

# Home Range and Habitat Selection of the Suwannee Alligator Snapping Turtle (Macrochelys suwanniensis) in the Suwannee River, Florida

Authors: Thomas, Travis M., Enge, Kevin M., Suarez, Eric, Schueller, Paul, Bankovich, Brittany, et al.

Source: Chelonian Conservation and Biology, 22(2): 146-155

Published By: Chelonian Research Foundation and Turtle

Conservancy

URL: https://doi.org/10.2744/CCB-1583.1

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at <a href="https://www.bioone.org/terms-of-use">www.bioone.org/terms-of-use</a>.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

### Home Range and Habitat Selection of the Suwannee Alligator Snapping Turtle (Macrochelys suwanniensis) in the Suwannee River, Florida

## Travis M. Thomas<sup>1,\*</sup>, Kevin M. Enge<sup>2</sup>, Eric Suarez<sup>3</sup>, Paul Schueller<sup>2</sup>, Brittany Bankovich<sup>2</sup>, and Erin H. Leone<sup>2</sup>

<sup>1</sup>Nature Coast Biological Station, University of Florida, Cedar Key, Florida USA [travis.thomas@ufl.edu];

<sup>2</sup>Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, Gainesville, Florida USA [kevin.enge@myfwc.com, paul.schuller@myfwc.com, brittany.bankovich@myfwc.com, erin.leone@myfwc.com];

<sup>3</sup>Division of Habitat and Species Conservation, Florida Fish and Wildlife Conservation Commission, West Palm Beach, Florida USA [eric.suarez@myfwc.com]

\*Corresponding author

Abstract. - Effective management of a species requires that resource managers know critical aspects of its ecology, including information on home range and habitat use. We conducted the first telemetry study on the Suwannee alligator snapping turtle (Macrochelys suwanniensis), and we examined movements at an upper river (UR) site and a lower river (LR) site in the Suwannee River in Florida, USA. We estimated home range size with kernel density estimates (KDE) using the FishTracker GIS toolbox, and we examined potential differences in KDEs with Generalized Linear Models (GLMs). We also used GLMs (family = binomial) to examine habitat selection for M. suwanniensis. We used an information-theoretic approach to rank and select the most parsimonious models. Overall, our models revealed that M. suwanniensis possessed larger 90% KDEs in the LR site than the UR site, and in both sites, turtles moved into the floodplain during flooded conditions. Remarkably, these movements continued even after water levels receded and the aquatic links were severed. Interestingly, M. suwanniensis selected shallow water with some type of subsurface cover, especially large woody debris (LWD). Instream LWD is likely extremely important, especially during low water levels when undercut banks and other bank habitats are unavailable, so the removal of LWD, including deadhead logs, could negatively affect the species. Minimum flows have been established in the drainage, but river water levels have declined an estimated 40% since human settlement, partly because of groundwater withdrawal outside the drainage, potentially imperiling this state Threatened species.

KEY WORDS. – acoustic telemetry; *Chelydridae*; dynamic; *FishTracker*; kernel density estimator; spatial ecology

Understanding how animals use the landscape is important for wildlife management (Morrison et al. 1998). Home range has traditionally been defined as the area an animal uses for feeding, mating, and taking care of young (Burt 1943), whereas habitat selection is the process that an animal uses to select a nonrandom set of available habitats (Morris 2003). Most estimators of animal movements were designed for terrestrial species that move freely throughout the landscape (Calhoun and Casby 1958; Dixon and Chapman 1980), but many species are either associated with restricted, fragmented habitats or confined to largely linear pathways such as rivers (Redpath 1995; Taylor 1997; Major and Gowing 2001). Assessing movements can be somewhat challenging for riverine species, including freshwater turtles.

Linear home range (LHR) is an extremely common home range estimation method for freshwater turtles (Harrel et al. 1996; Riedle et al. 2006; Shipman and Riedle 2008; Moore et al. 2014). Linear methods are simple

and can provide home range estimates in geographically restricted environments (Kay 2004). Improvements in technology and recent developments in geographic information systems (GIS) have allowed ecologists to intensify their research on animal movements (Nilsen et al. 2008). In fact, the area traversed by an animal can be considered a probability function, not a continuous distribution (Getz et al. 2007). All home range analyses have limitations, and no single method is appropriate in all settings (Kenward et al. 2001). Most conventional analyses of home range do not consider physical constraints, such as barriers, or the cost of traversing alternate possible paths between points; instead, they typically infer a straight-line path between sequential relocations. This approach has obvious limitations, especially in constrained environments such as rivers (Laffan and Taylor 2013).

Macrochelys is a genus of highly aquatic freshwater turtles restricted to rivers and associated wetlands that drain into the Gulf of Mexico from Florida to Texas (Pritchard 2006). Macrochelys consists of 2 recognized species, the alligator snapping turtle (M. temminckii) and the Suwannee alligator snapping turtle (M. suwanniensis; Thomas et al. 2014). The latter species is restricted to a single river drainage in Georgia and Florida (Enge et al. 2021b). Macrochelys suwanniensis is listed as Threatened in Florida and has an uncertain population status in the main stem Suwannee River (Thomas et al. 2022). Several telemetry studies conducted on M. temminckii in Louisiana, Missouri, Kansas, Oklahoma, and Texas found they moved extensively throughout available aquatic habitat and used microhabitats that tended to have greater underwater structure and denser canopy cover (Sloan and Taylor 1987; Shipman et al. 1995; Harrel et al. 1996; Riedle et al. 2006; Munscher et al. 2021). Macrochelys rarely move over land, except nesting females and hatchlings leaving the nest (Mount 1975; Pritchard 2006), and telemetry studies have not documented terrestrial activity (e.g., Harrel et al. 1996; Riedle et al. 2006; Howey and Dinkelacker 2009). Most studies of M. temminckii movements were conducted in sloughs, impoundments, altered river systems, or smaller streams (Harrel et al. 1996; Riedle et al. 2006; Shipman and Riedle 2008; Munscher et al. 2021). Little information exists on Macrochelys movements in large, free-flowing rivers, and home range and habitat selection are unknown for M. suwanniensis. Therefore, we conducted an acoustic telemetry study to better understand aspects of M. suwanniensis movements in the Suwannee River in Florida, USA. Our objectives were to 1) estimate M. suwanniensis home range sizes, and 2) determine habitat selection in the Suwannee River. The Suwannee River is a dynamic system that changes ecologically from its headwaters to its mouth (Hornsby et al. 2000), so we examined *M. suwanniensis* movements in 2 different sites: an upper river (UR) site and a lower river (LR) site. We hypothesized that male M. suwanniensis would have larger home ranges due to larger body sizes, and home range estimates would be larger in the LR site because the river channel is wider. We also hypothesized that M. suwanniensis habitat selection would be similar to that of M. temminckii and that M. suwanniensis would utilize deep pools and select areas associated with underwater structure (e.g., log jams, fallen trees, submerged logs) and dense canopy cover in both sites. Results from this study could help identify critical habitats used by M. suwanniensis, leading to better conservation and management strategies for this species, which is listed as Threatened in Florida and Georgia and proposed for federal listing as Threatened (US Fish and Wildlife Service 2021).

#### **METHODS**

Study Sites. — The Suwannee River is the second largest river by drainage in Florida and serves as a key geological and ecological break between the peninsula and panhandle regions (Neill 1957; Bermingham and Avise

1986). The Suwannee River flows unaltered  $\sim$  378 km from the Okefenokee Swamp in southeastern Georgia to the Gulf of Mexico on the Dixie-Levy County line in Florida, and it exhibits changes in water chemistry and biological productivity (Ceryak et al. 1983; Hornsby et al. 2000). We selected 2 different sites to account for these differences: an upper river (UR) site and a lower river (LR) site that best represented this dynamic river system (Fig. 1). The UR site lies within the Okefenokee Swamps and Plains subregion and is a typical low-nutrient, acidic, 'blackwater' stream that is characterized by deeply incised limestone banks with a narrow channel that is 30-50 m wide (see Hornsby et al. 2000). Water flow is extremely variable, and water levels fluctuate greatly depending on rainfall (surface runoff). The UR site reaches flood stage when water levels are > 22.5 m above mean sea level at the US Geological Survey (USGS) river gage at White Springs (gauge 02315500). However, the floodplain typically remains inundated for long periods after the river crests.

Our LR site is situated in the Middle River Calcareous Reach and exhibits several changes related to greater flows and a larger drainage area. The channel has deeper pools and is wider (up to 100 m). Several major artesian springs are present, and the floodplain is broad and mainly consists of bottomland hardwood plant communities. The floodplain in the LR site is inundated more frequently, and the site reaches flood stage when water levels are > 7.6 m above mean sea level, the flood level for the USGS river gage at Branford (Gage 02320500). Water levels in the Suwannee River are dynamic in nature, so there is no 'normal' river level. Therefore, we considered 2 different river states in both sites, flooded (i.e., inundated floodplain) and unflooded (i.e., no standing water in the floodplain).

Turtle Captures. — At each site, we captured M. suwanniensis with large hoop-net traps (122-cm diameter with 6.4-cm mesh) baited with fresh fish. We set traps with the funnel opening facing downstream, parallel to the current, in the late afternoon and checked traps the next morning. We collected the following data on each captured M. suwanniensis: straight midline carapace length (CL), precloacal tail length (PTL), mass, and sex-age class. Straight-line measurements were taken to the nearest 1 mm with either 40-cm or 95-cm aluminum tree calipers (Haglöf, Sweden). Mass was taken with a 10-kg, 20-kg (Pesola, Switzerland), or 100-kg (Rubbermaid Pelouze, Saratoga Springs, NY, USA) spring scale. We determined sex by CL and PTL measurements (see Dobie 1971). We individually marked each turtle by implanting a passive integrated transponder tag in the ventrolateral tail muscle (Trauth et al. 1998) and by drilling holes in posterior marginal scutes using a numbering system (Cagle 1939).

Acoustic Telemetry. — We attached acoustic telemetry tags (CT-05-48-E; CT-82-2-E; Sonotronics, Tucson, AZ, USA) to 20 *M. suwanniensis* to investigate home range size and habitat selection in the Suwannee River. We equipped 9 adult males and 2 adult females in the LR

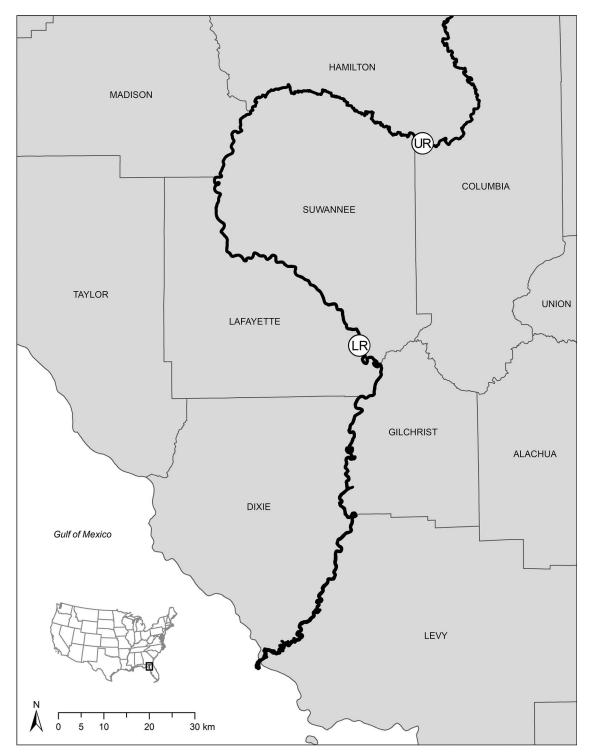


Figure 1. Map of study area showing the upper river (UR) site and lower river (LR) site in the Suwannee River in Florida.

site and 4 adult males, 3 adult females, and 2 juveniles in the UR site. We attached transmitters on the posterior carapace marginals by threading cable ties through drilled holes and securing them to the carapace with marine epoxy (PC marine; PC Products, PA, USA). All attached transmitters were <5% body mass, and tagged individuals were released at their capture site. From December 2012 through December 2013, we attempted to locate turtles weekly during the day at each site for  $\sim 1$  yr. In

addition, we located turtles at night at least once per month throughout the year. Inclement weather prevented field activities on several occasions. We located turtles with a digital ultrasonic receiver (USR-08; Sonotronics) by trolling a towable hydrophone (TH-2; Sonotronics) until a signal could be detected. Then, we used a directional hydrophone (DH-4; Sonotronics) to determine the turtles' exact location. Turtle locations were marked using a handheld global positioning system unit (Garmin [Olathe,

KS, USA] GPSMAP 64st,  $\pm$  3.6-m error). At each turtle location, we determined the microhabitat used (i.e., no structure, subsurface rock, undercut bank, large woody debris [LWD], or undetermined), and we recorded the following habitat measurements for each location: water depth (m) of turtle with a handheld portable depth finder (Hawkeye [Stuart, FL, USA] Digital Sonar PX), percent canopy cover with a densiometer (Geographic Resource Solutions, Arcata, CA, USA), and distance (m) to nearest bank with a laser range finder (Leupold RX1000i; Leupold & Stevens Inc., Beaverton, OR, USA). We used side-scan sonar (Humminbird 998c Side Imaging system; Johnson Outdoors, WI, USA) to help identify subsurface structure when water clarity was poor. We used ArcGIS 10 (ESRI, Redlands, CA, USA) to generate a series of random locations at each site to represent habitat availability, and we subsequently collected the above habitat measurements for a random location after locating each turtle.

Home Range. — We estimated home range size using FishTracker (Laffan and Taylor 2013), an ArcGIS toolbox for calculating kernel density estimators (KDE) of animal home ranges in habitats with hard boundaries. The FishTracker method incorporates a raster-based cost surface to define boundaries to animal movement. In the case of a dynamic river system like the Suwannee River, habitat availability varies with river stage. To account for fluctuating river levels, we created 4 cost levels specific to the Suwannee River: 1 = river channel, 3 = floodplain wetlands within maximum river stage, 5 = maximum riverstage, and 10 = above maximum river stage. We created maximum river stage extent by first adjusting the 2013 maximum river stage reading from the nearest USGS gaging station to the center of each study site by accounting for river slope. We used a 5-m digital elevation model (FWC 2009) to reclassify areas as either above or below the maximum river stage at each site. Areas within the maximum river stage that contained wetland habitats (e.g., cypress) were identified from a landcover map (FWC 2014). Random noise (±5%) was added to the cost surface to allow smoother paths in the sinuous river channel. We calculated home range size using KDE, and we used the mean daily movement distance at each site (UR = 180 m, LR = 420 m) as the bandwidth (search radius). We used 2 masks in the KDE process that represented the river channel and the floodplain wetlands accessible at maximum river stage. We then summarized a KDE for each turtle with 90th, 50th, and 25th percentiles. The 90th percentile represented an estimate of total area used, the 50th percentile represented median use, and the 25th percentile represented core use areas.

We used Generalized Linear Models (GLMs) to investigate home range size, and we fit several linear regression model sets to examine potential differences in the 90th percentile KDE between sites, sex-age class, or body size (CL) in the river during unflooded and flooded periods. We fit a set of 7 models for each response variable. These model sets represented all combinations of

the effects of site, sex-age class, and CL additively on the response variable. For each model set, we used model selection to determine which combination of predictor variables was most plausible (Burnham and Anderson 2002) by calculating Akaike's Information Criterion (AIC; Akaike 1973) with a small sample size adjustment (AIC<sub>c</sub>; Hurvich and Tsai 1989) and relative Akaike weights (Burnham and Anderson 2002). We considered all models with relative Akaike weights greater than 1/10th the weight of the top model to have notable plausibility.

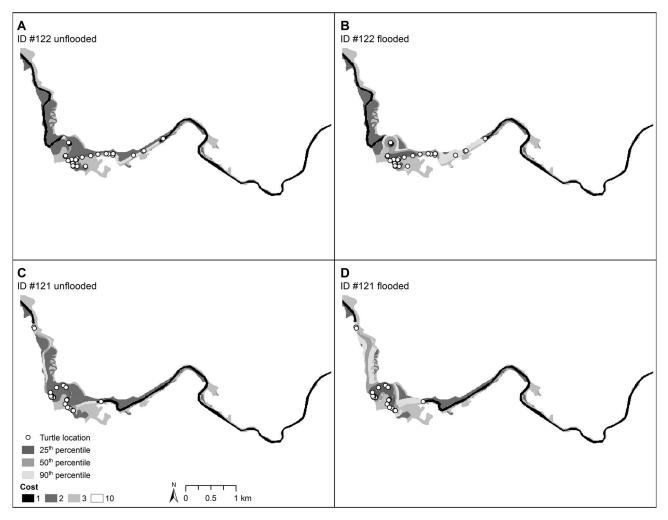
Habitat Selection. — We used GLMs (family =binomial) to determine which variables influenced M. suwanniensis habitat selection. We classified data as a binary variable where turtle locations were coded as 1 and random locations were coded as 0. This approach allowed us to estimate the probability of a turtle being found at a location and the associated habitat conditions there relative to the habitat conditions at random locations. We modeled the probability of M. suwanniensis location as a function of season, microhabitat, water depth, canopy cover, and distance from the riverbank. We scaled all continuous predictor variables to a mean of 0 and standard deviation of 1 (i.e.,  $[x_i - mean(x)/SD(x)]$ ), which allowed us to directly compare the magnitude of their effects.

We used an information-theoretic approach to determine the combination of predictor variables that made the observed data most plausible (Burnham and Anderson 2002). We used AIC with AIC<sub>c</sub> and relative Akaike weights to determine the relative plausibility of each model. We considered all models with relative Akaike weights greater than 1/10th the weight of the top model to have notable plausibility. We were primarily interested in microhabitat type, so we included its effect in all models. The candidate set of models represented all combinations of the remaining predictor variables as well as the interaction between microhabitat and site. All parameter estimates or test statistics were considered significant if their confidence intervals did not contain zero, and all statistical analyses were performed in Program R (version 4.0.3; R Core Team 2020).

#### **RESULTS**

In 2012–2013, we collected 372 locations for 8 M. suwanniensis in the UR site and 427 locations for 8 M. suwanniensis in the LR site. We failed to locate 1 turtle after 6 locations in the UR site and 2 turtles soon after release (< 12 locations) in the LR site. One large male M. suwanniensis was found dead  $\sim$  1 mo after tagging in the LR site. We did not include lost and deceased individuals in analyses.

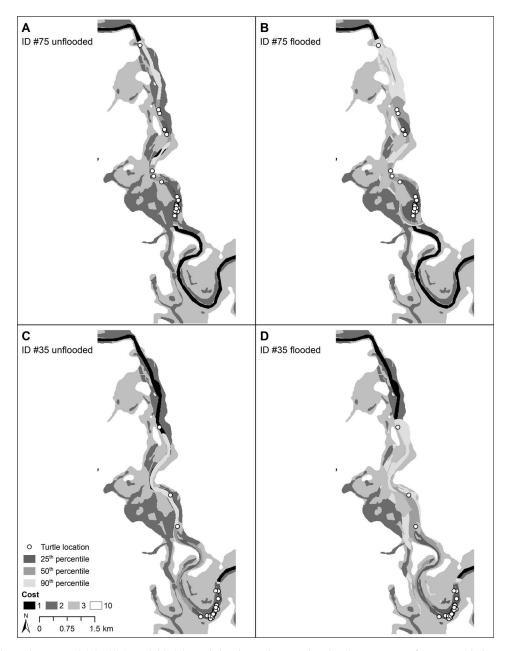
Home range. — The results produced by FishTracker GIS toolbox accounted for flooded river conditions and lateral turtle movements into the floodplain (Figs. 2 and 3). Interestingly, one of our largest adult males (ID # 22;



**Figure 2.** FishTracker mean 25%, 50%, and 90% kernel density estimates showing home ranges for Macrochelys suwanniensis ID #122 (A and B) and ID #121 (C and D) in both unflooded and flooded river states in our upper river site in the Suwannee River, Florida, 2012–2013.

51.5 kg) in our LR site possessed the smallest home range size (90th percentile KDE) in both river states (17.7 ha unflooded; 54.1 ha flooded). Although males possessed larger mean home ranges than did females and juveniles during flooded and unflooded river states (Table 1), the most plausible model for both river states included only the effect of site (Table 2). The model that included the effects of site and CL carried notable relative Akaike weight, but the effect of CL on 90th percentile KDE was not significant for either river state (unflooded 95% CI, -0.05-0.1; flooded 95% CI, -0.06-0.29). The best supported model for both river states indicated that the 90th percentile KDE was smaller in the UR site than the LR site (unflooded mean estimate = -28.8; 95% CI, -43.14 to -14.53; flooded mean estimate = -82.8, 95% CI, -116.81 to -48.75). When river levels rose and water filled the floodplain, 15 of 18 telemetered M. suwanniensis moved from the river channel into the inundated floodplain. These floodplain areas remained inundated for long periods, but when water levels fell, aquatic connections to the river channel disappeared. Surprisingly, 3 males and 2 females continued moving between the river channel and floodplain, even when this required crossing land.

Habitat Selection. — The most parsimonious and best supported model for the probability of turtle location included the effects of canopy cover and water depth, along with the effect of microhabitat. However, 3 additional models carried notable relative Akaike weight (Table 3). All models carrying notable relative Akaike weight included the effect of water depth. The most plausible model was between 1.6 and 4.4 times more plausible than any other model carrying notable relative Akaike weight. Parameter estimates from the top model indicated significant effects of microhabitat structure and water depth (Table 4). Turtles were far less likely to be found in locations that lacked underwater structure (Table 4). The microhabitat type of large woody debris (LWD) had a strong effect on turtle location (Table 4). Undercut bank habitat also had a relatively large effect on turtle location, but there was a considerable amount uncertainty in this estimate (Table 4). Interestingly,



**Figure 3.** FishTracker mean 25%, 50%, and 90% kernel density estimates showing home ranges for Macrochelys suwanniensis ID #75 (A and B) and ID #35 (C and D) in both unflooded and flooded river states in our lower river site in the Suwannee River, Florida, 2012–2013.

water depth had a significant negative effect on the probability of M. suwanniensis location, indicating that turtles were less likely to be found in deeper water. The magnitude of the effect of water depth was much greater than the effect of canopy cover, which was not statistically significant (Table 4). The probability of a turtle using a location remained > 0.90 in water < 0.9 m deep and > 0.80 in water < 2.7 m deep. However, as water depth approached 5 m, the probability of a turtle being found in that location decreased to around 0.57 (Fig. 4). Overall, our results indicate that M. suwanniensis are more likely to use shallow water with cover than open water lacking structure.

#### DISCUSSION

Our study is the first to report on movements of *M. suwanniensis*, which used all available aquatic areas of the river, including springs (artesian), spring runs, and inundated floodplains. Interestingly, the *FishTracker* KDE accounted for lateral turtle movements in the floodplain. This method allowed us to calculate statistically robust KDEs for turtles that are linearly confined to river channels and their associated wetlands. Furthermore, the *FishTracker* method accounted for movements that are not incorporated in simple linear measurements of home range. Typically, estimates of LHR use the distance between the farthest

**Table 1.** Mean 25%, 50%, and 90% kernel density estimates (ha) produced by *FishTracker* for 9 male (M), 5 female (F), and 2 juvenile (J) *Macrochelys suwanniensis* by sex and site (upper river [UR] site and lower river [LR] site during unflooded and flooded river conditions in the Suwannee River, Florida, USA, 2012–2013. Estimates are presented as means ± standard error.

	Home range (unflooded)			Home range (flooded)			
	25%	50%	90%	25%	50%	90%	
Sex							
M	$9.4 \pm 2.1$	$18.9 \pm 4.3$	$34.1 \pm 7.8$	$25.1 \pm 5.6$	$50.3 \pm 11.3$	$90.5 \pm 20.3$	
F	$5.3 \pm 1.7$	$10.7 \pm 3.4$	$19.3 \pm 6.2$	$15.8 \pm 4.2$	$31.6 \pm 8.4$	$56.9 \pm 15.2$	
J	$4.3 \pm 1.1$	$8.7 \pm 2.3$	$15.5 \pm 4.0$	$5.3 \pm 2.1$	$10.7 \pm 4.3$	$19.2 \pm 7.7$	
Site							
UR	$3.5 \pm 0.3$	$7.1 \pm 0.7$	$12.7 \pm 1.3$	$8.2 \pm 1.3$	$16.5 \pm 2.6$	$29.7 \pm 4.6$	
LR	$11.5 \pm 1.9$	$23 \pm 3.9$	$41.6 \pm 7.1$	$31.2 \pm 4.6$	$62.6 \pm 9.3$	$112.5 \pm 16.7$	

upstream and downstream localities and do not include more nuanced movements. Most (15 of 18) of our tagged *M. suwanniensis* made movements outside of the river channel that would not have been included in estimates of LHR using other home range analytical approaches. Therefore, the application of the *FishTracker* GIS toolbox could prove useful for estimating freshwater turtle home ranges in dynamic riverine environments and in confined linear river systems where turtles may move between the river channel and floodplain wetlands.

In the Suwannee River, approximately 83% of telemetered *M. suwanniensis* moved into floodplains once they became inundated. Floodplain areas may be important to *M. suwanniensis* because they provide access to resources that are unavailable or scarce in the river channel, and prey items such as crayfish, amphibians, mammals, and mast are widely available in these areas (Mount 1975; Ernst et al. 1994; Sloan et al. 1996; Elsey 2006). Surprisingly, 5 adult turtles repeatedly moved between the floodplain and the river channel, making overland movements when these habitats were no longer connected

**Table 2.** Model selection results for Generalized Linear Models (GLM) for 90th percentile kernel density estimates (KDE) for *Macrochelys suwanniensis* during unflooded and flooded river states in the Suwannee River, Florida, USA, 2013–2014. The table has the included effects (CL = carapace length), difference (delta) in Akaike's Information Criterion (corrected for small sample size;  $AIC_c$ ) between the current model and the top model (ΔAIC<sub>c</sub>), and relative Akaike weights (ω<sub>i</sub>).

Model	$\Delta AIC_c$	$\omega_i$
KDE unflooded		
Site	0	0.74
Site + CL	3.08	0.16
CL	4.85	0.07
Site + Sex	6.98	0.02
Site + Sex + CL	10.95	0
Sex	12.81	0
KDE flooded		
Site	0	0.65
Site + CL	1.78	0.27
CL	4.75	0.06
Site + Sex	7.19	0.02
Sex + CL	8.99	0.01
Site + Sex + CL	10.67	0
Sex	15.07	0

by water. Our study is the first telemetry study to document (infer) overland movements by *Macrochelys*, although individuals other than nesting females have occasionally been observed on land (Ewert et al. 2006; Enge et al. 2021a). However, our study inferred overland movements made by 2 large males (> 50 kg), which suggests that these movements may be less rare than previously thought.

Our analyses indicated differences in home range size (90th percentile KDE) between the upper river (UR) and lower river (LR) sites. This finding supported our hypothesis that M. suwanniensis in the LR site would have larger home ranges. This is likely because the FishTracker KDEs accounted for site-specific complexities at the landscape level. For example, the LR site possesses a much wider channel and a more extensive floodplain, and turtles in the LR site took advantage of these areas. Turtles also used floodplains in the UR site, but the river channel and associated floodplains are much smaller there. Thus, the differences in home range size could potentially be explained by different habitat availability between our two sites. Our home range results are difficult to compare directly to other studies using estimates of LHR, which varied widely among sex, location, and age groups. For example, Harrel et al. (1996) found that the mean LHR of juvenile male M. temminckii (3.5 km) was larger than that of juvenile females (1.4 km) in a slow-flowing bayou in Louisiana. In contrast, Munscher et al. (2021) found that adult female M. temminckii averaged longer movements and larger LHRs than males in an urban bayou in Texas.

**Table 3.** Model selection results of the probability of *Macrochelys suwanniensis* locations including the effects (DFB = distance from bank), the number of parameters (K), difference (delta) in Akaike's Information Criterion (corrected for small sample size; AIC<sub>c</sub>) between the current model and the top model ( $\Delta$ AIC<sub>c</sub>), and relative Akaike weights ( $\omega_i$ ). Only models carrying notable Akaike weight are shown, and all models included the effects of site and microhabitat.

0.40
0.25
0.15
0.09
(

Table 4. Parameter estimates from the most parsimonious and most plausible model of probability of <i>Macrochelys suwanniensis</i>
location and habitat, including the mean parameter estimate, the standard error (SE), lower and upper 95% confidence intervals (LCI
and UCI), the z-score, and the $p$ -value. UR is upper river site.

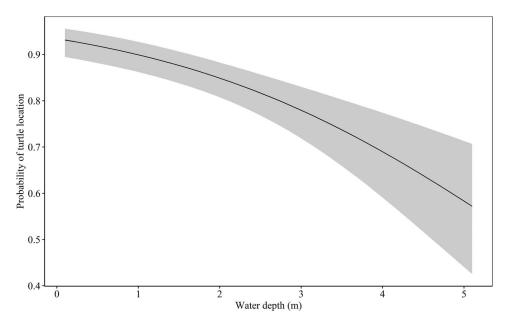
Parameter	Estimate	SE	LCI	UCI	z-value	<i>p</i> -value
Intercept (UR site, large woody debris)	1.03	0.19	0.66	1.41	5.48	< 0.001
Canopy	0.17	0.10	-0.03	0.37	1.71	0.088
Depth	-1.06	0.20	-1.46	-0.66	-5.17	< 0.001
No structure	-4.38	0.30	-4.96	-3.79	-14.69	< 0.001
Subsurface rock	-0.49	0.46	-1.39	0.41	-1.07	0.287
Undetermined	-0.33	0.39	-1.10	0.43	-0.86	0.392
Undercut bank	0.94	0.62	-0.28	2.17	1.51	0.130

Riedle et al. (2006) found that female *M. temminckii* in small Oklahoma streams tended to have larger LHRs than did males, whereas Shipman and Riedle (2008) found no differences in mean LHRs (1.8 km) between sexes in a Missouri stream. We failed to find differences in 90th percentile KDE among sex or age groups, but our sample size was small for female and juvenile turtles.

Our study was the first to examine *M. suwanniensis* habitat selection and found support for some of our hypotheses. For example, we found that *M. suwanniensis* selects habitats with underwater structure, similar to *M. temminckii* (Harrel et al. 1996; Riedle et al. 2006; Howey and Dinkelacker 2009; Munscher et al. 2021). Large woody debris (LWD) had a strong effect on turtle location and is likely an important resource for *M. suwanniensis*. Instream LWD is especially important during low water levels when bank-associated habitats are unavailable. Our results also suggest that undercut banks could be an important habitat type; however, there was a lot of uncertainty around this estimate. This uncertainty could be due to the reduced probability of a randomly selected and measured point falling directly on an undercut bank.

In fact, only 3 of our randomly selected points included undercut bank as the microhabitat type. Overall, our findings support the notion that M. suwanniensis are cryptic and secretive animals that may feel safer in and around cover. Canopy cover has been identified as an important factor in M. temminckii habitat selection, with turtles preferring denser canopy cover (Riedle et al. 2006; Howey and Dinkelacker 2009; Munscher et al. 2021). Interestingly, we found little evidence that canopy cover significantly affected habitat selection, likely because the dark-colored, tanninstained water in the Suwannee River makes overhead cover superfluous. Surprisingly, we found that M. suwanniensis occasionally uses clear-water artesian springs and spring runs, but turtles in these habitats remained completely hidden from sight under undercut banks. Unaltered floodplain springs could provide important refuges for M. suwanniensis along the Suwannee River, but more research is needed.

We found that *M. suwanniensis* selected shallower depths when sedentary, possibly because these selected microhabitats (e.g., LWD, undercut banks) were more likely to be located near riverbanks. Also, shallower depths could be preferred for ease in breathing. Some



**Figure 4.** The predicted probability of *Macrochelys suwanniensis* location as a function of water depth (m) in the Suwannee River, Florida, 2012–2013. The black line indicates the mean prediction and the gray region indicates 95% confidence intervals.

telemetry studies have found *M. temminckii* associated with deeper pools (Lescher et al. 2013; Moore et al. 2014). In Oklahoma, Riedle et al. (2006) found that turtles selected deeper depths in midwinter than in early summer, possibly for thermoregulation, but Moore et al. (2014) found no selection for water temperature, which varied little among sites. In an oxbow lake in Texas, *M. temminckii* selected a narrow range of microhabitats that were significantly warmer and less variable in temperature than were random sites (Fitzgerald and Nelson 2011). *Macrochelys suwanniensis* were active (made movements) year-round in the Suwannee River, possibly because the more southerly latitude and the input of warm artesian spring water resulted in greater thermal stability.

Rivers can be dynamic systems, and as water levels fluctuate, habitat availability potentially changes. In the Suwannee River, water levels can rise and fall rapidly, possibly affecting the availability of habitats highly selected by M. suwanniensis. During low water levels, important habitats such as undercut banks and LWD associated with banks are less available, possibly making instream submerged LWD extremely important. This is a conservation concern because instream LWD is sometimes removed from the Suwannee River. The State of Florida initiated a program in 2000 that resulted in the removal of > 16,000 deadhead logs (submerged pine and cypress timber) from state waters in 8 yrs, but this is likely a conservative estimate (Kaeser and Litts 2008). The removal of LWD from the Suwannee River could negatively affect this state Threatened species. Although minimum flows have been established in the drainage, water levels have decreased an estimated 40% in the Suwannee River since human settlement (Knight and Clarke 2014). The Suwannee watershed is relatively undeveloped, but high rates of groundwater withdrawals in adjacent more developed areas in Florida (Knight and Clarke 2014) could negatively affect this imperiled species.

#### ACKNOWLEDGMENTS

The Florida Fish and Wildlife Conservation Commission (FWC) is responsible for the management of the State of Florida's wildlife. No specific permission was required for conducting research because the research was conducted by the permitting agency. However, all animals were handled with great care, and we followed the proper guidelines from the Herpetological Animal Care and Use Committee of the American Society of Ichthyologists and Herpetologists. We thank M. Ruccolo for assisting with telemetry, A. Kaeser for assisting with side-scan sonar, and R. Butryn for assisting with analyses. We thank D. Steen and F. Bled for providing helpful comments on a previous version of this manuscript. The team at Sonotronics, specifically M. Gregor, provided equipment and technical support. The Wildlife Research Section of FWC's Fish and Wildlife Research Institute

supplied funds from the Nongame Wildlife Trust Fund to conduct this study.

#### LITERATURE CITED

- AKAIKE, H. 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov, B.N. and Csaki, F. (Eds.). 2nd International Symposium on Information Theory. Budapest: Akademia Kiado, pp. 267–281.
- Bermingham, E. and Avise, J.C. 1986. Molecular zoogeography of freshwater fishes in the southeastern United States. Genetics 113:939–965.
- Burnham, K.P. and Anderson, D.R. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Second edition. New York: Springer-Verlag, 488 pp.
- Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346–352.
- CAGLE, F.R. 1939. A system of marking turtles for future identification. Copeia 1939:170–173.
- Calhoun, J.B. and Casby, J.U. 1958. Calculation of Home Range and Density of Small Mammals. Public Health Monograph No. 55. Washington, DC: US Department of Health, Education, and Welfare, 24 pp.
- CERYAK, R., KNAPP, M.S., AND BURNSON, T. 1983. The geology and water resources of the Upper Suwannee River Basin, Florida. Tallahassee: Bureau of Geology, Division of Resource Management, Florida Department of Natural Resources and Suwannee River Water Management District, 165 pp.
- DIXON, K.R. AND CHAPMAN, J.A. 1980. Harmonic mean measure of animal activity areas. Ecology 61:1040–1044.
- Dobie, J.L. 1971. Reproduction and growth in the alligator snapping turtle, *Macroclemys temmincki* (Troost). Copeia 1971:645–658.
- ELSEY, R.M. 2006. Food habits of *Macrochelys temminckii* (alligator snapping turtle) from Arkansas and Louisiana. Southeastern Naturalist 5:443–452.
- ENGE, K.M., SMITH, B.S., TALLEY, B.L., CANNON, T., THOMAS, T.M., AND CATIZONE, D. 2021a. Coastal observations of alligator snapping turtles in the Florida panhandle. Florida Field Naturalist 49:138–147.
- ENGE, K.M., THOMAS, T.M., JOHNSTON, G.R., STEVENSON, D.J., JENSEN, J.B., STEGENGA, B.S., CHANDLER, H.C., AND MOLER, P.E. 2021b. Distribution and relative abundance of the Suwannee alligator snapping turtle (*Macrochelys suwanniensis*). Chelonian Conservation and Biology 20:184–199.
- Ernst, C.H., Barbour, R.W., and Lovich, J.E. 1994. Turtles of the United States and Canada. Second edition. Washington, D.C.: Smithsonian Institution Press, 682 pp.
- EWERT, M.A., JACKSON, D.R., AND MOLER, P.E. 2006. *Macrochelys temminckii*—alligator snapping turtle. In: Meylan, P.A. (Ed.). Biology and Conservation of Florida Turtles. Chelonian Research Monographs 3:58–71.
- Fitzgerald, L.A. and Nelson, R.E. 2011. Thermal biology and temperature-based habitat selection in a large aquatic ectotherm, the alligator snapping turtle, *Macroclemys temminckii*. Journal of Thermal Biology 36:160–166.
- FLORIDA FISH AND WILDLIFE CONSERVATION COMMISSION (FWC). 2009. Florida Statewide 5-Meter DEM. https://www.arcgis.com/home/item.html?id=4d2faae736ff4738a1e60ecb3efd637d (15 May 2021).
- FLORIDA FISH AND WILDLIFE CONSERVATION COMMISSION (FWC). 2014. Florida Cooperative Land Cover Map Version 3. https://myfwc.com/research/gis/wildlife/cooperative-land-cover/ (15 May 2021).

- Getz, W.M., Fortmann-Roe, S, Cross, P.C., Lyons, A.J., Ryan, S.J., and Wilmers, C.C. 2007. LoCoH: nonparametric kernel methods for constructing home ranges and utilization distributions. PloS One 2(2):p.e207.
- HARREL, J., ALLEN, C., AND HEBERT, S. 1996. Movements and habitat use of subadult alligator snapping turtles (*Macro-clemys temminckii*) in Louisiana. American Midland Naturalist 135:60–67.
- HORNSBY, D., MATTSON, R.A., AND MIRTI, T. 2000. Surface water quality and biological monitoring. Annual Report 1999. Live Oak, FL: Suwannee River Water Management District Technical Report WR-00-04, 148 pp.
- Howey, C.A.F. and Dinkelacker, S.A. 2009. Habitat selection of the alligator snapping turtle (*Macrochelys temminckii*) in Arkansas. Journal of Herpetology 43:589–596.
- Hurvich, C.M. and Tsai, C. 1989. Regression and time series model selection in small samples. Biometrika 76:297–307.
- KAESER, A.J. AND LITTS, T.L. 2008. An assessment of deadhead logs and large woody debris using side scan sonar and field surveys in streams of southwest Georgia. Fisheries 33: 589–597.
- KAY, W.R. 2004. Movements and home ranges of radio-tracked Crocodylus porosus in the Cambridge Gulf region of Western Australia. Wildlife Research 31:495–508.
- KENWARD, R.E., CLARKE, R.T., HODDER, K.H., AND WALLS, S.S. 2001. Density and linkage estimators of home range: nearest-neighbor clustering defines multinuclear cores. Ecology 82:1905–1920.
- KNIGHT, R.L. AND CLARKE, R.A. 2014. Florida springs—a waterbudget approach to estimating water availability. Journal of Earth Science and Engineering 6:59–72.
- Laffan, S.W. and Taylor, M.D. 2013. FishTracker: a GIS toolbox for kernel density estimation of animal home ranges that accounts for transit times and hard boundaries. In: Piantadosi, J. and Boland, J. (Eds.). 20th International Congress on Modelling and Simulation. Adelaide, Australia: Modelling & Simulation Society, pp. 1617–1623.
- Lescher, T.C., Tang-Martínez, Z., and Briggler, J.T. 2013. Habitat use by the alligator snapping turtle (*Macrochelys temminckii*) and eastern snapping turtle (*Chelydra serpentina*) in southeastern Missouri. American Midland Naturalist 169:86–96.
- Major, R.E. and Gowing, G. 2001. Survival of red-capped robins (*Petroica goodenovii*) in woodland remnants of central western New South Wales, Australia. Wildlife Research 28:565–571.
- Moore, D.B., Ligon, D.B., Fillmore, B.M., and Fox, S.F. 2014. Spatial use and selection of habitat in a reintroduced population of alligator snapping turtles (*Macrochelys temminckii*). Southwestern Naturalist 59:30–37.
- Morris, D.W. 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia 136:1–13.
- Morrison, M.L., Marcot, B.G., and Mannan, R.W. 1998. Wild-life–Habitat Relationships Concepts and Applications. Second edition. Madison: University of Wisconsin Press, 435 pp.
- MOUNT, R.H. 1975. The Reptiles and Amphibians of Alabama. Auburn: Alabama Agricultural Experiment Station, 345 pp.
- Munscher, E., Gladkaya, V., Stein, J., Butterfield, B.P., Adams, R., Gray, J., Tuggle, A., Weber, A.S., Norrid, K., and Walde, A. 2021. Movements of western alligator snapping turtles, *Macrochelys temminckii* (Testudines, Chelydridae), in an urban ecosystem: Buffalo Bayou, Houston, Texas. Herpetology Notes 14:985–994.

- NEILL, W.T. 1957. Historical biogeography of present-day Florida. Bulletin of the Florida State Museum, Biological Sciences 2:175–220.
- NILSEN, E.B., PEDERSEN, S., AND LINNELL, J.D.C. 2008. Can minimum convex polygon home ranges be used to draw biologically meaningful conclusions? Ecological Research 23:635–639.
- PRITCHARD, P.C.H. 2006. The Alligator Snapping Turtle: Biology and Conservation. Second edition. Malabar, FL: Krieger, 140 pp.
- R CORE TEAM. 2020. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- REDPATH, S.M. 1995. Habitat fragmentation and the individual: tawny owls, *Strix aluco*, in woodland patches. Journal of Animal Ecology 64:652–661.
- RIEDLE, J.D., SHIPMAN, P.A., FOX, S.F., AND LESLIE, D.M. 2006. Microhabitat use, home range, and movements of the alligator snapping turtle, *Macrochelys temminckii*, in Oklahoma. Southwestern Naturalist 51:35–40.
- Shipman, P.A., Edds, D.R., and Shipman, L.E. 1995. Distribution of the alligator snapping turtle (*Macroclemys temminckii*) in Kansas. Transactions of the Kansas Academy of Science 1903:83–91.
- SHIPMAN, P.A. AND RIEDLE, J.D. 2008. Status and distribution of the alligator snapping turtle (*Macrochelys temminckii*) in southeastern Missouri. Southeastern Naturalist 7:331–338.
- SLOAN, K.N., BUHLMANN, K.A., AND LOVICH, J.E. 1996. Stomach contents of commercially harvested adult alligator snapping turtles, *Macroclemys temminckii*. Chelonian Conservation and Biology 2:96–99.
- SLOAN, K.N. AND TAYLOR, D. 1987. Habitats and movements of adult alligator snapping turtles in northeast Louisiana. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 41:343–348.
- TAYLOR, J. 1997. An Introduction to Error Analysis: The Study of Uncertainties in Physical Measurements. Second edition. Sausalito, CA: University Science Books, 343 pp.
- Thomas, T.M., Granatosky, M.C., Bourque, J.R., Krysko, K.L., Moler, P.E., Gamble, T., Suarez, E., Leone, E., Enge, K.M., and Roman, J. 2014. Taxonomic assessment of alligator snapping turtles (Chelydridae: *Macrochelys*), with the description of two new species from the southeastern United States. Zootaxa 3768(2):141–165.
- Thomas, T.M., Enge, K.M., Suarez, E., and Johnston, G. R. 2022. Population Status of the Suwannee Alligator Snapping Turtle (Macrochelys Suwanniensis) in the Suwannee River, Florida. Chelonian Conservation and Biology 21:2–10.
- Trauth, S.E., Wilhilde, J.D., and Holt, A. 1998. Population structure and movement patterns of alligator snapping turtles (*Macroclemys temminckii*) in northeastern Arkansas. Chelonian Conservation and Biology 3:64–70.
- US FISH AND WILDLIFE SERVICE. 2021. Endangered and threatened wildlife and plants; 12-month petition finding and threatened species status with Section 4(d) rule for Suwannee Alligator Snapping Turtle. Federal Register 86:10814–18034.

Received: 9 March 2023

Revised and Accepted: 18 May 2023 Published Online: 17 January 2024 Handling Editor: Jeffrey A. Seminoff