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Autecological Study of Gulf Coast Box Turtles (*Terrapene carolina major*) in the Florida Panhandle, USA, Reveals Unique Spatial and Behavioral Characteristics

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Abstract.—**Terrapene carolina major* (Gulf Coast Box Turtle) is an unresolved taxonomic lineage from the Florida Panhandle and Gulf of Mexico Coastal Plain in the USA. Like other box turtles, *T. c. major* is vulnerable to increasing anthropogenic pressures. To date, no intensive or comparative ecological or behavioral studies have been published on this lineage of box turtles. We conducted a radio-telemetry study of 21 adult *T. c. major* in the Florida Panhandle in 2016 and 2017 to evaluate seasonal home range, habitat use and selection, and behavior. We calculated summer home range size using minimum convex polygons (MCP) and fixed kernel density estimators (KDE). We evaluated habitat use using Geographic Information Systems (GIS) to determine proportions of different habitat types within 100% MCPs of individuals and habitat selection was evaluated using generalized linear models. Unlike most other studies of *T. carolina* lineages, females had significantly larger home ranges than males, while males had higher home range fidelity than females. The generalized linear models indicated males used forested wetlands and females used coniferous forests significantly more than other habitats. Approximately 23% of total radio-location observations for both sexes were aquatic environments that included areas primarily in Floodplain Swamps, Mixed Wetland Hardwoods, and Wet Coniferous (*Pinus* spp.) Plantations. Our observations indicated that *T. c. major* demonstrates unique behavioral and ecological characteristics, and while the phylogenetic relationships and evolutionary significance of this lineage remains unclear, we recommend *T. c. major* be managed as a distinct taxon of *T. carolina* when evaluating conservation and management decisions.**

Key Words.—habitat use; home range; movement; radio-telemetry; spatial ecology; territoriality

Introduction

Spatial ecology studies are necessary to understand how a species interacts with its environment and the greater landscape. Conclusions drawn from these studies aid in the development of species management plans. Effective and adaptive management plans have become particularly important for turtle species, and globally, turtles are one of the most threatened vertebrate groups with approximately 61% of species considered threatened or endangered (Lovich et al. 2018). Turtles are threatened primarily by growing anthropogenic pressures of habitat loss and fragmentation, over-collecting for the pet trade, and climate change (Klemens 2000; Dodd 2001). *Terrapene carolina* (Eastern Box Turtle) is also affected negatively by this suite of threats and is currently listed as Vulnerable on the Red List of the International Union for Conservation of Nature's Red List (van Dijk 2011).

Terrapene carolina are generally one of the most terrestrial North American emydids, preferring lowland woodlands and dry forested areas (Stickel 1950; Dodd 2001; Donaldson and Echternacht 2005). Some *T. carolina*, however, have been reported to use aquatic environments, particularly during the summer and spring (Stickel 1950; Madden 1975; Donaldson and Echternacht 2005; Rossell et al. 2006; Weiss 2009). Both home range estimates and habitat use and selection varies between populations based on seasonal environmental variables, life-history characteristics, and anthropogenic pressures. While this variation can present challenges when comparing lineages (e.g., *T. c. carolina*, *T. c. triunguis*, *T. c. major*, etc.) or populations, the information obtained offers insight into the specific populations being assessed and potential conservation threats facing those local populations. Theoretically, key biological processes can be protected if preferred or ideal habitats are identified and conserved as part of a connected landscape.

Terrapene c. major (Gulf Coast Box Turtle) is found only along the Gulf Coastal Plain and has the largest body size of the five extant *T. carolina* lineages (Dodd 2001). Older adult males of *T. c. major* tend to have flared posterior marginal scutes of the carapace, an hourglass shaped first costal scute, and may occasionally have a white blotched head (Minx 1996; Dodd 2001; Farrell et al. 2006). Another unique trait of *T. c. major* is the suspected tendency for individuals to frequently use water bodies, more so than other *T. carolina* lineages (Donaldson and Echternacht 2005; Farrell et al. 2006), and it is very similar to the habits of *T. coahuila* (Brown 1974). Compared to other living *T. carolina* lineages, relatively little is known about the ecology and behavior of *T. c. major*. Previous studies of *T. c. major* have been limited to controlled laboratory experiments or genetic analyses (Ensign 1954; Anton 1990, Butler et al. 2011; Martin et al. 2013). To better understand the life-history characteristics of *T. c. major* and provide scientifically rigorous information for conservation planning, more ecological studies need to be conducted across the range of *T. c. major*. Our primary objectives of this study were to: (1) estimate the seasonal home range size and structure of *T. c. major* adults within a population in the Florida Panhandle, (2) assess the differences in home range structure and movement between males and females, (3) evaluate the similarities and differences of habitat use between males and females, and (4) describe the behavioral characteristics of the species.

Materials and Methods

Study site.—We initiated a study in northwestern Florida, USA, in 2014 to assess the status of *T. c. major* by evaluating home range size, movement patterns, habitat use, population estimates, and vulnerability to road mortality. We established five radio-telemetry study sites in March 2016, with most telemetry occurring during the summers (May to August) of 2016 and 2017. To reduce the risk of illegal collection, exact study locations are not provided. The total area we studied that encompassed all radio-telemetry locations was approximately 619.4 ha with an average individual site size of 123.6 ha (± 32.72 standard deviation; range, 82.4–158.1 ha). Sites were located within a 14 kilometer (km) total linear distance (ranging from 2–7 km apart). The mean percentage of habitat characterized as roads within the sites was 2.3% ± 1.13% (range, 0.9–3.6%) based on the Florida Land Cover data. The dominant habitat types of the study sites included Mixed Wetland Hardwoods, Floodplain Swamp, Hydric Pine (*Pinus* spp.) Flatwoods, and Coniferous Plantations (Florida Natural Areas Inventory. 2010. Guide to the natural communities of Florida. Florida Natural Heritage Program, Tallahassee, Florida, USA. Available online at http://fnai.org/PDF/FNAI-Natural-Community-Classification-Guide-2010_20150218.pdf. [Accessed 23 September 2016]). All five sites were similar in canopy composition and were dominated by *Nyssa aquatica* (Water Tupelo), *Nyssa sylvatica* (Black Tupelo), *Taxodium distichum* (Bald Cypress), *Pinus elliottii* (Slash Pine), *Pinus taeda* (Loblolly Pine), *Acer rubrum* (Red Maple), and various *Quercus* (Oak) species (Fig. 1).

Descriptive statistics of body size.—We collected morphometric data from captured individuals during both years of study to compare male and female body size. We captured individuals that we radio-tagged during the study period via visual surveys and we captured additional individuals opportunistically while radio-tracking. During an initial capture event, we measured the straight, midline carapace length (CL), total plastron length (PL), shell height (SH), and weight (to 1 g) using a 300 mm caliper and digital pharmaceutical balance; we also noted any injuries or deformities. We conducted Welch's two-sample *t*-tests (α = 0.05) with log transformations (due to skewness of the data) to determine whether males and females had similar body size metrics. We determined a sexual dimorphic index (SDI) using the mean CL of males and females (Gibbons and Lovich 1990).

Radio-telemetry.—In March 2016, we captured 20 adult *T. c. major* (11 males, nine females) at five sites and fitted each individual with a 15.3 g radio transmitter (150 MHz, model R1860; Advanced Telemetry Systems, Isanti, Minnesota, USA) and a temperature logging ibutton (Maxim Integrated Products, iButtonLink, LLC, Whitewater, Wisconsin, USA) using a two-part putty plumbing epoxy. We placed the transmitter and ibutton on the right posterior carapace, so we did not inhibit mating or walking (Fig. 2). The weight of the transmitter, ibutton, and epoxy did not exceed more than 5% of the body weight of a turtle, well below the weight recommended (American Society for Ichthyologists and Herpetologists [ASIH] 2004. Guidelines for use of live amphibians and reptiles in field and laboratory research. ASIH, Lawrence, Kansas, USA. Available online at https://asih.org/sites/default/files/documents/resources/guidelinesherpsresearch2004.pdf. [Accessed 7 April 2016]). We apportioned males and females roughly equally between the five study sites (Site 1: three males, one female; Sites 2-5: two males, two females) and we gave a unique identification number to each turtle by filing notches into the marginal scutes (Ernst et al. 1974).

From May to August 2016 and 2017, we located each radio-tagged individual twice a week for 14–15 weeks using a 148–174 MHz telemetry receiver (R1000,

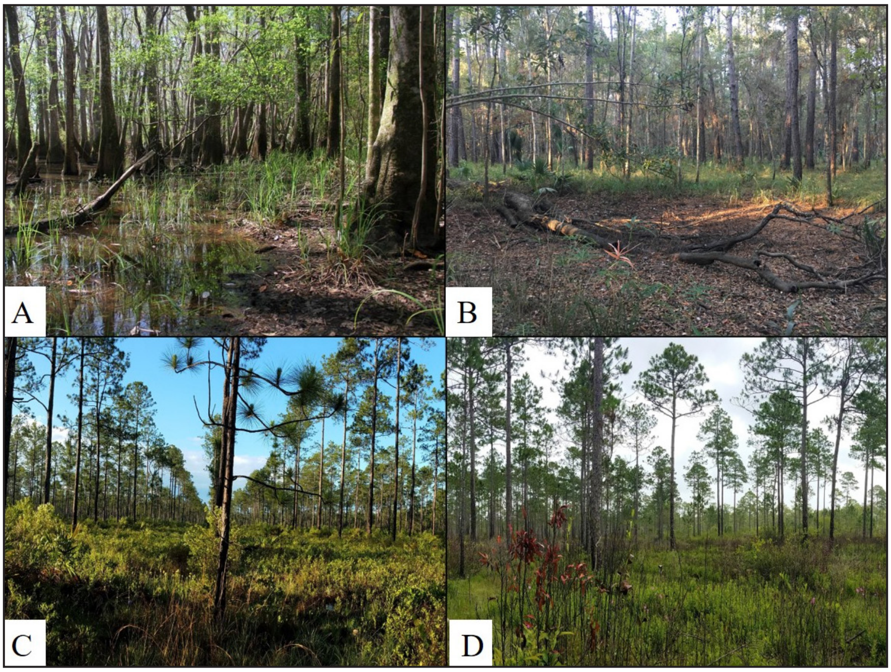

Figure 1. Examples of habitats where *Terrapene carolina major* (Gulf Coast Box Turtle) were commonly observed in the Florida Panhandle, USA. (A). Floodplain swamp (Photographed by Michael T. Jones). (B). Mixed wetland hardwood, seasonally inundated (Photographed by Jonathan D. Mays). (C). Coniferous plantation (Photographed by Jessica R. Meck). (D). Mesic flatwoods (Photographed by Jessica R. Meck).

Communication Specialist Inc., Orange, California, USA) and an antenna called the Rubber Ducky (RA-23, Telonics, Mesa, Arizona, USA). We obtained one additional location during the months of November 2016, December 2016, and March 2017. In December 2016, we found one radio-tagged male (M104) dead, 8 mo after we found that it had a hind limb dislocation from unknown causes. In March 2017, we fitted an additional male (M95) with a radio transmitter at the same site as the dead male to maintain the relatively equal sex ratio between sites. We used only May to August data collected for all home range, movement, habitat selection, and behavior analyses to maintain consistency. During each location event, we recorded turtle identification number, date, time, air temperature (°C), weather, distance to water (meters), turtle behavior, dominant habitat type within 5 m, and GPS location (Garmin GPS Map 78, Garmin Ltd., Olathe, Kansas, USA). We avoided physical contact with the radio-tagged turtles during location events to minimize any influence on natural behaviors.

Home range and movement.—We used five methods to calculate home range each year to maximize the comparability with other studies. We created two minimum convex polygons (MCP) and three fixed kernel density estimators (KDE) using the package adehabitatHR (Calenge 2006) in RStudio (version 1.1.383) and the statistical software R, version 3.3.3 (R Core Team 2016). We determined 100% and 95% MCPs. We calculated 100% MCPs to include potential female nesting movements. We calculated three kernel estimations by using the default h = href (the reference default bandwidth) and calculated the area (hectares) of 95%, 75%, and 50% of the points to determine activity areas. We conducted Welch's two-sample *t*-tests ($\alpha = 0.05$) with log transformations (due to skewness of the data and unequal variance) to determine whether males and females exhibit similar home range sizes and

Figure 2. *Terrapene carolina major* (Gulf Coast Box Turtle) male #122 (M122) with a radio transmitter and temperature logging ibutton fixed onto the right posterior carapace to lessen the chance of the turtle being caught on vegetation. (Photographed by Jessica R. Meck).

Table 1. The grouping of habitat types of the Florida Land Cover GIS raster data (www.fgdl.org/metadataexplorer/explorer.jsp) into five categories: Coniferous Plantation, Wet Coniferous Forest, Forested Wetland, Other Natural, and Other Disturbed. Habitat types listed were habitats within the 21 radio-tracked *Terrapene carolina major* (Gulf Coast Box Turtle) 100% Minimum Convex Polygons (MCP) for the 2016 and 2017 field seasons (May to August) combined. Groupings were determined by the definitions provided by the Florida Land Cover Classification System (Kawula 2014). One asterisk (*) are for habitats found only in 2017 female MCPs, and two asterisks (**) are for habitats found in female MCPs both field seasons.

Group	Habitat Type	Description
Coniferous Plantation	Coniferous Plantation**	Actively managed upland pine plantation, not seasonally inundated.
Wet Coniferous Forest	Hydric Pine Flatwoods Mesic Flatwoods** Wet Coniferous Plantation Wet Flatwoods**	Pine dominated canopy (natural or plantation), sandy substrate, and typically seasonally inundated/saturated.
Forested Wetland	Alluvial Forest Baygall* Floodplain Swamp Mixed Wetland Hardwoods Other Wetland Forested Mixed	Forested area where canopy can be primarily deciduous or mixed with pine and is seasonally or yearly inundated.
Other Natural	Mixed Scrub-Shrub Wetland Riverine	Habitats that totaled < 2% of all use and available points combined and occur naturally on the landscape.
Other Disturbed	Rural Open** Transportation Shrub and Brushland*	Habitats that are the result of a frequent or recent human disturbance and totaled < 2% of all use and available points combined.

movement patterns. We also conducted an incremental core area analysis using 100% MCPs from 2016 and 2017 separately to determine if enough locations were obtained to accurately represent a home range of an individual (Hanski et al. 2000).

We determined the mean daily distances (DPD) for each individual for both years during the months of May to August. The DPD was calculated by dividing the distance since last location by the number of days elapsed. We also measured maximum linear distances (MLD) between the two farthest location points from May to August for each individual to the nearest meter in ArcMap (version 10.5.1) and conducted Welch's two-sample *t*-tests ($\alpha = 0.05$) with log transformations (due to the right-skewed distribution of the raw data) to evaluate male and female DPD and MLD changes between years.

Home range fidelity.—Using the 100% MCPs for both years of data, we calculated the percentage of area used both years for each individual using the following equation described in Refsnider et al. (2012):

$$[\text{Area overlap} / (\text{Area}_{\text{year1 MCP}} + \text{Area}_{\text{year2 MCP}} - \text{Area Overlap})] \times 100.$$

We performed a Welch's two-sample *t*-test ($\alpha = 0.05$) with log transformations (due to right skew distribution of the raw data) to determine if males and females had similar home range overlap between years.

Habitat use and selection.—We used Spatial Analyst tools (Esri, Redlands, California, USA) to extract the habitat type of each telemetry location for all 21 individuals to compare our field observations to the Florida Land Cover raster datafile (10 m resolution, www.fgdl.org/metadataexplorer/explorer.jsp). We extracted 15 habitat types and determined that the Land Cover raster datafile highly corresponded to our field observations (88%). The extracted habitat types were grouped into one of five categories based on dominant canopy composition and overall inundation: Coniferous Plantation, Wet Coniferous Forest (inclusive of Hydric Pine Flatwoods, Mesic Flatwoods, Wet Coniferous Plantation, and Wet Flatwoods), Forested Wetland (Alluvial Forest, Baygall, Floodplain Swamp, Mixed Wetland Hardwoods, and other wetland forested mix), other natural (Mixed Scrub-Shrub Wetland and Riverine), and other disturbed (shrub and brushland, rural open, and transportation) to simplify the analysis (Table 1). We based groupings on the Florida Land Cover Classification System definitions (Kawula 2014). We generated 100 random points within each 100% MCP and evaluated habitat selection by using a Generalized Linear Model (GLM) in R using a binary (telemetry location or random point) response, habitat type as the predictor, individual turtle as a fixed effect, and evaluated the model using a goodness of fit test. We summarized habitat use by calculating the area of each habitat group within each 100% MCP in ArcMap to determine the percentage of habitat groups for each individual and by sex. We analyzed the 2016 and 2017 field season data separately.

Behavior.—We categorized observed activities into three groups (alert, quiescent, and aquatic) for both years to determine if males and females were similar; we also wanted to determine if males and females were similar in overall aquatic use. Alert activities included alert on surface, mating, nesting, feeding, walking, and fighting where individuals were not in a body of water (> 0 m to water). Quiescent activities included complete form (individual covered > 90% by substrate, inactive), partial form (individual was covered < 90% by substrate, inactive), and concealed (individual could not be visually observed, e.g., located in underground burrow) where individuals were not in a body of water (> 0 m to water). Aquatic activities included submerged, soaking (partially submerged), and activities where the distance to water was 0 m. We then calculated the percentage of each categorized activity for all individuals for both years separately and conducted a Chi-square Analysis (α = 0.05) to determine if males and females were displaying similar activities.

We pooled radio-observations involving fighting turtles and evaluated them for territorial relationships. We designated winners and losers of fights when possible based on the position and behavior of each turtle when found. We designated winners as those individuals displaying dominant behaviors, such as mounting the opponent, flipping the opponent, chasing the opponent, or biting the opponent. Losers were individuals that were submissive (i.e., mounted by the opponent, flipped over, trying to escape, or being bitten). Upon observing the fighting behavior, the observer waited ≥ 5 m away for the turtles to finish the encounter. If the turtles appeared to have been disturbed by the presence of the observer, we processed the turtles (e.g., morphological measurements, behavioral notes, GPS location).

Results

Descriptive statistics of body size.—We found and measured 334 unique *T. c. major* adults (n = 182 male, n = 152 female) within the study sites from 2016 to 2017. The mean male CL was 182.3 ± 11.94 (standard deviation) mm (range, 149–208 mm), mean PL was 159.3 ± 11.28 mm (range, 135–194 mm), mean SH was 78.1 mm ± 5.14 mm (range, 62–89 mm), and mean weight was 961.0 ± 177.28 g (range, 614–1,416 g). The mean female CL was 160.8 ± 11.18 mm (range, 123–193 mm), mean PL was 142.6 ± 11.93 mm (range, 104–174 mm), mean SH was 76.7 ± 4.98 mm (range, 61–91 mm), and mean weight was 782.6 ± 149.42 g (range, 410–1194 g). A total of 15 individuals, all males, had a CL ≥ 200 mm. Males were significantly larger for all body metrics compared to females (CL: t = -16.89, df = 313.9, P = < 0.001; PL: t = -13.87, df = 301.7, P = < 0.001; SH: t = -2.55, df = 321.8, P = 0.011; weight: t = -9.42, df = 301.2, P = < 0.001). The sexual dimorphic index (SDI) for the sampled individuals is -1.14. Of the 432 unique individuals we found (including juveniles), approximately 9% (22 males, 14 females, two juveniles) had damaged or missing nuchals. Some individuals had clearly been struck by vehicles, equipment, or an unknown source, but others were likely damaged during mating or fighting (see Behavior section).

Home range and movement.—The mean number of locations for each individual was 30 (range, 29–31) in 2016 and 28 (range, 26–30) in 2017. The incremental core area analysis for both 2016 and 2017 revealed that males and females reached an asymptote at a mean of 30 locations, indicating a sufficient number of locations were obtained. The largest and smallest 100% MCP calculated from both years was 45.4 ha and 0.2 ha, respectively (Table 2). Females had significantly larger home ranges than males for all calculations and for both years (Table 3). Mean DPD from both years combined ranged from 3.0 m to 39.7 m (Table 2). Both male and female DPD decreased significantly between years (male: t = 4.42, df = 20.0, P = < 0.001; female: t = 2.94, df = 13.1, P = 0.013). Females made significantly larger movements than males for both years (2016: t = 4.13, df = 17.9, P = < 0.001; 2017: t = 3.46, df = 13.5, P = 0.004).

Home range fidelity.—The individual total area used over two years (100% MCPs) for the 19 turtles we tracked both years ranged from 0.6 ha to 45.6 ha. Female total area used averaged 15.1 ± 11.96 (standard deviation) ha and males averaged 1.2 ± 0.62 ha. The percentage overlap of total area used between 2016 and 2017 for females averaged 21.3% (range, 2.9–49.8%) and males averaged 43.8% (range, 8.4–72.4%). Males used significantly more of the same area from year to year than females (t = -2.62, df = 11.1, P = 0.023).

Habitat use and selection.—In 2016, Forested Wetlands were used significantly more than Wet Coniferous Forests (estimate = 0.862, Z = 2.677, df = 1,434, P = 0.007) and other natural habitats (estimate = 1.006, Z = 2.025, df = 1434, P = 0.043). In 2017, no habitat group was used significantly more or less than other available habitats detected in male home ranges (estimate = 0.001, Z = -0.123, df = 1,393, P = 0.902). One habitat group, Coniferous Plantations, were not used by males in 2016 or 2017. In 2016, Coniferous Plantations were used significantly more by females than Forested Wetlands (estimate = 0.078, Z = 2.116, df =

Table 2. Average home range and movement calculations for *Terrapene carolina major* (Gulf Coast Box Turtle) in the Florida Panhandle, USA, for 2016 and 2017. Home range (minimum convex polygons [MCPs] and kernel density estimators [KDEs]) are reported in hectares and distance per day (DPD) and maximum linear distance (MLD) is reported in meters. An asterisk (*) indicates a significant difference was found between males and females.

	2016		2017	
Parameter	Male	Female	Male	Female
95% MCP	0.7 ± 0.35	5.9 ± 3.88*	0.7 ± 0.40	8.8 ± 13.11*
	0.2–1.4	1.1–10.7	0.1–1.3	0.5–42.5
100% MCP	0.9 ± 0.47	7.9 ± 4.90*	0.9 ± 0.43	10.9 ± 13.37*
	0.2–1.8	1.9–17.0	0.2–1.4	0.8–45.4
95% KDE	2.7 ± 2.45	21.5 ± 16.34*	2.8 ± 2.34	34.1 ± 44.86*
	0.6–9.5	4.2–53.5	0.4–8.7	1.8–148.0
75% KDE	1.3 ± 1.28	9.5 ± 6.82*	1.4 ± 1.20	15.6 ± 21.66*
	0.3–5.0	1.9–20.8	0.2–4.4	0.9–70.6
50% KDE	0.7 ± 0.68	4.3 ± 3.18*	0.7 ± 0.61	6.5 ± 8.74*
	0.2–2.7	0.7–9.1	0.1–2.2	0.5–28.7
DPD	12.0 ± 5.21	23.0 ± 8.47*	5.8 ± 1.94	13.3 ± 7.32*
	6–26	15–40	3–8	4–30
MLD	180.6 ± 73.75	528.1 ± 221.90*	169.9 ± 66.96	614.6 ± 323.92*
	84–326	263–1,021	66–301	147–1,259

1,166, P = 0.034) and Wet Coniferous Forests (estimate = 0.077, Z = 2.054, df = 1,166, P = 0.041). In 2017, Wet Coniferous Forests were used significantly more by females than Forested Wetlands (estimate = 1.254, Z = 4.666, df = 1,142, P = < 0.001) and other disturbed habitats (estimate = 2.266, Z = 2.131, df = 1,142, P = 0.033). All five habitat groups were present in female home ranges both years.

Male 2016 individual MCPs averaged 21.2% Wet Coniferous Forest, 74.9% Forested Wetlands, and 5.0% other natural habitats. Only three individuals (M122, M104, and M97) had Wet Coniferous Forest present in their MCP, whereas the other individuals had primarily Forested Wetland. Other natural habitats were relatively small portions of overall MCPs. Male 2017 individual MCPs averaged 22.7% Wet Coniferous Forest, 76.5% Forested Wetland, 0.3% other disturbed habitats, and 0.5% other natural habitats. Similar to 2016, three individuals (M122, M97, and M95) had a high percentage of Wet Coniferous Forest present whereas other individuals had a high percentage of Forested Wetlands in their 100% MCP. Only two individuals had other disturbed and natural habitats (M108 and M27, respectively). Female 2016 individual MCPs averaged 7.1% Coniferous Plantation, 25.9% Wet Coniferous Forest, 64.1% Forested Wetlands, 2.2% other disturbed habitats, and 0.7% other natural habitats. Three individuals (F7002, F145, and F131) had no Wet Coniferous Forest present in their MCP. Similar to males, other disturbed and other natural habitats were small portions of overall MCPs and only one female, F119, had all five habitat groups. Female 2017 individual MCPs averaged 5.8% Coniferous Plantation, 28.5% Wet Coniferous Forest, 63.2% Forested Wetland, 2.1% other disturbed habitats, and 0.4% other natural habitats. Only one individual (F7002) did not have any coniferous habitat present in her MCP, and F23 was the only individual who had all five habitat groups.

Behavior.—We categorized 519 activity observations (288 male, 231 female) in 2016 and 516 (290 male, 226 female) in 2017. In 2016, total observed male activities were 33% alert, 20% aquatic, and 47% quiescent and in 2017 activities were 25% alert, 32% aquatic, and

Table 3. Results of the log-transformed Welch's two-sample t-tests (df = degrees of freedom) for the home range and movement calculations between male and female *Terrapene carolina major* (Gulf Coast Box Turtle) in the Florida Panhandle, USA, during the 2016 and 2017 field seasons.

	2016			2017		
Results	t	df	P-value	t	df	P-value
95% MCP	5.69	12.2	< 0.001	3.77	11.6	0.003
100% MCP	6.88	14.9	< 0.001	5.35	12.8	< 0.001
95% KDE	5.18	14.7	< 0.001	4.48	13.8	< 0.001
75% KDE	4.94	14.5	< 0.001	4.11	13.5	0.001
50% KDE	4.52	14.2	< 0.001	4.01	14.0	0.001
DPD	4.13	17.9	< 0.001	3.46	13.5	0.004
MLD	5.96	17.6	< 0.001	5.08	13.9	< 0.001

Table 4. Date, turtle identification (ID), outcome, carapace straight, midline length (CL), and weight (g) of eight radio-tagged *Terrapene carolina major* (Gulf Coast Box Turtle) individuals in the Florida Panhandle, USA, involved in putative fighting during the 2016 and 2017 field seasons (May to August). The asterisk (*) indicates that M95 was not radio-tagged in 2016 but was tagged in 2017 to replace M104.

Fight	Date	Turtle ID	Outcome	CL	Weight	Notes
1	14 March 2016	M109	Winner	204.6	1415	M109 chasing M129
		M129	Loser	197	1211	
2*	14 March 2016	M95	Winner	166	834	M134 flipped, M95 upright
		M134	Loser	171	768	
3	17 March 2016	M151	Loser	189	1220	M44 biting M151's leg
		M44	Winner	176	851	
4	24 May 2016	M97	Winner	175.9	917	M98 inside shell, M97 alert
		M98	Loser	184	971	
5	9 June 2017	M95	Winner	166	834	M371 on his side, M95 alert
		M371	Loser	169	739	
6	13 June 2017	M97	Loser	175.9	917	M97 mounted by M134
		M134	Winner	171	768	
7	13 June 2017	M109	Winner	204.6	1415	M129 on his back, M109 alert
		M129	Loser	197	1211	
8	8 August 2017	M97	Unknown	175.9	917	Facing each other, alert
		M98	Unknown	184	971	

43% quiescent. Female observed activities in 2016 were 34% alert, 16% aquatic, and 50% quiescent and in 2017 activities were 36% alert, 24% aquatic, and 39% quiescent. In 2016 there was no significant difference between male and female activity (χ^2 = 0.992, df = 2, P = 0.609) whereas in 2017 there was a significant difference between male and female activity, with males using aquatic locations more than females (χ^2 = 8.73, df = 2, P = 0.013).

We observed eight fighting encounters during the 2016 and 2017 field seasons involving four male radio-tagged individuals (Table 4). We observed an additional eight fights in 2016 and 2017 with non-radio tagged individuals. We did not see females fighting in either year, but we occasionally found females near (< 5 m) fighting males. We also observed males biting the nuchal and anterior carapace of opponents causing the nuchal and marginals to break and bleed in some cases (Fig. 3). Two pairs of males were observed fighting both years, M97 with M98 and M109 with M129. Based on our observations, M97 won the fight against M98 in 2016, but was disturbed by the observer in 2017 and the fighting stopped before conclusion. An additional fight occurred between M97 and M134 in 2017 where M97 lost. Both years, M109 appeared to have won a fight with M129, where M129 was flipped onto his side in 2017 and these fights were the only two of the seven conclusive fights where the winner had a larger CL.

We confirmed two females nested during our study, one in a non-inundated forested wetland and one in an open recreational area. We discovered radio-tracked female F7002 covering her nest on top of a heavily soiled root mass from a fallen tree in a non-inundated forested wetland 19 June 2017 at 1100 (Fig. 4). An additional unknown female was observed by a biologist of the U.S. Forest Service and she was reported to have nested in an open area under a pine tree 21 June 2016. We do not know the fate of either nest.

Discussion

Body size.—We found that males were significantly larger than females across all body metrics, suggesting this population of *T. c. major* is sexually dimorphic. It is not uncommon for populations of *T. carolina* to show sexual size dimorphism and on average, males tend to be larger than females and reach greater maximum sizes (Dodd 2001). Other *Terrapene* studies that reported a sexual dimorphism index include Dodd (1997) with *T. c. bauri* in Florida (-1.05) and Gibbons and Lovich

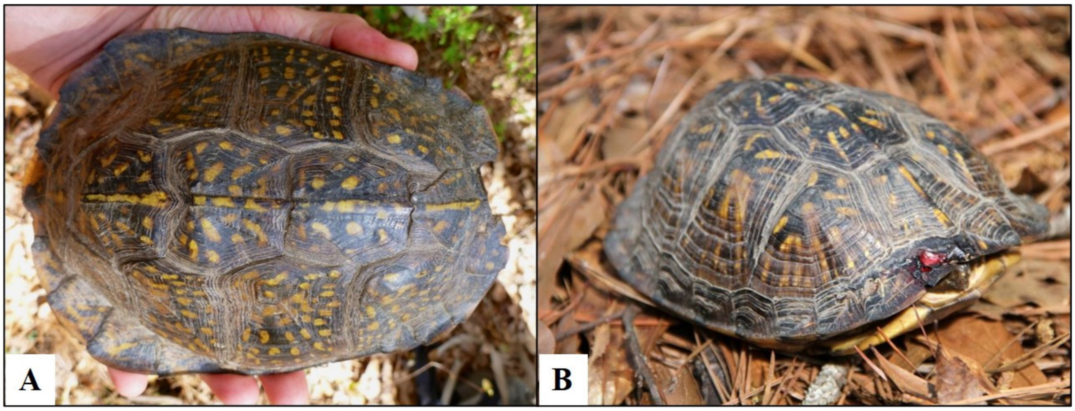

Figure 3. (A). A male *Terrapene carolina major* (Gulf Coast Box Turtle) with nuchal and anterior marginal damage (Photographed by Jonathan D. Mays). (B). A young male *T. c. major* with recent anterior marginal damage from suspected fighting. (Photographed by Michael T. Jones).

(1990) with *T. c. carolina* in Indiana (-1.06). There is no conclusive explanation as to why male *Terrapene* have evolved to be larger than females. Berry and Shine (1980) suggested that among turtles, the degree of sexual dimorphism depends on the male mating strategies. Males would be larger than females if males exhibited combat and/or forcible insemination. In our population of *T. c. major*, we observed males fighting with other males. Dodd (2001) explained that larger male *T. c. bauri*, had a mechanical advantage. Larger males have larger plastron concavities, allowing for a better fit during copulation with the female and the ability to grasp the carapace of a female during courtship. This mechanical advantage would also apply to *T. c. major*.

Home range and movement differences.—Although most studies of *T. carolina* lineages have not found differences between male and female home range size (Stickel 1950; Cook 2004; Bernstein et al. 2007; Kapfer et al. 2013; Kiester and Willey 2015), we found females had significantly larger home ranges than males and averaged an order of magnitude larger; eight (2016) and 11 (2017) times larger than males. Females on average also moved more between locations compared to males. While this study took place during *T. carolina* nesting season, potential nesting movements do not fully explain this difference; the significant difference of the 50% kernel estimations indicate females move, even within their core activity areas, more frequently and farther compared to males. We also found that males exhibited significantly higher home range fidelity over the two summer seasons compared to females.

Based on these observed differences in home range size and fidelity, we think *T. c. major* males may be displaying elements of territoriality. Brown and Orians (1970) established the standard definition for territoriality in mobile animals by describing the following three requirements an animal must meet to be considered territorial: (1) a fixed location, (2) defense against intruders, and (3) exclusivity of an area. Additionally, Maher and Lott (2000) summarized that in general for many species, food predictability is linearly correlated with territoriality, describing other determinants as an inverted U shape. Examples of other determinants are intruder pressure, population density, and food distribution, where levels are required to be intermediate for fighting and territories to be established. This suggests that depending on the species life-history characteristics, the influence of other determinants vary when the cost-benefit ratio is ideal to warrant a defended territory.

Our data suggest *T. c. major* males meet the first two requirements of Brown and Orians (1970) definition;

Figure 4. Radio-tagged female *Terrapene carolina major* (Gulf Coast Box Turtle) #7002 (F7002) after completing a nest atop the fallen root mass of a tree in a non-inundated forested wetland on 19 June 2017. (Photographed by Jessica R. Meck).

fixed location and defense against intruders. High site fidelity is an indicator of a fixed location, and on average males used 43.8% of the same area year to year, with two individuals using more than 70% of the same area. Another consideration is the size of the location, and males had significantly smaller home ranges than females across all calculations. If territoriality is the case in our study, a smaller area is easier to defend because it requires less energy (Maher and Lott 2000). The males we tracked, even at the 100% MCP level, averaged < 1 ha both years, compared to females who averaged 9 ha. Comparatively, average MCP estimates across *T. c. carolina* populations range from < 2 ha (Aall 2011; Donaldson and Echternacht 2005) to > 7 ha (Baker 2009; Willey 2010), but males and females typically have the same size home range. Additionally, we observed multiple males fighting, of which two radio-tagged males fought with the same opponent both years suggesting defense against intruders. Fighting the same opponent both years also suggests that the individuals have some home range overlap or territories that border each other. Other turtle species that have been observed fighting, such as *Glyptemys insculpta* (Wood Turtle) and *Gopherus polyphemus* (Gopher Tortoise), are known to establish dominance hierarchies, which were shown to affect reproductive success but not exclude individuals from a defined area or territory (McRae et al. 1981; Kaufmann 1992). Therefore, it seems possible that *T. c. major* males may also be establishing dominance hierarchies and that population density and food resources are at appropriate levels to warrant the potential costs of losing a fight (Maher and Lott 2000).

We had no evidence to support the third characteristic of territories, exclusivity of an area. Two males, M151 (radio-tagged) and M44 (not radio-tagged) were consistently in the same area, with M44 found 10 times on the same date as M151 with a mean distance of 25.4 m apart, indicating neither individual was excluding the other from the area. On the contrary, measuring exclusivity in reptiles, such as turtles, would be extremely difficult based on their ecology. Unlike birds or mammals that have either vocal, chemical, or a combination of cues to warn or detect intruders in their territory (Rosell and Thomsen 2006; Brumm and Ritschard 2011; Shonfield et al. 2012), box turtles have no known cues that would allow them to detect if another individual is in the area, particularly at a considerable distance. Research suggests that when finding mates, male box turtles rely heavily on close-range visual cues (Belzer and Seibert 2009), so it would be assumed that detecting another male would be the same. Box turtles are also not able to traverse rapidly within their home ranges to patrol or seek intruders, therefore the classic definition of territoriality put forth by Brown and Orians (1970) likely rules out the possibility that any turtle species can be territorial, because they cannot be exclusive. Future ecology studies of freshwater turtles may warrant a reevaluation of territorial characteristics specific to turtle species. Whether this lineage is establishing hierarchies or territories, our observations are ecologically unique compared to other *T. carolina* lineages. Additional research needs to be conducted to further explore male body size influence on fighting outcomes and reproductive success, movement patterns of the losing male individuals, and seasonal changes in behavior (i.e., fighting frequency).

Habitat selection and aquatic behavior.—The landscape of our study sites was predominantly Forested Wetlands, Coniferous Plantations, and Wet Coniferous Forests, and both sexes spent approximately 23% of their time in aquatic conditions. Females selected Coniferous Plantations or Wet Coniferous Forests over Forested Wetlands whereas males selected Forested Wetlands. Both sexes, however, had Forested Wetlands as the dominant habitat within their 100% MCP, suggesting that females may seek other sources of aquatic micro-environments upland and males seek non-aquatic micro-environments in the forested wetlands. Similar behavior has been observed in *T. c. carolina* at the population level in South Carolina, USA (Roe et al. 2018). Additionally, our primary data collection occurred during the summer months, the driest time of the year in the region, limiting our interpretation of *T. c. major* ecology and behavior to these summer months. A long-term, multi-season study with a higher frequency of radio-tracked locations may indicate that *T. c. major* is more aquatic throughout the year.

In total, 15 habitat types were used in male and female home ranges combined, indicating the presence of a highly mosaic landscape. As expected, females had a larger number of habitat types than males in their significantly larger home ranges. As indicated by the 50% kernel estimations, larger female home ranges cannot be explained by nesting movements alone, but it may partially explain it. The landscape in our study sites is predominantly Forested Wetlands, which are typically unsuitable for nesting due to lack of unsaturated, open habitat. We found that females selected for upland coniferous habitats, indicating these habitats may be highly important for females in the region for successful reproduction. Of the two nesting sites observed, one was in an upland setting and another was a hummock in a Forested Wetland. We believe both of these habitats are important given their overall use by females. Most coniferous habitats in our study area are managed with prescribed fire primarily during the winter months, allowing for more open canopy and exposure to the sandy substrate (Kawula 2014), ideal for nesting turtles and other reptiles. Additionally, the Gulf Coastal Plain has many habitats and species that rely and have evolved with fire, such as *Pinus palustris* (Longleaf Pine; Blaustein 2008). *Terrapene c. major* females may seek these fire-dominated coniferous habitats for nesting given their low canopy cover (i.e., more solar radiation getting to the forest floor) and substrate qualities, but probably use other habitats based on availability. Future studies focusing on nesting behavior and associated habitat selection should be conducted to better understand the relationship between *T. c. major* and prescribed fire habitats.

While upland coniferous habitats may be important for nesting, Forested Wetlands, in turn, may serve as a resource for access to mates, similar to streams and hibernacula for *G. insculpta* (Brown et al. 2016; Kaufmann 1992). During our limited late fall-early winter and spring trips, we observed females using the Forested Wetlands, possibly for better thermoregulation in colder temperatures, and as a result, they encounter males for mating opportunities. During our study, we encountered 13 separate matings, seven of which were located within Forested Wetlands and two in an ecotone of Forested Wetlands and upland Deciduous Forests. While the sample size is small and potential bias in visual detectability is undeterminable (i.e., Forested Wetlands may be easier to survey for mating compared to upland habitats), future investigations into *T. c. major* mating should consider incorporating a habitat component.

Conservation and evolutionary implications.—Our investigation of *T. c. major* body size, spatial ecology, and behavior revealed significant differences in the manner of habitat use by males and females. Males maintain smaller home ranges with higher fidelity within forested wetlands and exert dominance via fighting, while females use a much larger area with lower fidelity in diverse habitats. From an evolutionary perspective, fighting between males may drive gene selection toward larger, more aggressive males that are capable of securing mating opportunities through dominance. Furthermore, *T. c. major* is the closest living genetic lineage to the extinct *T. c. putnami* (Giant Box Turtle; Martin et al. 2013), indicating *T. c. major* may attribute its size and behavior to *T. c. putnami.* If further genetic analyses support this theory, then it is even more vital that conservation efforts effectively preserve the evolutionary potential of *T. c. major*.

The different ways that males and females used the landscape during our study indicates they may be susceptible to different threats. Based on our observations, females do not rely on the Forested Wetlands during the summer months and move more frequently, making them more vulnerable to road mortality, collection, and anthropogenic landscape alterations, such as timber operations (Howey and Roosenburg 2013), whereas males would be more sensitive to changes in Forested Wetlands. Future conservation efforts should take into consideration high home range variability and strive to develop plans that cater to creating or managing large, protected areas with diverse habitats. Additional studies are warranted in other locations with higher road densities or in suburban habitats.

While the systematic relationships of *T. c. major* remain unclear, this lineage has demonstrated unique spatial and behavioral characteristics compared to other *Terrapene* and should be considered a unique taxon from a conservation and management perspective. A recent genetic study aiming to characterize the hybridization and introgression of box turtles in the southeastern U.S. suggested at least one *T. c. major* population sampled had no evidence of introgression with *T. c. carolina* or *T. c. triunguis* (Three-toed Box Turtle; Martin et al. 2019). If in fact introgression is not occurring between the three lineages in places, it is imperative that long-term autecological assessments are established for *T. c. major* to better inform conservation decisions that ensure this unique lineage remains on the landscape.

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