Movement and Space Use in Southern Populations of Spotted Turtles (*Clemmys guttata*)

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Abstract - Effective protection of habitats for rare or declining species depends on a fundamental understanding of species' movements and space use. We studied the spatial ecology of 2 populations of *Clemmys guttata* (Spotted Turtle) in southeastern Georgia. We attached radio transmitters to 29 individuals and located them for a 9-month (April–December) period during 2016. We found that home ranges of individual Spotted Turtles were generally small, varying from 0.38 to 6.14 ha at Site 1 and from 0.39 to 8.21 ha at Site 2 (95% minimum convex polygon estimates). Estimates for the space used by the population as a whole varied from 26.7 to 49.4 ha at Site 1 and 11.1 to 14.5 ha at Site 2. Movement distances decreased from ~15 m/day during the spring to <5 m/day in late summer and fall. Our results indicate that some Spotted Turtle populations in Georgia utilize relatively small areas of interconnected wetland complexes. Protecting wetland complexes along with the surrounding upland habitat will allow Spotted Turtle populations to move between wetlands and exploit riparian areas during certain times of the year without suffering the negative effects of fragmentation.

Introduction

A hallmark of effective conservation is to protect habitat and manage it in ways that maintain habitat quality, minimize fragmentation, and limit external effects on communities living in the protected area (Geldmann et al. 2013, Watson et al. 2014). To be successful, these protected areas must provide the space and resources necessary for individuals to complete all aspects of their life cycle without adding additional stressors or sources of mortality that could reduce population stability over the long-term (Dennis et al. 2006, Dodd 2016, Soulé et al. 2003). The amount of space and resources required by a population or metapopulation varies dramatically over both long (i.e., habitat patch quality changing over time) and short (i.e., seasonal) time scales (Börger et al. 2008, Whited et al. 2007). For example, seasonally available resources may encourage individuals to move into specific locations during certain times of the year (Hyslop et al. 2009, Walker et al. 2016). Thus, it is critical to understand how individuals of a species use space when making decisions for land conservation and management, especially when focusing on rare or declining species that are susceptible to small environmental changes (Browne and Hecnar 2007).

Recent status assessments indicate that turtles are one of the most endangered groups of animals on the planet (Lovich et al. 2018, Rhodin et al. 2018, Turtle Taxonomy Working Group 2017). Turtle species face numerous threats including

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habitat loss, degradation, and fragmentation as well as overharvest for consumption and the pet trade, climate change, and subsidized predation (Ernst and Lovich 2009, Gibbons et al. 2000). Furthermore, chelonian biology (e.g., long times to sexual maturity and low egg and hatchling survival) generally makes turtle populations susceptible to declines when adult mortality rises, which can result from exploitation or changing environments (Congdon et al. 1983, 1987; Heppell 1998). Turtle movements, particularly female movements to and from nesting sites or long-distance movements between habitat patches, expose individuals to increased threats (e.g., road mortality; Walston et al. 2015). Increased mortality events can directly affect population structure and stability (Congdon et al. 1993, Dupuis-Désormeaux et al. 2017).

Clemmys guttata (Schneider) (Spotted Turtle) is an example of a declining turtle species where conservation-relevant data describing its spatial ecology are needed. Spotted Turtles are small freshwater turtles with an expansive range stretching from southern Canada to the southeastern United States. Spotted Turtle populations have declined across much of this range, primarily because of habitat loss and collection for the pet trade (Browne and Hecnar 2007, Ernst and Lovich 2009). Currently, Spotted Turtles are listed as endangered in Canada, are a candidate for federal listing under the US Endangered Species Act, and are listed as Endangered on the IUCN Red List (van Dijk 2011). At the southern end of their range, Spotted Turtles are state-listed in South Carolina and Georgia, and status assessments to clarify their status in Georgia, South Carolina, and Florida are currently underway.

While the species occupies a large geographic area, most of the published research on Spotted Turtles has been conducted in the northern portion of their range. Research on other turtle species with large ranges has indicated that northern and southern populations can differ significantly in multiple aspects of their ecology (Iverson et al. 1993, 1997). Specifically, northern Spotted Turtle populations tend to support larger individuals, larger population sizes spread across large wetland complexes, larger clutch sizes, and a shorter annual activity period when compared to a South Carolina population (Ernst and Lovich 2009; Haxton 1998; Litzgus and Brooks 1998; Litzgus and Mousseau 2004a, b; Milam and Melvin 2001). Litzgus and Mousseau (2003, 2004a, 2004b) currently provide the best available ecological data from a southern Spotted Turtle population, and, to date, no research from Georgia or Florida populations has been published (but see Barnwell et al. [1997] and Stevenson et al. [2015] for analyses of distribution records in Florida and Georgia, respectively). The lack of spatially and temporally relevant data, including descriptions of turtle movements and space use, is a key challenge for the conservation of this species in Georgia and Florida.

Here, we describe the results of a radio telemetry study of 2 populations of Spotted Turtles in the Coastal Plain of southern Georgia. Our primary goal was to quantify the space used by individuals and by the population as a whole, identifying differences between sexes and populations. We identified how individual turtles move through their environments, giving particular attention to long-distance movements that could expose individuals to additional threats or reveal important behaviors. We highlighted factors that may contribute to increases in activity and movement distances throughout the year and provide a general description of the environments that turtles used over the course of the study. The data presented here provide a better understanding of space use, movement, and natural history in southern Spotted Turtle populations and have direct applications to the conservation of these populations.

Field Site Description

We monitored Spotted Turtle populations at 2 sites in the Coastal Plain of southeastern Georgia. Both study sites consisted primarily of floodplain swamps and were characterized by typically shallow (<1 m), tannin-stained water. *Taxodium distichum* (L.) Rich. (Bald Cypress), *Nyssa biflora* Walter (Swamp Black Gum), and *Acer rubrum* L. (Red Maple) were dominant in the canopy, and *Cephalanthus occidentalis* L. (Buttonbush) was common in the subcanopy. Both sites were surrounded by a matrix of deciduous forests, planted *Pinus* (pines), and riparian habitats. Site 1 was located in the Altamaha River drainage and consisted of floodplain swamp bordering a 1st-order stream. This site was influenced by *Castor canadensis* L. (American Beaver) activity and also contained old agricultural and drainage ditches. Site 1 had standing water for the duration of the study period. Site 2 was located in the Ogeechee River drainage (~145 km from Site 1), bordering a 3rd-order stream. Site 2 dried completely by the middle of May, refilled for a couple of weeks in mid-June, and then dried again by the end of June, remaining mostly dry for the duration of the study. At Site 2, precipitation events occasionally produced small, shallow pools after the site dried; these flooded pools were generally no more than a few meters in diameter. Specific locations of study sites are withheld throughout because of collecting concerns.

Methods

Radio telemetry

From March to early May 2016, we opportunistically attached 5.0-g radio transmitters (Model: SOPR-2190, Wildlife Materials International, Inc., Murphysboro, IL) to adult Spotted Turtles at both sites. Turtles were captured as part of ongoing efforts to monitor their populations, both using modified crab traps (Chandler et al. 2017b) and by hand during visual encounter surveys. We initially planned to attach transmitters to an equal number of turtles at both sites, but after a month of trapping, it became apparent that this would not be possible because of a smaller population size at Site 2 (H.C. Chandler, unpubl. data). We ultimately attached transmitters to 18 turtles at Site 1 (10 males and 8 females) and 11 turtles at Site 2 (6 males and 5 females). At Site 1, we captured more adult turtles than were included in the study, and we attached radio transmitters to individuals as they were captured through the sampling period, while attempting to maintain an even sex ratio (i.e., some captured adult male turtles were not included in the study). The midline carapace length (Iverson and Lewis 2018) varied from 96.0 to 109.5 mm (mean = 103.7 ± 1.0 SE) for male turtles and from 90.1 to 110.9 mm (mean = 99.8 ± 1.6 SE) for female turtles.

We glued transmitters to the left rear side of each turtle's carapace using a waterproof epoxy. We oriented transmitters so the antenna trailed behind the turtle as it moved, reducing the chances of the antenna becoming entangled in the environment. We placed transmitters mostly on the pleural scutes and off of the marginal scutes to reduce the stress towards the edges of the shell. The total weight of the transmitters and epoxy was always less than 10% of the individual's body mass. After attaching transmitters, we verified that they were working and released turtles near their point of capture within 24 hours.

We began using radio telemetry to locate turtles on 1 April (a week after the first transmitters were attached). The total number of turtles with transmitters attached gradually increased over the following month and a half until the final 2 transmitters were attached on 16 May, which coincided with the end of our standardized turtle trapping. The frequency with which we located turtles varied seasonally and by site. While turtles were still active in late spring and early summer, we located all turtles twice a week. At Site 1, we continued with this effort until mid-August, after which we switched to tracking once a week until the end of October. At Site 2, we switched to locating turtles once a week at the end of June (due to logistical constraints and the drying of the site, which led to lower activity levels) and continued with this effort until the end of October. During November and December, we were only able to locate turtles once every 2 weeks at both sites because of logistical constraints. We removed transmitters and epoxy from turtles on 22 and 29 December (Sites 1 and 2, respectively).

When each turtle was located, we recorded a general description of the turtle's position, state, and the habitat that it was occupying or moving through at the time. We noted whether the individual was in the water or on land and indicated whether or not the turtle was active and visible to the observer or in cover. We classified turtles as active if they were moving in water or on land or sitting in the open with their heads out of the shell (i.e., not in cover). If an individual was in cover, we described the type of cover that the turtle was occupying. When an individual was observed in the water, we also measured the water depth at the turtle's position using a meter stick.

Statistical analyses

We calculated Spotted Turtle home-range sizes at both sites using 3 different estimation methods. All home-range calculations were conducted using the R package 'adehabitatHR' (Calenge 2006). First, we estimated home-range sizes using 95% minimum convex polygons (MCP). Second, we calculated a utilization distribution for each individual, which creates a probability density function that predicts the probability of an individual occurring at that location based on all of the locations for that individual (Worton 1995). We estimated utilization distributions using both bivariate normal and Epanechnikov kernels. For both methods, we used the ad hoc method to calculate the smoothing parameter (Silverman 1986, Worton 1995). We estimated home-range sizes for the 2 kernel methods by calculating the area in which there was a 95% probability of locating an individual at any given time. We calculated home-range sizes using 3 estimation methods because there is little consensus on the best method to use (Powell 2000) and using multiple estimation techniques allows for comparisons with a wider range of previous and future studies. We examined the effect of sex and site on home-range estimates using a two-tailed *t*-test assuming unequal variances. We compared the variances between groups using an *F*-test. We applied a natural logarithmic transformation to home-range estimates to improve violations of the normality assumption. To estimate the area used by our entire study population at each site (population range), we applied the same 3 home-range estimation techniques to all of the turtle locations at each site. We also calculated the percent overlap of all home ranges at both sites using 95% Epanechnikov kernels.

In addition to home-range sizes, we also calculated the straight-line distances between consecutive locations for each individual turtle using the R package 'adehabitatL' (Calenge 2006). We classified long-distance movements as those greater than 100 m, which represented the approximate 90th percentile in the movement distance data. For analysis, we standardized all distances by the number of days between each location. We fit a linear mixed model, including individual turtle as a random effect, to test the effects of sex, site, and month on movement distances between tracking events. We applied a natural logarithmic transformation to the distance data after adding 1 to all data points to eliminate values of zero. We also fit a simple linear regression model to examine the effect of precipitation on movement distances by calculating the total amount of precipitation that occurred between tracking events. Movement distance data were again transformed using a natural logarithm. We downloaded daily precipitation data from the PRISM Climate Group using the approximate centroid of each study site (PRISM Climate Group, Oregon State University; http://prism.oregonstate.edu). All analyses were conducted in R (R Core Team 2018).

Results

Over the 9-month tracking period, we successfully radio-tracked 29 Spotted Turtles from 2 Georgia populations. We collected a total of 1267 observations of the 29 turtles, with each turtle being located an average of 47 times at Site 1 (min–max: 20–52) and 42 times at Site 2 (min–max: 36–45). Only 1 turtle from Site 1 lost a transmitter, likely due to a failed predation event, before we removed transmitters at the end of the tracking period. Teeth marks were observed on the transmitter, and this individual was recaptured alive the following year (identified via shell notches).

Spotted Turtle home ranges were generally small (less than 10 ha) and did not significantly differ between sites or sexes (Tables 1, 2). However, there was higher variance in the home-range sizes of female turtles when compared to male turtles (e.g., coefficient of variation for MCP home ranges: males = 48.7; females = 123.0), regardless of which estimation method was used (MCP: $F_{12,15} = 10.3$, $P < 0.001$; Epanechnikov: $F_{12,15} = 5.3$, $P = 0.003$; bivariate normal: $F_{12,15} = 3.8$, $P = 0.017$).

Female turtles accounted for the 3 largest and 4 smallest home ranges. There was significant variation in the size of the estimated home ranges depending on the calculation method (Tables 1, 2). Home-range estimates from 95% MCP varied from 0.38 to 6.14 ha at Site 1 and from 0.39 to 8.21 ha at Site 2. Kernel density estimates of home-range sizes were larger using both the Epanechnikov kernel (Site 1: 0.95–11.75 ha; Site 2: 0.65–16.04 ha) and the bivariate normal kernel (Site 1: 1.27–17.35 ha and Site 2: 0.86–22.52 ha) (Table 1).

Estimates for the population range varied from 26.7 to 49.4 ha at Site 1 and 11.1 to 14.5 ha at Site 2, depending on the estimation method. We observed significant overlap in space use at both sites, with some individual's home ranges completely encompassed by the home ranges of other individuals. Furthermore, at both sites the

Table 1. Home-range estimates for 29 Spotted Turtles from 2 sites in southern Georgia based on 3 different estimation methods. Epanechnikov kernel estimates were calculated using both 95% and 50% probability of locating a turtle in the given area. The percent area difference between these 2 measures is given in the last column. All home-range sizes are presented in hectares.

ID	Sex	95% MCP	Bivariate normal kernel 95%	Epanechnikov kernel 95%	Epanechnikov kernel 50%	% area difference
Site 1						
15	F	0.38	1.34	0.95	0.19	19.9
9	F	0.44	1.27	0.97	0.22	22.2
3	F	0.39	1.33	0.99	0.19	19.5
8	M	0.54	1.55	1.07	0.23	21.8
27	M	0.39	1.93	1.26	0.25	19.5
279	F	0.57	1.90	1.38	0.36	25.8
6	M	0.92	2.19	1.65	0.40	24.2
53	F	1.11	3.45	2.34	0.38	16.1
16	M	1.59	4.17	2.63	0.52	19.7
29	M	2.73	4.63	2.72	0.46	17.1
2	F	1.08	5.43	3.31	0.96	29.0
18	M	1.56	4.78	3.35	0.75	22.3
28	F	1.27	5.57	3.74	0.90	24.2
13	M	1.15	5.80	3.75	0.60	16.0
12	M	2.60	8.58	5.82	1.90	32.6
11	M	2.96	15.22	8.28	1.93	23.3
56	M	2.27	12.74	8.32	1.19	14.3
25	F	6.14	17.35	11.75	2.09	17.8
Site 2						
13	F	0.39	0.86	0.65	0.15	23.6
20	F	0.93	2.37	1.59	0.36	22.4
21	M	1.08	3.83	2.60	0.76	29.2
3	M	1.21	3.72	2.81	0.86	30.6
5	M	1.63	4.39	3.16	1.02	32.3
6	M	1.29	5.06	3.34	0.86	25.6
8	M	1.70	6.21	4.66	1.04	22.3
19	F	1.45	7.38	4.85	1.30	26.7
18	M	2.77	9.02	5.48	1.32	24.0
17	F	4.97	17.80	10.98	2.83	25.7
27	F	8.21	22.52	16.04	4.73	29.5

home ranges of at least 10 individuals partially overlapped, and there were clearly defined areas where turtles congregated (Fig. 1). At Site 1, the average home-range overlap for all individuals was 22.0%, while at Site 2 the average overlap was 42.0% (95% Epanechnikov kernels). Across both populations, most individuals spent a large portion of their time in an area much smaller than the home or population range. For example, the estimate of the area required to locate individuals with 50% probability accounted for just 14.3–32.6% of the area needed to locate individuals with 95% probability at Site 1 and 22.3–32.3% at Site 2 (Epanechnikov kernel estimates) (Table 1). At the population level, 88% of locations at Site 1 and 82% at Site 2 fell within an area that was approximately half of the population range (MCP estimates).

Some individuals at both sites remained active for the duration of the tracking period, especially at Site 1 where there was more standing water available. There was a significant effect of both month ($F_{8,1208} = 8.86$, $P < 0.001$) and site ($F_{1,27} = 4.23$, $P = 0.049$) on the average straight-line distance moved between tracking events, but sex had no effect on these movement distances ($F_{1,25} = 0.06$, $P = 0.81$). Individuals at Site 1 tended to move farther than individuals at Site 2 (mean = 11.3 and 7.9 m/day, respectively; $P = 0.040$). Movement distances also tended to be longer during the early part of the tracking period (April–June) than during late summer and fall (Table 3). The random effect for individual included in the mixed-effects model explained less than 2% of the overall variation in the residuals. Finally, the amount of precipitation since the previous tracking event had a positive effect on the distances moved at Site 1 ($P < 0.001$, $R^2 = 0.04$) and Site 2 ($P < 0.001$, $R^2 = 0.05$).

Table 2. Mean home-range sizes (SE in parentheses) for Spotted Turtles in 2 Georgia populations (*n* = 18 and 11 at Sites 1 and 2, respectively). Home ranges were calculated using 3 different estimation methods (minimum convex polygon [MCP], a utilization distribution with an Epanechnikov kernel, and a utilization distribution with a bivariate normal kernel). Average home ranges are presented by site and sex (16 males and 13 females). We used *t*-tests to test for differences between groups. All home range sizes are presented in hectares.

	95% MCP	95% kernel density (Epanechnikov)	95% kernel density (bivariate normal)
Site 1	1.56 (0.34)	3.57 (0.72)	5.5 (1.57)
Site 2	2.33 (0.69)	5.11 (1.37)	7.56 (2.02)
t-test	$t = 1.23$, $P = 0.23$	$t = 1.06$, $P = 0.30$	$t = 0.94$, $P = 0.36$
Male	1.65 (0.20)	3.81 (0.55)	5.86 (0.95)
Female	2.10 (0.72)	4.58 (1.40)	6.81 (2.06)
t-test	$t = –0.64$, $P = 0.53$	$t = –0.58$, $P = 0.57$	$t = -0.65$, $P = 0.52$

Figure 1 (following page). Overlap in home ranges for 2 populations of Spotted Turtles in southern Georgia calculated using a utilization distribution and 95% Epanechnikov kernel. (A) Site 1 includes home-range estimates for 18 individuals, and (B) Site 2 includes home-range estimates for 11 individuals.

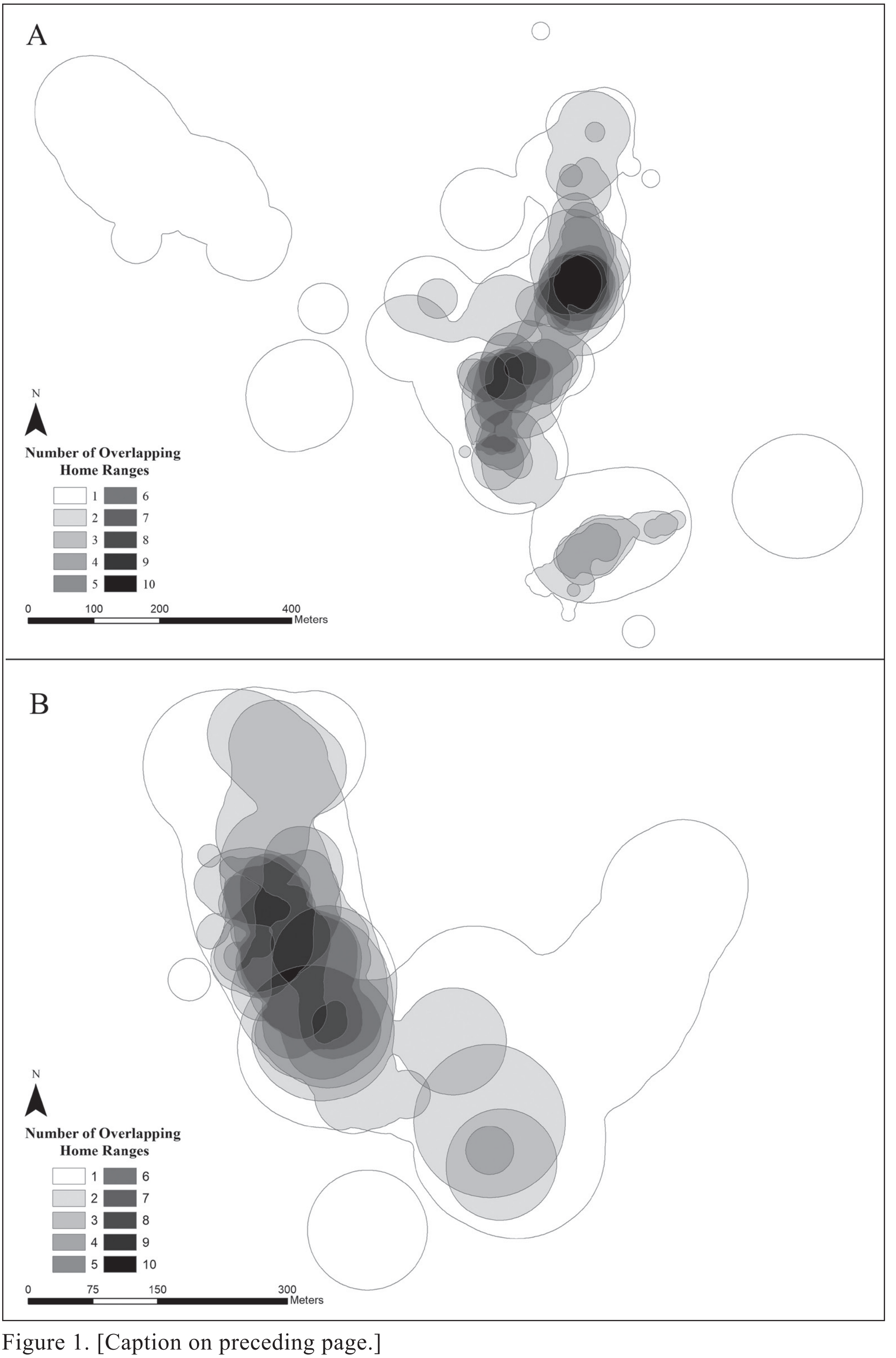

Figure 1. [Caption on preceding page.]

Approximately 73% of straight-line distance movements between tracking events were less than 50 m and only 145 of 1237 (11.7%) were greater than 100 m (min–max: 0–519) (Fig. 2). Long-distance movements greater than 100 m occurred over the entire tracking period, but movements of this distance were most common during April–June (Table 3). At Site 2, the entire wetland was mostly dry by the end of May, but turtles continued to move both short and long (i.e., >100 m) distances. Further, we observed multiple instances of turtles congregating in small floodplain pools away from the areas where they spent the majority of the 9-month period (i.e., some individuals moved long distances to locate the only available flooded habitat). For example, during the first week of September, 4 turtles moved an average of

Table 3. Straight-line distance movements between tracking events for 29 Spotted Turtles at 2 sites in southern Georgia summarized by month. Movement distance metrics were calculated for each individual and then averaged across all individuals in the 2 populations. Standard errors are in parentheses.

	Mean movement distance (m/day)	Mean maximum distance (m)	# of movements >100 m	
			Mean	Total
April	14.5 (1.4)	118.1 (12.6)	0.8 (0.2)	22
May	15.0 (1.3)	156.7 (13.4	1.2 (0.2)	34
June	15.0 (1.8)	154.7 (17.4)	1.3 (0.2)	37
July	8.5 (1.2)	93.5 (15.8)	0.6 (0.2)	18
August	4.8 (0.5)	117.8 (18.5)	0.5 (0.1)	14
September	4.3 (0.9)	53.6 (12.7)	0.1 (0.1)	3
October	6.3 (1.0)	105.3 (21.3)	0.4 (0.1)	12
November	2.0 (0.3)	48.3 (6.7)	0.1 (0.1)	2
December	2.9 (0.7)	39.9 (10.2)	0.1 (0.1)	3

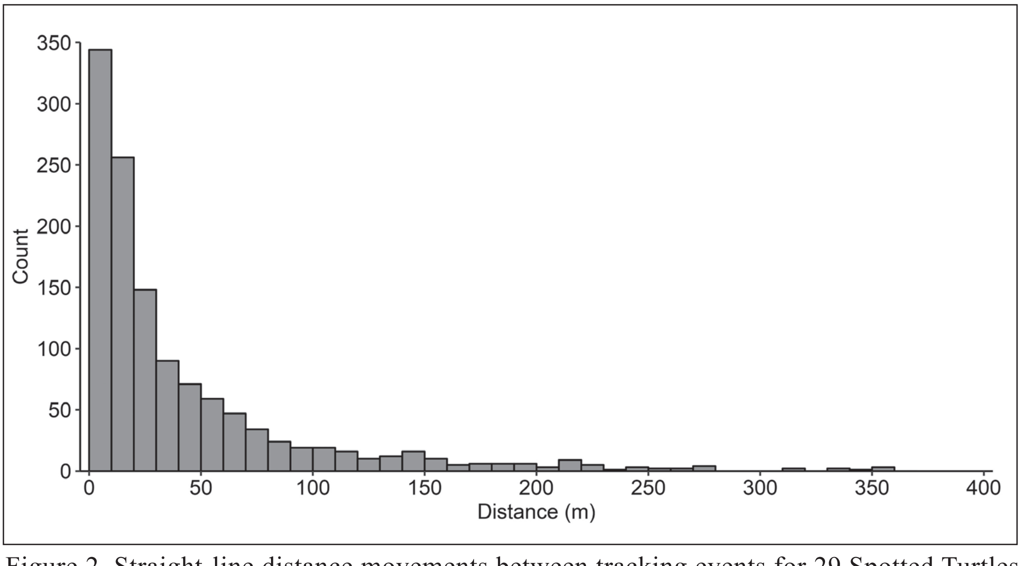

Figure 2. Straight-line distance movements between tracking events for 29 Spotted Turtles at 2 sites in southern Georgia. Count is defined as the total number of movements for all turtles within each 10-m interval. Two movements of 402 and 519 m were omitted for clarity.

281 m from dry swamp to a single, small, flooded pool before returning to the dry swamp over the next 2 months (Fig. 3).

Spotted Turtles in both populations utilized a matrix of flooded, often discontinuous wetland habitats, moving over land and through water to reach different parts of the surrounding wetlands. At Site 1, turtles were located in water 73.2% of the time, while at Site 2, turtles were found in the water only 25.8% of the time. Of the 626 observations where a water depth was recorded, turtles were located in

Figure 3. Home-range estimates (calculated using a utilization distribution and 95% Epanechnikov kernel) and point locations of 4 Spotted Turtles from a southern Georgia population in 2016. Individuals made straight-line movements of 219, 220, 280, and 404 m from dry floodplain swamp to a single flooded pool and subsequently moved away from the flooded area over the next 2 months. Large symbols and dates indicate the day each individual was located before making the long movement (August 31), the day all 4 individuals were found in close proximity (September 8), and the day that each individual was found after moving away from that area (September 14–October 24).

>300 mm of water just 3% of the time. At Site 1, turtles utilized both natural wetland habitats and adjacent man-made wetlands, specifically old agricultural and drainage ditches. The population at Site 2 inhabited entirely natural floodplain swamp. Spotted Turtles were located in cover 77.4% of the time (i.e., the turtle was not visible and was under some sort of cover object). Individuals utilized a variety of cover objects when in the water and on land, including thick mud and leaf litter, fallen trees or braches, stump holes or root masses, undercut banks, and/or thick vegetation.

Discussion

Both southern Georgia populations of Spotted Turtles occupied relatively small areas with well-defined activity centers where turtles clustered. Activity centers were used by a majority of the radio-tracked individuals and included centrally located portions of the wetlands where male and female turtles congregated during March and April, likely for courtship and mating (Litzgus and Mousseau 2004b), which we observed at both sites. Some individuals moved away from activity centers by early summer, but many turtles continued to spend large amounts of time in the same general areas throughout the remainder of the year. Size estimates for the population range in these Georgia populations were smaller than those observed in a southern Ontario population during flooded conditions (Yagi and Litzgus 2012). Even the estimate of the pre-flooding population range for that Ontario population was much larger than our estimates for Site 2 and similar to the highest estimate for Site 1 (Yagi and Litzgus 2012). Others have reported Spotted Turtle populations using wetland complexes that are much larger than those in our study (Graham 1995, Milam and Melvin 2001, Ward et al. 1976). Individuals in our study populations inhabited a majority of the available wetlands during at least part of the year, and these 2 populations are likely restricted to the wetland complexes where we observed individuals (i.e., there are few, if any, adjacent wetlands within a distance that would be suitable for regular use). Site 1 had a larger wetland area than Site 2 and held water for much longer, which likely contributed to the larger population range, lower home-range overlap, and longer average movement distances that we observed.

Similar to the population range, estimated home-range sizes for most individuals in our study were small, although there were exceptions at both sites. Average MCP home-range sizes tended to be smaller than estimates for populations in South Carolina and North Carolina (Litzgus and Mousseau 2004b, O'Bryan 2014). The home-range estimates (MCP) for some northern populations were larger than our Georgia estimates (Rasmussen and Litzgus 2010, Yagi and Litzgus 2012), while others were either smaller or similar to what we observed (Milam and Melvin 2001). A small number of individuals had considerably larger home ranges than a majority of the other turtles. Some of these differences can likely be attributed to individual variation in habitat use (e.g., the 2 individuals with the largest home-range estimates spent the majority of their time farther away from activity centers and needed to travel further to reach mating aggregations in spring). However, some of the larger home ranges (and long movements from May–July) were characteristic of female turtles moving to nesting habitats and then returning to their original locations (Joyal et al. 2001). Overall, individuals in our 2 study populations appear to use less space, on average, than individuals in many other Spotted Turtle populations that have been studied. These home-range estimates can now be used to predict how likely individuals are to move between certain wetlands or to encounter landscape features that could increase mortality events (e.g., roads). Logistical constraints prevented us from tracking turtles over multiple years, and it is likely that our home-range estimates would be larger with additional years of data from these same turtles (Bekoff and Mech 1984, Rasmussen and Litzgus 2010). Further, some of the overlap in home ranges that we observed could be attributable to an increased chance of locating turtles in the same area after the first radio transmitters were attached. However, we did attempt to representatively sample all of the available flooded habitat at both sites when attaching transmitters.

Unlike northern Spotted Turtle populations (Lovich 1988, Milam and Melvin 2001, Rasmussen and Litzgus 2010), we documented individuals active in the water (when available) and making both short- and long-distance movements throughout the duration of the tracking period. We did observe a decrease in movement distances between tracking events during the summer months, but turtles continued to move over land and in the water during this period. This continuity of activity suggests that a summer aestivation period does not occur in these populations, especially when water is available for foraging (Litzgus and Mousseau 2004b). Thick forested wetlands may keep water temperatures below the threshold triggering summer inactivity (Ernst 1976). Interestingly, individuals at Site 2 continued to move short distances throughout the summer even though most of the water dried by the end of May. We suspect that many of these turtles continued to actively forage in damp leaf litter and shallow puddles after precipitation events (Ernst 1976). Short movements followed by burrowing into the leaf litter may also be a method for minimizing predation risks during periods of terrestrial exposure (Bennett et al. 1970, Litzgus and Brooks 2000).

Similar to observed activity during the summer months, individuals were also active in the fall and early winter. There was a brief increase in activity in late September and October that is likely attributable to a fall courtship period (Litzgus and Mousseau 2006). In fact, we observed multiple instances of male turtles actively pursuing and climbing onto female turtles during this fall period, although direct copulation was never observed. We also observed turtles active in the water (i.e., swimming or sitting in the water with their heads out of the shell) when transmitters were removed in late December. Spotted Turtles have now been documented as active in all 12 months of the year in Georgia when combining our results with previous data (Stevenson et al. 2015). Winter activity is somewhat common in southern populations of Spotted Turtles, with turtles often active during periods of warm winter weather (Litzgus and Mousseau 2004b; J. Mays, Florida Fish and Wildlife Conservation Commission, Gainesville, FL, unpubl. data; Ward et al. 1976). Georgia's warm climate appears to facilitate a much longer activity season for Spotted

Turtles than is available in northern portions of the range (Ernst and Lovich 2009). A longer active season likely has multiple benefits for these southern populations, including a second mating season, multiple clutching, and expanded foraging opportunities (Litzgus and Mousseau 2003, 2006). However, a longer activity period may also have other trade-offs for these populations, including a longer time spent avoiding predators and necessitating additional energy intake over the course of an entire year.

Spotted Turtles at both sites used their environments in similar ways over the 9-month study period. Turtles were generally located in shallow water, when available, and often sheltered under some kind of cover object. Root-masses and large fallen trees were often used for cover, and these structures likely represent an important microhabitat for Spotted Turtles (Litzgus and Mousseau 2004b). At a coarse scale, we were able to detect a positive effect of precipitation on movement distances, although precipitation explained only a small percentage of the overall variation in movement distances. After precipitation events, turtles were often observed in shallow depressions that were recently inundated by rising water levels. We suspect that this is a foraging behavior, potentially capitalizing on recently submerged invertebrates and allowing turtles to more easily capture prey items. However, additional data are needed to further examine the effects of this and other environmental factors on Spotted Turtle behavior. Fine-scale movement data combined with more detailed climate and water-level data at study sites (e.g., Chandler et al. 2017a) are the first steps to identifying the relationships between environmental factors and turtle behavior.

Globally, freshwater turtle populations are declining because of a myriad of threats. There is a growing body of literature documenting how freshwater turtle populations navigate their environments and the space required to support viable populations (e.g., Arvisais et al. 2002, Beaudry et al. 2008, Bennett et al. 2010, Roe and Georges 2008). These data have important conservation implications, including identifying both wetland and adjacent terrestrial habitats that need protection (Congdon et al. 2011, Roe and Georges 2007) and identifying potential threats to populations (Ferronato et al. 2016, Gibbs and Shriver 2002). A broad understanding of these ecological processes for each species over broad geographic areas is crucial for making effective conservation and management decisions.

Our study adds to the growing amount of published data on Spotted Turtles from across their large range (Ernst and Lovich 2009) and provides additional insights into the ecology of southern populations. In both study populations, Spotted Turtles used a network of disjunct flooded areas that were often not directly connected by flooded habitats. Many of the longer movements observed in our study occurred at least partially over land, which is common for both Spotted Turtles (Joyal et al. 2001, Litzgus and Mousseau 2004b) and other freshwater turtle species (Congdon et al. 1987, Pittman and Dorcas 2009, Roe and Georges 2008). Thus, for habitat protection to be successful for Spotted Turtle populations in Georgia, wetlands and surrounding uplands must be protected and managed to provide the aquatic and terrestrial habitats (e.g., riparian areas) that these populations require. Further, wetland complexes with multiple small wetlands should be protected as a single unit and not divided (i.e., by roads; Howell and Seigel 2019) in such a way that would limit the ability of turtles to move from one wetland to another or create a new source of mortality or access for collectors. The high percentage of road records in Georgia (Stevenson et al. 2015) indicates that fragmentation could already be a concern for many Georgia Spotted Turtle populations. Finally, Spotted Turtles are currently listed as unusual in Georgia, mostly because of a paucity of records and published data. Additional surveys, further ecological research, and continued monitoring are needed in both Georgia and Florida to better understand this species at the southern extent of its distribution.

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