
SPATIAL ECOLOGY, MOVEMENTS, AND HABITAT SELECTION OF *CLEMMYS GUTTATA* IN A TEMPORALLY DYNAMIC WETLAND SYSTEM IN NORTH CAROLINA, USA

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Abstract.—Turtle populations are in decline worldwide, requiring immediate conservation and management actions. For species with broad geographic ranges that cover diverse environmental contexts, region-specific information on declining species could inform more targeted management plans. I examined the ecology of a Spotted Turtle (*Clemmys guttata*) population in a temporally dynamic wetland system in the Southeastern Plains ecoregion of North Carolina. Turtles selected forested wetlands and streams while avoiding open wetlands and river habitats, but used terrestrial habitats minimally and randomly. Turtles responded to wetland drying by remaining in wetlands and maintaining modest levels of activity during short-duration drying events (< 1 mo), but moved very little during longer droughts (7 mo). Turtles had prolonged active seasons (February–October) as long as wetlands and streams were flooded, with movement rates peaking in late spring at 23.6 ± 3.7 m/d (mean \pm standard error). Turtles had large home ranges (14.1 ± 4.3 ha) that often included multiple local stream networks used as movement corridors between forested wetland patches and as activity centers when wetlands dried. I suggest that conservation plans for *C. guttata* include large management areas that protect a network of streams and adjacent forested swamps in the Southeastern Plains and perhaps other lowland ecoregions in the Southeastern U.S. Because terrestrial habitats were not used for extended refuge during drought, certain low-impact land uses in adjacent terrestrial areas are not likely to negatively impact *C. guttata* populations, but terrestrial forests would still be important in maintaining overland travel corridors.

Key Words.—drought; estivation; home range; forested wetland; radiotelemetry; Spotted Turtle; stream; temporary wetland

INTRODUCTION

Turtles are among the most imperiled vertebrates worldwide, with more than half of species listed as threatened or already extinct in modern times and requiring conservation action (Buhlmann et al. 2009a; Tuberville et al. 2014; Lovich et al. 2018; Van Dyke et al. 2019; Stanford et al. 2020). Declines result from a variety of factors, including the loss, degradation, and fragmentation of habitats, overexploitation in pet and food trades, road mortality, disease, invasive predators, climate change, and environmental pollution (Lovich et al. 2018; Stanford et al. 2020). Turtles are particularly vulnerable to such threats owing to their slow somatic growth, delayed sexual maturity, and variable but high mortality in embryonic and juvenile life stages (Brooks et al. 1991; Congdon et al. 1993, 1994; Heppell 1998; Dodd et al. 2016). Such life history characteristics limit population growth and prolong recovery rates in most turtle species (Hall et al. 1999; Keevil et al. 2018; but see Fordham et al. 2007).

Many turtle species are geographically restricted to relatively small areas, including several whose range occurs only within a specific habitat type or local

watershed basin (Buhlmann et al. 2009a). In such cases, collecting ecological information, identifying threatening processes, and monitoring population dynamics may be relatively straightforward, thus facilitating the implementation of conservation and management strategies (Sterrett et al. 2015; Selman and Jones 2017). For turtle species with large geographic ranges, populations may experience environments that differ in the spatial distribution and availability of resources, climate, the frequency and intensity of disturbances, and other factors that influence behavior, life history, and population dynamics (St. Clair et al. 1994; Iverson et al. 1997; Markle and Chow-Fraser 2014; Janzen et al. 2018; Roe et al. 2018). In such cases, it may be necessary to design region- or habitat-specific management plans to maintain unique genetic diversity and evolutionary histories, and to facilitate the identification of variable behaviors, threats, knowledge gaps, and more effective conservation and management solutions (Mockford et al. 2007; Wallace et al. 2010; Averill-Murray et al. 2012; Eiseberg et al. 2019; Roe et al. 2021).

Wetlands have declined appreciably in the USA over the past few centuries (Hefner and Brown 1984;

Dahl 1990; Davidson 2014), especially for shallow forested wetlands that have been drained or modified to other wetland types by agriculture and forestry practices (Knoeff and Royle 2004). The loss and degradation of wetlands and other aquatic habitats has contributed to population declines in many aquatic and semi-aquatic turtles (Gibbs 1993; Chessman 2011; Stanford et al. 2020), but detailed information of how and when wetlands are used, along with specific habitat preferences is important for effective conservation and management applications. Wetlands are dynamic systems in space and time, typically requiring complex behavioral, physiological, or morphological responses in animals to survive in such environments. Wetlands are often patchily distributed within a terrestrial matrix, and the environment can differ widely among different wetlands or within a given wetland over time, especially in temporary wetlands (i.e., wetlands that periodically dry; Euliss et al. 2004; Bauder 2005). Such spatial and temporal heterogeneity results in variable habitat quality with respect to environmental conditions and resource availability, either requiring animals to move to a more suitable waterbody, or remain in place to await the return of favorable conditions. Freshwater turtles demonstrate a range of responses to wetland drying, including movement to other wetlands (Roe and Georges 2007) or nearby terrestrial environments (Buhlmann and Gibbons 2001; Rees et al. 2009; Zaragosa et al. 2015), or remaining within the dry wetland (Kennett and Christian 1994). Responses often differ among species (Gibbons et al. 1983; Christiansen and Bickham 1989) and populations (Ligon and Peterson 2002), and can even vary among individuals in the same population (Roe and Georges 2008). Wetland drying is a disturbance that can thus affect freshwater turtle behavior (i.e., movements, home range, habitat selection), as well as their energy and water relations, growth, survival, and reproduction (Christiansen and Bickham 1989; Kennett and Georges 1990; Roe and Georges 2008; Roe et al. 2008). The behavioral responses of turtles to wetland drying can also have important conservation implications, including the need to include adjacent terrestrial buffer zones, overland travel corridors, and other nearby waterbodies in management plans (Burke and Gibbons 1995; Semlitsch and Bodie 2003; Roe and Georges 2007; Beaudry et al. 2008).

The Spotted Turtle (*Clemmys guttata*) is a semi-aquatic freshwater species with a broad geographic distribution in eastern North America (Ernst et al. 1994). *Clemmys guttata* is a species of conservation concern throughout most of its range, with its listing as Endangered by the International Union for the Conservation of Nature (IUCN; van Dijk 2011) and in Canada (Committee on the Status of Endangered Wildlife in Canada 2004), and it is a candidate for listing

under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 2015). Aspects of *C. guttata* ecology and life history are variable across its range (Lovich 1988; Litzgus and Mousseau 2003, 2006), but most detailed studies of *C. guttata* ecology are from the Great Lakes region of North America (Litzgus and Brooks 2000; Rasmussen and Litzgus 2010; Yagi and Litzgus 2012; Rowe et al. 2013) and northeastern parts of their range (Graham 1995; Haxton and Berrill 1999; Joyal et al. 2001; Buchannan et al. 2017; O'Dell et al. 2021). The only detailed ecological studies of southern populations are from South Carolina (Litzgus and Mousseau 2004), Georgia (Chandler et al. 2019), and North Carolina in the U.S. (O'Bryan et al. 2016). Additional region-specific information on *C. guttata* ecology, including habitat associations and selection, movements, activity, home range, and responses to spatial and temporal environmental heterogeneity is necessary to implement successful management and conservation practices for populations in areas that have historically received less attention from biologists.

Here, I examined *C. guttata* behavior in a temporally dynamic stream and wetland system in the Southeastern Plains of North Carolina. I expected the activity season of *C. guttata* would be extended because of longer periods of thermal suitability compared to more northern locations similar to other southern populations (Litzgus and Mousseau 2004; Chandler et al. 2019), but that activity would be constrained to periods of surface water availability (Haxton and Berrill 2001; Rowe et al. 2013). I also expected that wetland drying would affect movements, home range size, and habitat selection, with turtles either seeking refuge in nearby terrestrial forests or other waterbodies that remain flooded (Haxton and Berrill 1999; Litzgus and Brooks 2000; Milam and Melvin 2001; Yagi and Litzgus 2012; O'Dell et al. 2021) and moving long distances over large areas in response to flood-drought cycles. Such ecological information will improve our understanding of *C. guttata* behavior in response to natural hydrologic fluctuations, and assist land managers in designing more effective conservation plans in the southern part of their range.

MATERIALS AND METHODS

Study site.—I studied turtles on public and adjacent private lands in the Southeastern Plains Level III Ecoregion, or Atlantic Southern Loamy Plains and Southeastern Floodplains and Low Terraces Level IV Ecoregions (Griffith et al. 2002) in North Carolina, USA. I have not given the specific location of the study site due to poaching concerns. Environments included extensive bottomland swamp forests and streams with Bald Cypress (*Taxodium distichum*), tupelo (*Nyssa* spp.), Tuliptree (*Liriodendron tulipifera*), Sweetgum

(*Liquidambar styraciflua*), Red Maple (*Acer rubrum*), and Atlantic White Cedar (*Chamaecyparis thyoides*). Swamp forests and streams were tannin-stained, shallow, and with variable hydrology of intermittent flows that frequently dried during the study (Fig. 1). River levels were also variable, but permanent flows remained in the channelized portions throughout the study period. The surrounding uplands were comprised of mixed pine and hardwood forests with Loblolly (*Pinus taeda*) and Longleaf Pine (*P. palustris*), oaks (*Quercus* spp.), and hickory (*Carya* spp.) as canopy cover, with an understory of Fetterbush (*Lyonia lucida*), blueberry (*Vaccinium* spp.), and Mountain Laurel (*Kalmia latifolia*).

Radiotelemetry.—I captured five turtles during Visual Encounter Surveys along streams and in adjacent shallow wetlands during spring flooding, and four turtles while radiotracking other turtles in these same areas. I equipped turtles with radiotransmitters (RI-2B, 6 g, Holohil Systems Ltd., Carp, Ontario, Canada) using 5-minute epoxy gel (Devcon, Solon, Ohio, USA). From May 2017 to May 2020, I tracked nine turtles (five females and four males) for periods of 10–21 mo (15.3 ± 1.0 mo; mean \pm standard error). Upon initial capture, I measured midline carapace length (CL) to the nearest 0.1 mm using vernier calipers and mass to the nearest gram using a spring scale. I determined sex by observing tail length and plastron curvature, with males having thicker and longer tails and more concave plastrons compared to females (Ernst et al. 1994). I located telemetered turtles using a receiver (R-1000, Communication Specialists, Orange, California, USA) and Yagi antenna at a frequency of once per week from April–October and at least once per month from November–March. At each location, I determined the coordinate position using a hand-held GPS (≤ 7 m accuracy) and plotted locations on maps using ArcMap 10.2.2.

Space use and movement variable estimation.—I calculated home range size, range length, and movement rate for each turtle. I used 100% minimum convex polygons (MCP) to estimate home range size, including all locations throughout the year. I measured movement rates as straight-line distances between sequential locations divided by the number of days elapsed between observations. I used Geospatial Modeling Environment (<http://www.spatialecology.com/gme>) and R (R Core Team 2017) as extensions of ArcMap 10.2.2 to estimate movement distances and home range sizes. I used the measure tool in ArcMap 10.2.2 to estimate range length as the maximum distance between any two locations.

Habitat.—I used the U.S. Geological Survey (USGS) Land Cover layer (30 \times 30 m resolution, 2011 Edition, amended 2014) to define the spatial distribution of habitats. Habitat classes within the study area



FIGURE 1. Swamp forest in flood (A) and dry (B) stage in the Southeastern Plains ecoregion of North Carolina, USA. (Photographed by John Roe).

included woody wetland, emergent herbaceous wetland, evergreen forest, deciduous forest, mixed forest, shrub/scrub, and grassland, while cultivated crops and pasture/hay environments were present immediately outside the study area. I mapped stream and river networks by walking each watercourse following heavy rainfall, or paddling in boats. I collected coordinate positions of each channel using hand-held GPS units (GPS 72H, Garmin, Olathe, Kansas, USA) and digitized the network as polylines using ArcMap 10.2.2. By mapping watercourses during high water, I was able to include areas where surface water was present on a temporary basis. Watercourses were classified as temporary if they were observed to dry at any point in the study period, or permanent if surface water was present continuously. I also observed water levels in streams and adjacent swamp forests, and noted whether surface water was present or absent at least once every two weeks. I observed water levels at three standardized locations where streams exited swamp forests and crossed under a service road and then entered the main river floodplain, locations that all allowed me to visually observe the variety of aquatic habitats used by turtles in this study. To assess habitat use, I measured the Euclidian distances from turtle locations to the nearest permanent and

temporary streams, as well as to the nearest patch of each habitat class.

Statistical analyses.—I performed statistical analyses with SPSS v. 25.0 (SPSS Inc., Chicago, Illinois, USA). Where appropriate, I examined the assumptions of homogeneity of variances and normality; when data failed to meet assumptions, I transformed data to approximate normal distributions or equal variances. If transformations did not rectify parametric assumptions, I used appropriate non-parametric tests. I accepted statistical significance at $P < 0.05$, and report values as mean \pm 1 standard error unless otherwise stated. I examined variation in space use using Multivariate Analysis of Variance (MANOVA), with home range size (MCP) and range length as the dependent variables, sex as the independent variable, and carapace length as a covariate. I \log_{10} -transformed MCP, range length, and carapace length prior to analysis.

I used Linear Mixed Models to examine sources of variation in movement rates. I first tested a model using mean monthly movement rate (m/day) as the dependent variable, sex, month, and sex \times month as independent variables, \log_{10} carapace length as the covariate, and individual as the repeated variable. In the model above, each month had a minimum sample size of seven turtles and at least three individuals of each sex. I then calculated mean movement rates (m/day) during wet and dry periods for each individual ($n = 9$) and tested whether movement rate (dependent variable) varied according to hydrology (wet vs. dry), sex, and sex \times hydrology (independent variables), or carapace length (covariate), using individual as the repeated variable. I defined dry periods as any month where surface water was unavailable in the temporary streams and bottomland swamp forests during at least one of the water level observations.

Prior to analyses of habitat use and selection, I collapsed terrestrial (upland) habitats into categories with structural similarities including forest (deciduous, evergreen, and mixed forests), shrub/grass (shrub/scrub and grassland), and agriculture (cultivated crops and pasture/hay), but retained woody and emergent herbaceous wetlands as separate classes. I excluded agriculture from analyses because this class was outside the study area. I used Linear Mixed Models to examine variation in habitat use between wet and dry periods, with distance to the nearest patch of each habitat class or watercourse as dependent variables, sex, hydrology (wet vs. dry), and their interaction as independent variables, \log_{10} carapace length as a covariate, and individual as the repeated variable. Because distances to woody and emergent herbaceous wetlands remained strongly non-normal after transformations, I used Wilcoxon Signed Rank tests to compare wetland use between dry and

wet periods, and Mann-Whitney U tests to compare sexes. In the above analyses, I calculated two distance values per individual (mean distances to each habitat class during wet periods and dry periods) as dependent variables, and ran separate analyses for forest, shrub/grass, woody wetlands, emergent herbaceous wetlands, streams, and rivers.

To assess habitat selection, I used Euclidian distance analysis (Conner and Plowman 2001; Conner et al. 2003). Using the Create Random Points tool in ArcMap 10.2.2, I generated random points paired with each turtle location ($n = 269$) within the study area, defined as the MCP encompassing locations for the sample population of turtles (population range). I measured nearest distances from random points to each habitat class and watercourse type. To determine whether turtles used habitats in accordance with availability, I calculated a selection index by subtracting the values (distances to habitat features) for random locations from paired turtle locations, combining both wet and dry periods and sexes. For each turtle, I calculated a mean selection index for each habitat and compared selection indices to a vector of the value zero (assuming random use of habitats, see Conner et al. 2003) using Analysis of Variance (ANOVA), with selection index as the dependent variable and location (turtle or random) as the independent variable. Because transformations failed to normalize the distribution of selection indices for wetlands and temporary streams, I compared selection indices to a vector of the value zero using Mann-Whitney U tests. In the above analyses, habitats used more frequently than available have selection indices < 0 (distances closer than expected from random), habitats used less frequently than random have indices > 0 (distances farther than expected from random), while habitats used similar to availability have indices $= 0$ (distances equal to availability). This scale of habitat selection combined second and third order analyses of Johnson (1980), comparing turtle locations to habitats available within the population range given that turtles could have feasibly traveled to all areas within the population range (see Results).

RESULTS

The size of turtles ranged from 91.1–115.2 mm CL and from 115–240 g. Females were 108.9 ± 5.9 mm CL (mean \pm standard deviation [SD]) and 177.5 ± 18.5 g (SD), and males were 104.9 ± 9.3 mm CL (SD) and 179.0 ± 46.8 g (SD). Transmitters were 2.5–5.0% of turtle body mass. I obtained 29.9 ± 3.3 locations per turtle over a period of 15.3 ± 1.1 mo. Home range size and range length varied between 3.1–42.7 ha and 401–1719 m, respectively, but did not vary according to body size (Wilks' $\lambda = 0.762$, $F_{2,5} = 0.780$, $P = 0.507$) or between

TABLE 1. Space use and movement variables for Spotted Turtles (*Clemmys guttata*) in the Southeastern Plains ecoregion of North Carolina, USA. Values are mean \pm standard error, n = sample size.

Sex	n	Home range (ha)	Range length (m)	Movement rate (m/d)
Male	4	18.7 \pm 8.6	769.8 \pm 109.2	14.4 \pm 2.8
Female	5	10.5 \pm 3.9	726.6 \pm 249.7	10.8 \pm 1.3
Combined	9	14.1 \pm 4.3	745.8 \pm 139.2	12.6 \pm 1.5

sexes (Wilks' $\lambda = 0.934$, $F_{2,5} = 0.177$, $P = 0.843$; Table 1; Fig. 2). Movement rates ranged between 7.7–22.5 m/d, and varied by month ($F_{11,10,371} = 6.088$, $P = 0.004$), but not sex ($F_{1,33,910} = 2.364$, $P = 0.133$), sex \times month ($F_{11,10,360} = 1.262$, $P = 0.358$), or according to body size ($F_{1,25,002} = 0.003$, $P = 0.955$). Movements were lowest from November to January, increased through spring until peaking in May, then declined through summer and fall (Fig. 3). Movements were highly variable in both wet and dry periods, but did not differ between wet and dry periods for either sex (hydrology: $F_{1,9,801} = 1.104$, $P = 0.338$; hydrology \times sex: $F_{1,9,801} = 0.006$, $P = 0.942$; Fig. 4) or according to body size ($F_{1,9,002} = 3.830$, $P = 0.082$).

The population range covered 238.3 ha, with woody wetland the most common habitat class (55.0%), followed by evergreen forest (20.1%), mixed forest (8.2%), deciduous forest (5.6%), shrub/scrub (5.6%), emergent herbaceous wetland (4.5%), and grassland (0.7%). Wetlands covered 59.9% of the area, while terrestrial forests and shrub/grasslands covered 33.8% and 6.3% of the site, respectively. Bottomland swamps and temporary streams were dry for 14 of the 37 mo of the study period, representing $26.9 \pm 6.9\%$ (range, 13.3–64.3%) of the time each turtle was tracked.

Turtles primarily used woody wetland ($85.6 \pm 7.6\%$), followed by mixed forest ($4.9 \pm 4.9\%$), evergreen forest ($4.3 \pm 2.2\%$), shrub/scrub ($2.2 \pm 2.2\%$), emergent herbaceous wetland ($2.5 \pm 2.5\%$), and deciduous forest ($0.5 \pm 0.5\%$), but were never found in grassland habitat. Distances from turtle locations to each habitat class were similar between sexes, across body sizes, and consistent

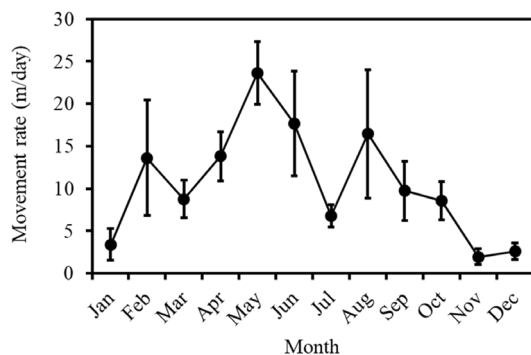


FIGURE 3. Monthly movement rates (mean \pm standard error) for Spotted Turtles (*Clemmys guttata*) in the Southeastern Plains ecoregion of North Carolina, USA.

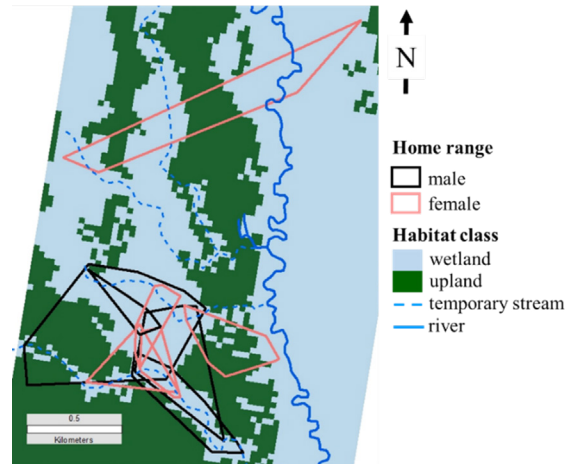


FIGURE 2. Home ranges (100% minimum convex polygons) for male and female Spotted Turtles (*Clemmys guttata*) in the Southeastern Plains ecoregion of North Carolina, USA.

between wet and dry periods for terrestrial forests (sex: $F_{1,12,887} = 0.587$, $P = 0.457$; hydrology: $F_{1,12,841} = 0.028$, $P = 0.870$; sex \times hydrology: $F_{1,12,841} = 0.015$, $P = 0.904$; CL: $F_{1,12,784} = 4.138$, $P = 0.063$), shrub/grasslands (sex: $F_{1,12,810} = 1.894$, $P = 0.192$; hydrology: $F_{1,12,735} = 0.255$, $P = 0.622$; sex \times hydrology: $F_{1,12,735} = 0.005$, $P = 0.946$; CL: $F_{1,12,642} = 0.480$, $P = 0.501$), woody wetlands (sex: $U = 8.5$, $P = 0.662$; hydrology: $W = 2.0$, $P = 0.655$), and emergent herbaceous wetlands (sex: $U = 8.0$, $P = 0.624$; hydrology: $W = 18.0$, $P = 0.594$). Distances from turtle locations to watercourses were also similar between

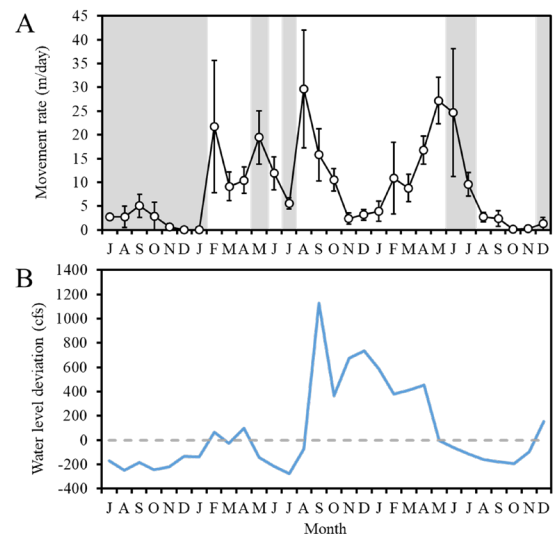


FIGURE 4. Monthly movement rates (mean \pm standard error) for Spotted Turtles (*Clemmys guttata*) and in swamp forests (A) and river flow deviations (cubic feet/second) relative to the 10-y average (B; 2010–2020) in the Southeastern Plains ecoregion of North Carolina, USA. Grey indicates periods when swamps and temporary streams were dry. Flow rates were collected from a station within 15 km of the study area and data were accessed from the U.S. Geological Survey National Water Dashboard.

TABLE 2. Distances (mean \pm SE) from Spotted Turtle (*Clemmys guttata*) locations and random points to habitat classes in the Southeastern Plains ecoregion of North Carolina, USA. Values are mean \pm standard error.

	Forest (m)	Scrub grassland (m)	Woody wetland (m)	Emergent herbaceous wetland (m)	Stream (m)	River (m)
Turtle	69.5 \pm 13.5	254.7 \pm 21.6	8.8 \pm 4.8	455.0 \pm 51.1	111.5 \pm 41.4	580.9 \pm 51.8
Random	56.2 \pm 6.3	252.5 \pm 11.5	17.4 \pm 1.4	272.9 \pm 18.7	180.1 \pm 12.3	425.0 \pm 20.2

sexes and consistent between wet and dry periods for temporary streams (sex: $F_{1,12,517} = 3.642$, $P = 0.080$; hydrology: $F_{1,12,340} = 0.032$, $P = 0.862$; sex \times hydrology: $F_{1,12,340} = 0.318$, $P = 0.583$) and the river (sex: $F_{1,12,545} = 3.950$, $P = 0.069$; hydrology: $F_{1,12,377} = 0.000$, $P = 0.985$; sex \times hydrology: $F_{1,12,377} = 0.063$, $P = 0.806$). Distances to temporary streams varied with body size, with smaller turtles maintaining closer proximity to streams (CL: $F_{1,12,118} = 5.16$, $t = 2.27$, $P = 0.042$), but body size did not affect distance to the river (CL: $F_{1,12,166} = 2.47$, $P = 0.142$). Distances from turtle locations to terrestrial habitat classes did not differ from random (forest: $F_{1,16}$

$= 0.874$, $P = 0.364$; shrub/grassland: $F_{1,16} = 0.006$, $P = 0.940$; Table 2; Fig. 5). Turtle locations were closer to woody wetlands ($U = 13.5$, $P = 0.014$) and temporary streams ($U = 9.0$, $P = 0.004$) than expected from random, but farther from emergent herbaceous wetlands ($U = 72.0$, $P = 0.004$) and the river than expected from random ($F_{1,16} = 9.53$, $P = 0.007$; Table 2; Fig 5).

DISCUSSION

Clemmys guttata occurs across a large geographic range and populations are thus exposed to heterogeneous environments that necessitate variable behavioral responses to local conditions. This study of a population in the Southeastern Plains of North Carolina reveals several insights into *C. guttata* ecology that are potentially important for their conservation and management. Turtles primarily used swamp forest habitats with a strong selection for areas in or near small temporary streams (especially for smaller individuals) while avoiding the larger, permanently flowing river. Turtles responded to drying of streams and swamp forests by remaining in the wetland and maintaining movements and surface activity for short duration periods of drying, but reduced movements during longer droughts. Movements occurred throughout much of the year (February–October), indicating a prolonged active season, and turtles traversed large home ranges that often included multiple local stream networks and extensive adjacent forested swamps. These behaviors are generally consistent with other southern populations of *C. guttata* in natural landscapes (Litzgus and Mousseau 2004; Chandler et al. 2019) and warrant region- or habitat-specific conservation and management strategies distinct from populations in the northern part of their range.

While capable of inhabiting a wide variety of aquatic environments (e.g., wet meadows, marshes, bogs, fens, vernal pools, streams, and adjacent floodplains; Ernst et al. 1994), wetlands occupied by *C. guttata* are generally shallow and dynamic habitats with temporally variable conditions, including changes in temperature, surface water availability and depth, food availability, and other variables (Litzgus and Brooks 2000; Litzgus and Mousseau 2004; Beaudry et al. 2009; Yagi and Litzgus 2012). In wetlands that temporarily dry, some *C. guttata* respond by seeking refuge in nearby terrestrial areas where they become inactive and await the return

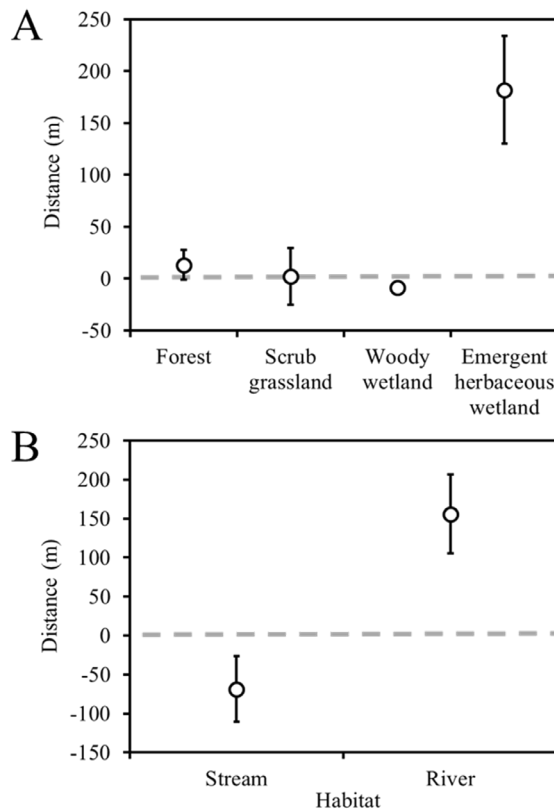


FIGURE 5. Euclidian distance-based selection indices (mean \pm standard error) for habitat classes (A) and watercourses (B) for Spotted Turtles (*Clemmys guttata*) in the Southeastern Plains ecoregion of North Carolina, USA. Habitats used more frequently than available have selection indices < 0 (distances closer than expected from random), habitats used less frequently than random have indices > 0 (distances farther than expected from random), while habitats used similar to availability have indices $= 0$ (distances equal to availability).

of flooding (e.g., Haxton and Berrill 1999; Litzgus and Brooks 2004; Yagi and Litzgus 2012; Buchanan et al. 2017; O'Dell et al. 2021). Other *C. guttata* may move to nearby isolated waterbodies offering different habitat types or longer hydroperiods (Graham et al. 1995; Joyal et al. 2001; Milam and Melvin 2001; Beaudry et al. 2008, 2009). In other circumstances, *C. guttata* may remain within a single wetland throughout flood-dry cycles (Ernst 1976; Ward et al. 1976; Ernst 1982; Rowe et al. 2013; Chandler et al. 2019). It should be noted that behavioral responses to wetland drying may be a general characteristic of a *C. guttata* population or variable among individuals within a population depending on local environmental conditions (e.g., season, quality, availability, and proximity to other aquatic and terrestrial habitats) and state variables (e.g., demographics, reproductive condition), as is the case for other species of freshwater turtles (Bodie and Semlitsch 2000; Chelazzi et al. 2007; Roe and Georges 2008; Rees et al. 2009). Streams and associated swamp forests used by turtles were dry for 38% of the time, with the longest drought conditions lasting up to 7 mo. While turtles made frequent movements within a wetland basin among localized deeper depressions (e.g., oxbows, ditches, stream channels, storm tip-ups) that held water longer as water levels dropped, and occasional movements to neighboring streams that required short-distance (< 100 m) overland movements, no turtles remained in upland terrestrial refuges for extended times, nor did any use the permanently flooded river when other wetlands were dry. Instead, all turtles resided in dry wetland habitats to await the return of flood conditions.

Freshwater turtles often become inactive when their wetlands dry and enter a state of estivation. Estivation is a behavioral strategy to reduce energy and water demands during drought conditions, and may also include physiological adjustments (Seidel 1978; Peterson and Stone 2000; Ligon and Peterson 2002; Roe et al. 2008; Buhlmann et al. 2009b). Whether estivation involves behavioral and/or physiological mechanisms, a critical aspect of enduring drought conditions is to select refuge sites that remain cool, humid, and concealed from predators, which is especially important for *C. guttata* given its small body size and high evaporative water loss rate compared to terrestrial species (Ernst 1968). Similar to other *C. guttata* populations in the southern part of their range (Litzgus and Mousseau 2004; Chandler et al. 2019), I typically found turtles buried in leaf litter, under logs and other woody debris, within root mounds or hummocks, or in dense shrubby vegetation when wetlands were dry. I suspect that refuge habitats available under the dense canopy cover within forested wetlands during dry periods were at least of comparable quality to those in terrestrial forests, but that overland migrations to and refuge within upland terrestrial forests

were unnecessary and may even expose turtles to other sources of injury or mortality (Beaudry et al. 2008; Cross and Bekker 2017). Infrequent use of terrestrial habitat was also observed in another *C. guttata* population in North Carolina, but this behavior may have been attributable to the availability of extensive flooded ditch networks in an anthropogenically reconfigured landscape (O'Bryan et al. 2016). The suitability of available refuge microenvironments within the wetland was also proposed as an explanation for other *C. guttata* populations remaining in dry wetlands during drought periods (Rowe et al. 2013; Chandler et al. 2019, 2020). Estivation in dry wetlands would also allow for more immediate responses to wetland reflooding and resumption of important aquatic activities (i.e., foraging and mating) compared to estivation in upland terrestrial refuges. *Clemmys guttata* populations throughout their range may enter estivation states of varying degrees depending on the duration of drought conditions, but they often maintain some surface activity and are quick to respond to wetland reflooding (Litzgus and Brooks 2000; Litzgus and Mousseau 2004; Yagi and Litzgus 2012; Rowe et al. 2013; Chandler et al. 2019). Similarly, turtles in my study were often active on the surface when streams and wetlands dried and continued to move at similar rates compared to wet periods. The failure to detect a significant effect of flood/dry conditions on movement rates may reflect the overall wet conditions of the study relative to long-term averages, including one of the largest hurricanes (Florence) to ever hit the region in September 2018, which resulted in record flood levels that persisted for several months. Movement rates were consistently low (< 5 m/d) during the earlier and more prolonged 7-mo drying event, but all subsequent dryings were of only short duration (i.e., several weeks) and likely did not capture full estivation behavior. It is also possible that the low sample sizes and broad hydrology classification I used was insufficient to detect changes in movement in response to wet-dry cycles in analyses. Nevertheless, estivation does not seem to be a seasonal phenomenon in this *C. guttata* population, but rather an episodic one depending on timing of flood-dry cycles. The only consistent period of inactivity was during overwintering (November-January), regardless of wet/dry conditions.

While numerous studies of *C. guttata* document habitat associations, relatively few demonstrate selection by comparing habitat use to availability (but see Milam and Melvin 2001; Rasmussen and Litzgus 2010; O'Bryan et al. 2016; O'Dell et al. 2021). I examined habitat selection with distance-based approaches, which offer potential advantages over classification-based approaches (e.g., compositional analysis), including lower sensitivity to locational errors, improved ability to identify important nearby habitat patches 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). Unlike other populations of *C. guttata* that demonstrate temporally variable habitat use and selection of a variety of aquatic and terrestrial habitat types (Litzgus and Brooks 2000; Rasmussen and Litzgus 2010; Beaudry et al. 2009; O'Dell et al. 2021), habitat use and selection were less dynamic in my study population. Turtles selected woody wetlands and temporary streams, avoided emergent herbaceous wetlands and the river, and used upland terrestrial forests and shrub/grasslands randomly, regardless of wetland hydrology. I caution that the small sample size and relatively small area where turtles were originally captured may have overlooked more variable habitat selection behaviors of individuals in the broader area. Nevertheless, this more simplistic habitat selection behavior may reflect the suitability of preferred forested wetlands and associated streams for all critical requirements in the annual cycle (e.g., feeding, reproduction, and refuge) and even during episodic disturbances (e.g., drought). It is noteworthy that females were rarely observed to leave a wetland, suggesting that even nesting may have occurred in or on the edges of wetlands as has been observed or suggested in other *G. guttata* populations (Litzgus and Mousseau 2004; Beaudry et al. 2010; Rowe et al. 2013; Chandler et al. 2019); however, the tracking frequency I used may have been insufficient to detect short-term nesting excursions.

Clemmys guttata often associates at least seasonally with open wetlands (Haxton and Berrill 1999; Beaudry et al. 2009; Rasmussen and Litzgus 2010; Rowe et al. 2013; O'Dell et al. 2021), but turtles in my study population avoided open emergent herbaceous wetlands in favor of forested wetlands. The closed canopy of forested wetlands may confer thermal advantages to *C. guttata* in warmer climates of the Southeastern U.S., allowing for prolonged activity during spring and summer seasons compared to thermal extremes that would be experienced in more open habitats (Chandler et al. 2020). The closer association of smaller individuals with streams likely reflects the longer duration of surface water availability this habitat feature offers compared to the adjacent bottomlands. Smaller individuals would be in greater water stress during drought given their high evaporative water loss rates and lower total body water (Foley and Spotila 1978; Finkler 2001), and may thus be at greater risk of desiccation if they become stranded in dry swamp forests far away from stream channels. To my knowledge, the closer association of smaller individuals to streams is the first documented case of size-dependent variation in habitat selection behavior in *C. guttata*, but further studies that examine a wider range of body sizes (including juveniles) would be necessary

to support this observation. That *C. guttata* avoided the river, despite it being within their movement range and the only source of available surface water during drought, is similar to their avoidance of other deeper, permanently flooded waterbodies elsewhere (Haxton and Berrill 1999; Milam and Melvin 2001; Rasmussen and Litzgus 2010). Avoidance of the river may be an artifact of initial capture locations, however, which were all in streams or adjacent swamp forests. Also, the relatively short duration of drying events observed in this study may not have been long enough to stress hydration and energy reserves in estivating turtles, and migration or dispersal to the river or other nearby permanent waterbodies may be necessary to survive more extended droughts, as has been observed in other semi-aquatic turtles (Roe and Georges 2008; Roe et al. 2008). I caution that the spatial configuration of habitats did not allow for a rigorous examination of selection for some habitats that were restricted to the edges of the study site or were otherwise of limited availability (e.g., grasslands, emergent herbaceous wetlands, river). I also acknowledge that the spatial resolution of broad-scale habitat classifications (30 × 30 m) would have overlooked important behavioral responses to finer-scale environmental heterogeneity in *C. guttata* (Litzgus and Mousseau 2004; Rasmussen and Litzgus 2010; O'Bryan et al. 2016).

Home range represents the area traversed during behaviors required for survival and reproduction over a defined time period (Burt 1943; Börger et al. 2006), making this an important ecological measure to compare how individuals or populations interact with their environments in space and time. Home ranges traversed by turtles in my study (14.1 ha) were considerably larger than *C. guttata* populations in the Northeastern U.S. (Ernst 1970; Graham 1995; Milam and Melvin 2001; Buchanan et al. 2017; O'Dell et al. 2021), the Great Lakes region of North America (Haxton and Berrill 1999; Rasmussen and Litzgus 2010; Yagi and Litzgus 2012; Rowe et al. 2013), and a southern population of the U.S. (Chandler et al. 2019), but were comparable to two other southern U.S. populations (Litzgus and Mousseau 2004; O'Bryan et al. 2016). The large home ranges likely reflect the expansive and continuous patches of suitable habitat in the forested swamps and stream networks available at my site. For example, the majority (55%) of the population range was comprised of woody wetlands, a strongly selected habitat class, perhaps allowing for extensive movements within it. Low elevation gradients along river basins in the Southeastern Plains region create extensive forested floodplain habitats bisected by slow-flowing, meandering streams, which is a similar landscape to a South Carolina *C. guttata* population with exceptionally large home ranges (Litzgus and Mousseau 2004). Much of my study site was on protected public

land and neighboring private properties managed for hunting clubs, timber harvest, and some agriculture. Consequently, the landscape was not heavily fragmented by roads and urban development, which are habitat alterations that constrain movements in turtles (Rubin et al. 2001; Edwards et al. 2004; Iglay et al. 2007; Patrick and Gibbs 2010). Another potential factor in the large home ranges was the spatial extent and long duration of flooding during the study period, coupled with long annual activity seasons. Indeed, home range sizes in other *C. guttata* populations increase with both hydroperiod length and in response to increased spatial extent of flooding (Yagi and Litzgus 2012; Rowe et al. 2013). Likewise, movements occurred from February–October if flooding permitted, indicating a considerably longer active season in southern compared to northern *C. guttata* populations (Lovich 1988; Litzgus and Mousseau 2004, 2006; Stevenson et al. 2015; Chandler et al. 2019). That males and females had similar home range sizes and seasonal movement patterns is consistent with most other *C. guttata* populations (Rasmussen and Litzgus 2010; Yagi and Litzgus 2012; Rowe et al. 2013; O'Dell et al. 2021, but see Litzgus and Mousseau 2004), indicating that resource needs generally overlap spatially for both sexes in forested wetlands and streams and that their movement responses to temporally dynamic flood-drought cycles were similar.

Management implications.—*Clemmys guttata* is a relatively well-studied species that nevertheless remains imperiled throughout much of its range. Unfortunately, the body of knowledge obtained through even the most rigorous studies is not easily or often translated into species recovery (Lovich and Ennen 2013). In many cases, the continued imperilment of *C. guttata* is likely due to a failure to implement management actions to address known threats; however, the disconnect between knowledge and management may in part be a product of the broad geographic range of *C. guttata*, with populations occurring in environments that differ in resource distribution, habitat types, climate, hydrology, disturbance regimes, and many other factors. Conservation and management plans for imperiled turtles must be flexible enough to allow for such regional variability (e.g., Wallace et al. 2010; Averill-Murray et al. 2012).

Identification of important habitat is essential for targeted conservation action, as such data could inform reserve design, restoration, translocation, and management of forest and wetland resources. My study is the first to highlight the importance of small temporary streams for *C. guttata*. Turtles used streams when traveling among distant patches of flooded swamp forest and for aquatic activity when adjacent bottomlands were dry, which was especially important for smaller

individuals. In addition to being an important habitat feature selected by *C. guttata*, streams are integral in the hydrologic regimes of adjacent swamp forests through over-bank flooding and perhaps groundwater connections as well. Smaller non-navigable streams are typically not included in the same habitat protection guidelines that larger navigable waterways have, and may thus be overlooked by conservation and management, which is especially true for streams that temporarily dry (Leibowitz et al. 2008). The quality of such streams and their hydrologic regimes may be especially sensitive to land management practices such as channelization, flow regulation, impoundment, draining, pollution, and siltation from surrounding land uses (Bodie 2001), all of which have heavily impacted stream communities in the Southeastern U.S. as a result of forestry, agriculture, and urban development (Sheldon 1988; Poff et al. 2006; O'Driscoll et al. 2010). The importance of stream management has been identified as critical for the conservation of several vertebrates including salamanders (Willson and Dorcas 2003; Price et al. 2006), fishes (Sheldon 1988; Colvin et al. 2019), and other species of freshwater turtle (Dodd 1990; Bodie 2001; Sung et al. 2015), including those that typically associate with lentic waterbodies (Somers et al. 2007; Pittman and Dorcas 2009; Smith and Cherry 2016). I recommend that streams be included as important habitat features in management and conservation plans for *C. guttata* in the Southeastern Plains and perhaps other ecoregions with comparable forested swamp habitat.

For semi-aquatic turtles that use terrestrial habitats for nesting, estivation, or overwintering, it is often recommended to extend habitat protection from the wetland some distance into adjacent uplands (Burke and Gibbons 1995; Buhlmann and Gibbons 2001; Semlitsch and Bodie 2003; Steen et al. 2012; Zaragoza et al. 2015). For *C. guttata* populations that regularly use uplands, suggested terrestrial buffer zones extend up to 400 m from the wetland boundary to include critical estivation and nesting habitats (Joyal et al. 2001; Milam and Melvin 2001; Beaudry et al. 2010; Buchanan et al. 2017). The more limited use of upland habitats by *C. guttata* in my study population may not warrant the same degree of terrestrial buffer zone protection, as estivation and presumably nesting occurred within the delimited wetland. Even though terrestrial habitats were not used by the turtles for extended periods, turtles made occasional short distance (< 100 m) overland movements between streams and patches of swamp forest, and the tracking frequency may have missed some short-duration terrestrial excursions. Habitat management practices and allowable land uses in uplands may be very different depending on whether the goal is to protect habitat used by animals for extended residency or to facilitate occasional movements between waterbodies.

Land uses and management practices in adjacent uplands should be tailored to maintaining waterbody connectivity in my *C. guttata* population, with less importance on providing terrestrial habitat for extended residency. Such a stratified approach to management of semi-aquatic vertebrate populations has been suggested as a means to balance wildlife conservation and land use in other species (deMaynadier and Hunter 1995; Semlitsch and Bodie 2003; Roe and Georges 2007).

The large home ranges of *C. guttata* suggest that extensive areas should be included in reserves to accommodate the needs of individuals through annual cycles and in response to anthropogenic and natural disturbance (Yagi and Litzgus 2012; Buchanan et al. 2017; Chandler et al. 2019; O'Dell et al. 2021). It should be noted that home range estimates and other behavioral measures were based on a small sample sizes and potentially biased by the behaviors of a few individuals that may be uncharacteristic of the population. My study was also limited by the short temporal period that coincided with extreme flooding, and that more prolonged drought or other disturbances could shift habitat or area requirements of individuals and the population as has been observed in other *C. guttata* populations (Yagi and Litzgus 2012; Chandler et al. 2019; O'Dell et al. 2021; Buchanan et al. 2017). For these reasons, I caution against interpreting the population range (combined area used by all turtles during the study) as the minimum area required to maintain a viable population (Yagi and Litzgus 2012; Chandler et al. 2019). Data on a small subset of a population collected over a brief period of time would also overlook infrequent extra-population movements that connect metapopulations via dispersal over broader spatial scales to facilitate gene flow or population reestablishment after local extirpation (Burke et al. 1995; Roe et al. 2009; Shoemaker and Gibbs 2013).

While the extended activity season of *C. guttata* in the southern part of their range has implications for the timing of critical biological cycles and life-history evolution (Litzgus and Mousseau 2003, 2006), regional activity patterns could inform the implementation of management actions as well. For example, timing of activity could influence *C. guttata* exposure to illegal collection. Periods of heightened movements and activity make turtles more visible, especially during mating season when *C. guttata* aggregates in higher densities (Litzgus and Mousseau 2004, 2006; Chandler et al. 2019). Similar to other southern populations (Litzgus and Mousseau 2006; Chandler et al. 2019), I observed two distinct mating seasons, with the only male/female pairings during February (3 pairings) and September–October (2 pairings). Management to minimize poaching may involve limiting access or patrolling known locations, including those in nature

reserves, which would be most effective if timed to periods of highest vulnerability (Garber and Burger 1995; Gong et al. 2017).

Clearly, the behaviors of *C. guttata* populations, their vulnerability to threats, and targeted management actions are variable over their broad distribution. I suggest caution when extrapolating results from particular locations to other sites across the geographic range of a species for use in conservation and management. This study broadens the understanding of *C. guttata* behavioral variation in the southern part of its range, but longer-term data and information for populations in other habitats and environmental contexts is required before making generalizations regarding best management practices for their conservation.

Acknowledgments.—I would like to thank Zach Lunn, Drew Baxley, Charles Gause, Zach Bayles, Maria Chavez, Kris Wild, Abbie Hudson, Dane Harvey, and Ryan McGirt for assistance with field research. Research was conducted under protocols Roe-2017 and Roe-2020 issued by the Institutional Animal Care and Use Committee of the University of North Carolina Pembroke (UNCP) and license SC00506 from the North Carolina Wildlife Resources Commission. Funding was provided by the Pembroke Undergraduate Research Center, UNCP Teaching and Learning Center, UNCP Biology Department, and the UNC Pembroke RISE program under the National Institutes of General Medical Sciences grant #5R25GM077634.

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