine turtles to facilitate the identification of variable behaviors, threats, knowledge gaps, and ultimately more effective conservation and management solutions across broad geographic areas (Wallace et al. 2010). In another example, the identification of variable patterns of habitat selection among populations of several bird species in response to differing land use practices has been useful in context-specific conservation planning in farmland systems (Whittingham et al. 2007). For *T. c. carolina*, preferred habitats were more strongly selected when they were less available. Land management practices for *T. c. carolina* in sandhills and perhaps other xeric environments would benefit from a complementary approach to habitat management, where special attention should be given to managing wet areas in addition to terrestrial forest resources, a strategy that might not be as important to populations

in coastal plain and other more mesic environments. Similar suggestions have been made for other *T. c. carolina* populations that require seasonal refuge in aquatic habitats (Donaldson and Echternacht 2005). Land managers could also benefit from knowledge of region-specific habitat selection when planning forest management practices (including prescribed fire) to project risks and responses of *T. carolina* to various plans and make modifications to minimize conflict if required (Platt et al. 2010; Currylow et al. 2012). Given the strength of selection for hardwood forests and other mesic habitats, we suspect that such habitat patches are critical refuges for *T. c. carolina* and other subspecies, especially in pyrogenic systems, and that maintenance of such forests patches in broader habitat mosaics would likely be important for population persistence. Despite the numerous limitations, these findings nonetheless improve our understanding of the various ways *T. c. carolina* interacts with its environment, with potential implications for developing a more targeted approach to land management and other conservation practices across their range.

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