

## Solving the Enigma of an Extralimital Suwannee Alligator Snapping Turtle (*Macrochelys suwanniensis*) Population in the Homosassa River, Florida

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**Abstract** - We conducted a study to determine the origin and provenance of *Macrochelys* sp. (alligator snapping turtles) in the Homosassa River >70 km from the nearest known population. In 2023–2024, we captured 14 males and 4 females in Pepper Creek, a Homosassa tributary. Genetic analyses of 16 turtles determined they were *M. suwanniensis* (Suwannee Alligator Snapping Turtle) that originated from near the confluence of the Santa Fe and Suwannee rivers, and they were parent–offspring or siblings. The population apparently resulted from 4 turtles escaping from a tourist attraction >40 years ago. Based on our capture–recapture model, there are ~33 (min–max = 22–55) individuals in Pepper Creek. Additional research is needed to better understand the health and conservation status of this population.

### Introduction

*Macrochelys* (alligator snapping turtles) are the largest freshwater turtles in North America and are endemic to Gulf of Mexico river basins of the southeastern US. Their natural populations historically occurred in 14 states, but they may now be entirely or functionally extinct in the wild in 4 states on the periphery of their range (Carr et al. 2023a). Past commercial harvest for meat decimated populations in some rivers and states (Carr et al. 2023a, Pritchard 1989). Florida prohibited sales in 1972, instituted a personal possession limit of 1 turtle in 1973, and prohibited all harvest in 2009 (Enge et al. 2021b). Alligator snapping turtles are popular as pets and exhibit animals because of their large size, interesting behavior, and prehistoric appearance. Thousands are produced annually in domestic turtle farms, and escaped or released specimens have been found outside their native range as far away as Italy, Spain, Korea, Japan, Taiwan, and Reunion Island (Carr et al. 2023a), with additional online reports from Ontario, the Czech Republic, Germany, Hungary, England, and South Africa. Two species are widely recognized, *M. temminckii* (Troost in Harlan) (Western Alligator Snapping Turtle) and *M. suwanniensis* (Thomas, Granatosky, Bourque, Krysko, Moler, Gamble, Suarez, Leone, Enge, and

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Roman (Suwannee Alligator Snapping Turtle). The 2 species can be distinguished both morphologically and genetically (Thomas et al. 2014). In Florida, the native range of the Suwannee Alligator Snapping Turtle is restricted to the Suwannee drainage, whereas the Western Alligator Snapping Turtle occurs from the Ochlockonee River west across the panhandle to the Perdido River (Enge et al. 2021b, 2023; Ewert et al. 2006). However, introduced turtles have been found in peninsular Florida in DeSoto, Duval, Hillsborough, Lake, Lee, Marion, Nassau, Orange, Pinellas, Polk, and Volusia counties (Enge et al. 2021b, 2025).

Outside the known range of alligator snapping turtles in southwestern Citrus County, FL, a turtle was filmed feeding on fish carcasses in 2020 along the Southeast Fork of the Homosassa River (K. Spratt, pers. observ.). Another turtle was photographed on 14 September 2021 with its claw stuck in the water-control structure (weir) on Pepper Creek (UF 201797; Fig. 1B), a dredged tributary in the Ellie Schiller Homosassa Springs Wildlife State Park (hereafter, the Park) owned by the Florida Department of Environmental Protection (FDEP). The carcass of a large turtle with a straight midline carapace length (CL) of 590 mm was salvaged from Pepper Creek on 15 September 2022 after being shot in the carapace (Fig. 1C). Examination of the skull and carapace suggested that this individual was a Suwannee Alligator Snapping Turtle (J. Bourque, Florida Museum of Natural History, Gainesville, FL, pers. comm.), which prompted further investigation because Western Alligator Snapping Turtles are typically bred on turtle farms for the pet trade and are thus more often found outside their native range than Suwannee Alligator Snapping Turtles (Enge et al. 2025). The Homosassa River discharges into the Gulf of Mexico ~70 km (straight-line distance) south of the Suwannee River, which is the closest river system with a naturally occurring population (Enge et al. 2021b). The proximity of these 2 rivers raised the possibility that this population might represent an undocumented, extralimital population of Suwannee Alligator Snapping Turtles, potentially originating from natural dispersal. Alternatively, due to the predominance of Western Alligator Snapping Turtles in the pet trade, it could represent a human-mediated introduction from released pets. Our objectives for this study were to (1) conduct capture–recapture surveys, (2) determine the species identity and possible source of the population, and (3) estimate population size. Ultimately, this research could help evaluate whether this occurrence reflected a natural assemblage or an introduced extralimital population resulting from anthropogenic releases.

### **Field-Site Description**

The Homosassa River is situated in the Crystal River Karst Plain Province, which is a narrow, low-elevation, coastal karst plain with abundant first- and second-magnitude springs that originate in a low marine escarpment along US Highway 19 and discharge to the Gulf as spring runs (Williams et al. 2022). The Homosassa River has multiple spring vents, including those in the Park's Main Spring Pool, a steep-sided basin measuring 27 m by 50 m with a maximum depth

of ~11 m (FDEP 2019). The Homosassa Springs Group is close to the coast and is considered an oligohaline (brackish) system that has alkaline, hard water with a relatively high chloride concentration (Nordlie 1990). The Southeast Fork tributary has at least 10 named spring vents that historically have always discharged fresh water, with very little influence from the high-chloride ground water (Jones et al. 2011, Yobbi 1992). The Southeast Fork merges with the Homosassa River ~300 m downstream of the Main Spring Pool (Fig. 2).

The headsprings were a popular train stop in the early 1900s, and a small tourist attraction was built there in the 1940s and expanded in 1964. The State of Florida acquired the wildlife park on 30 December 1988 to protect and preserve its first-magnitude spring, conserve habitat for endangered species, and provide



Figure 1. (A) Former Alligator Snapper pool along the Homosassa River, Citrus County, FL, in September 2024 (Photograph © K. Spratt). (B) A Suwannee Alligator Snapping Turtle with its claw stuck in the Pepper Creek weir on 14 September 2021 (Photograph © K. Spratt). (C) Shot turtle (590 mm CL) salvaged from Pepper Creek on 15 September 2022 (Photograph © K. Spratt). D. Trapped male (539 mm CL) on the bow of a pontoon boat on 13 April 2023 (Photograph © K.M. Enge).

exceptional public outdoor recreation opportunities to Florida residents and visitors (FDEP 2019). The Long River Bridge across the spring run near the western boundary of the Park has an underwater barrier of metal bars to prevent captive *Trichechus manatus latirostris* (Harlan) (Florida Manatee) undergoing rehabilitation from escaping during the summer. This barrier is removed in winter to allow entry of wild Florida Manatees and large fish into the Main Spring Pool (FDEP 2019). At least 47 freshwater or marine fish species occur in or near the headsprings, with marine species predominating in the winter and freshwater species predominating in the summer (SWFWMD 2017, Walsh and Williams 2003).

The upstream northern and eastern canals of the Pepper Creek drainage system are linear and were constructed prior to the 1950s, whereas the 1.4-km, winding section in the Park (Fig. 2) was dug in the 1960s and is lined with forested dredge-spoil piles (FDEP 2019). This channelized drainage system is ~4 km long and originates in urban areas of the town of Homosassa, which represents a major point source of stormwater pollution (FDEP 2019). Pepper Creek empties into the Southeast Fork ~150 m from its confluence with the Homosassa River (Fig. 2). The base flow of Pepper Creek is typically <0.14 m<sup>3</sup>/s but may be as high as 7.0 m<sup>3</sup>/s during large storm events (FDEP 2019). A weir system in the Park maintains sufficient depth for electric pontoon tour boats to operate on Pepper Creek, which is partially fed by small springs (FDEP 2019).

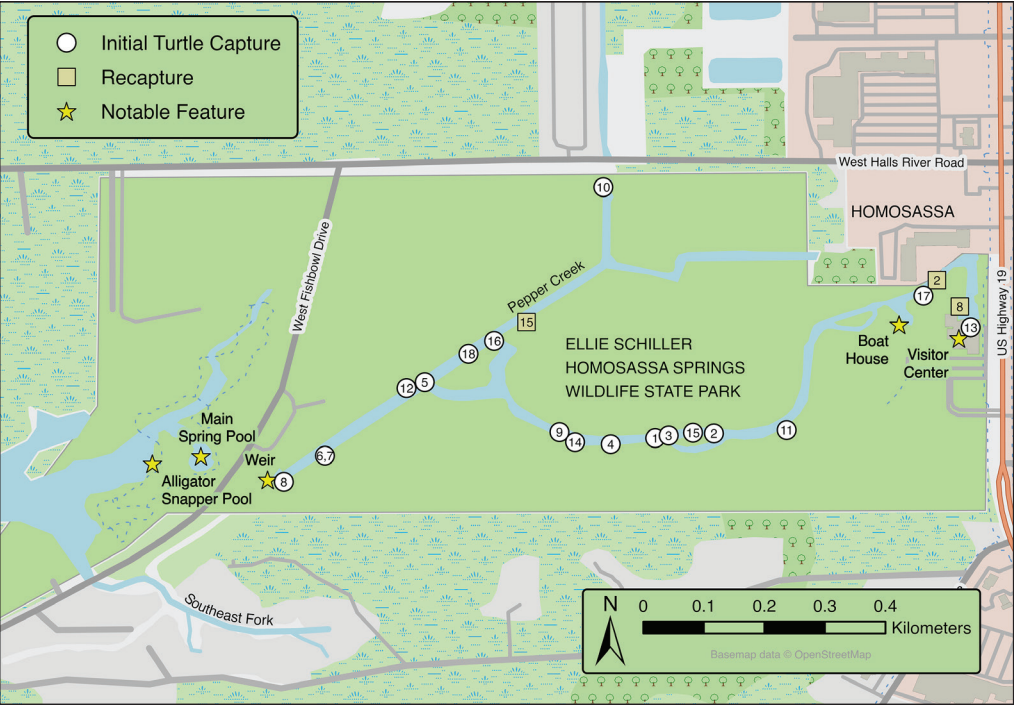


Figure 2. Map showing notable features in Ellie Schiller Homosassa Springs Wildlife State Park and captures (white circles) and recaptures (yellow squares) of 18 individual Suwannee Alligator Snapping Turtles in Pepper Creek, Citrus County, FL.

## Methods

### Turtle sampling

We captured turtles using large hoop-net traps (122-cm diameter with 6.4-cm mesh) with fingered throats baited with chunks of fresh fish and canned sardines. We set 14–16 traps in the 1.75-km section of Pepper Creek in the Park 3 times in 2023 and once in March 2024 for a total of 60 trap nights (Table 1). We also set 4 traps baited with fresh fish in the Southeast Fork of the Homosassa River in April 2023. We set traps in water <1.5 m deep in the late afternoon and checked them the following morning. We typically set traps with their openings facing downstream; however, because there was no discernable flow during low water levels when the creek was impounded by the weir, we sometimes set traps in other directions and successfully trapped turtles. While setting and checking traps on Pepper Creek, we opportunistically hand captured turtles observed from the boat.

On 27 June 2023, 9 people snorkeled the Southeast Fork and the nearby Homosassa River as far downstream as Mitten Cove looking for Alligator Snapping Turtles. On the same day, we set 12 traps in the linear upper reaches of Pepper Creek from 50 m east of US Highway 19 downstream to ~200 m south of West Halls River Road. We set a maximum of 4 traps in Pepper Creek north of West Halls River Road during the other 3 trapping sessions; however, as we did not capture any alligator snapping turtles there, we did not include these data when calculating catch per unit effort (CPUE; number of turtles captured per trap night) or population size.

We recorded the CL, head width, plastron length, precloacal tail length, tail length, and mass of captured turtles. We recorded length measurements to the nearest 1 mm using either a 40-cm or 95-cm aluminum tree caliper (Haglöf, Langsele, Sweden). We weighed turtles <20 kg to the nearest 10 g using 10-kg and 20-kg spring scales (Pesola, Baar, Switzerland) and turtles >20 kg to the nearest 0.5 kg with a 100-kg spring scale (Rubbermaid, Huntersville, NC). We considered individuals with a CL >330 mm and a PTL <115 mm to be adult females and individuals with a CL >370 mm and a PTL >115 mm to be adult males (Dobie 1971). We used a modified version of the Cagle (1939) method, where posterior marginal scutes were marked to give each turtle a unique number. We also inserted passive integrated transponder (PIT) tags (Biomark, Boise, ID) in the ventrolateral tail muscle (Trauth et al. 1998). All marking techniques are approved for turtles (Herpetological Animal Care and Use Committee 2004). We collected a small piece of tissue from the webbing of a hind foot for later genetic analyses to determine species identification and the river of origin (Apodaca et al. 2023).

### Genetic analyses

For genetic identification of turtles, we extracted DNA from webbing tissue clips of 18 Homosassa turtles using a Zymo QuickDNA Mini Prep Kit (Zymo Research, Irvine, CA) following manufacturer protocols. To directly combine our sequences with a previously established reference database (Apodaca et al. 2023), we precisely replicated the 3RAD library preparation methods of Apodaca et al.

(2023). Briefly, we digested the extracted DNA with restriction enzymes BamHI, ClaI, and MspI; dual-indexed each sample using unique internal adapters and Illumina-compatible primers; size-selected the digested fragments to 400–600 bp using a Pippin Prep (Sage Science, Beverly, MA); and sequenced the samples with a target depth of 5 million reads per individual on an Illumina NovaSeq Xplus system (San Diego, CA) with a 150-bp paired-end configuration. We assembled the raw reads following the same methods as Adams et al. (in press), using ipyrad v. 0.9.81 (Eaton and Overcast 2020) to assemble the sequences for Homosassa turtles with known, previously sequenced reference alligator snapping turtles from across their range. Like Adams et al. (in press), we used principal components analysis (PCA) and program Locator (Battey et al. 2020) to assign the Homosassa turtles to their point of origin. To determine whether the Homosassa turtles were related to each other, we calculated the kinship coefficient using the maximum likelihood estimator in SNPRelate (Zheng et al. 2012). Because the maximum likelihood estimator assumes a population of mostly unrelated individuals, we calculated kinship coefficients for all Suwannee Alligator Snapping Turtles, including all sequenced Homosassa turtles. Because estimates of relatedness can be biased by missing data, we only used biallelic SNPs present in at least 70% of individuals. To reduce the effects of linkage disequilibrium on our dataset, we restricted our dataset to 1 SNP per RAD locus using VCFtools (Danecek et al. 2011) and custom scripts (<[https://github.com/bmichanderson/RAD\\_scripts/blob/master/single\\_snp.py](https://github.com/bmichanderson/RAD_scripts/blob/master/single_snp.py)>).

### Population modeling

We used a Bayesian network approach (see Hobbs and Hooten 2025) to model Alligator Snapping Turtle abundance and detection probability. Our study site is isolated from other populations, and Alligator Snapping Turtles are long-lived with high annual survival rates, delayed sexual maturity, and limited ability to disperse over land (Thomas et al. 2023b, 2025). Based on these demographic and geographic considerations, we assumed population closure. Because the total population size ( $N_T$ ) remains unknown, we used a data-augmentation process, where observed encounter data are supplemented with all-zero capture histories by  $M$ , the maximum plausible number of individuals (Royle and Doazio 2012, Royle et al. 2007). We incorporated a hierarchical structure that included a latent state,  $z_i$ , to govern inclusion probability  $\psi$  using:

$$z_i | \psi \sim \text{Bernoulli}(\psi) \text{ for } i = 1, \dots, M,$$

where  $z_i = 1$  indicates that individual  $i$  is a member of the population. We derived total abundance using the following equation:

$$N = \sum_{i=1}^M Z_i,$$

where  $N$  is the sum of posteriors across all included individuals ( $z_i$ ) in the augmented captured history ( $M$ ). The data model was denoted as:

$$y_{i,t} | z_i, p \sim \text{Bernoulli}(z_i \cdot p) \text{ } i = 1, \dots, M; t = 1, \dots, T,$$

where the probability of detecting individual  $i$  during survey  $t$  is conditional on the latent state  $z$  for individual  $i$  for occasion  $t$  and per-occasion detection probability ( $p$ ). This formulation ensures that only individuals present ( $z_i = 1$ ) in the population are detected, while augmented individuals ( $z_i = 0$ ) contribute only to the structure of the encounter histories.

We assigned a moderately informative prior-to-capture probability,  $p \sim \text{Beta}(2.6, 19.4)$ , in part due to the cryptic nature of our study species along with low capture probabilities reported in previous studies (Enge et al. 2021b; Thomas et al. 2022, 2023b, 2025). This approach allowed us to place some prior mass on low detection probabilities (mean = 0.12), reflecting our expectation of lower per-occasion detection while allowing for substantial uncertainty. We specified a weakly informative prior-for-inclusion probability,  $\psi \sim \text{Beta}(2, 12)$ , to provide mild regularization without strongly influencing posterior estimates. We fit models and estimated posterior distributions using Markov chain Monte Carlo (MCMC) sampling implemented in JAGS (v. 4.3.1; Plummer 2025) using R (v. 4.5.0; R Core Team 2025) via the ‘R2jag’s package (v. 0.8.9; Su and Yajima 2024) running in RStudio (v. 2026.1.2.418; Posit Team 2026). We ran 3 parallel chains for 50,000 iterations each, following an initial adaptation phase and discarding the first 10,000 iterations of each chain as burn-in. We applied a thinning interval of 5, resulting in a total of 24,000 posterior samples across all chains. We assessed convergence using the rank-normalized split  $\hat{R}$  diagnostic (Vehtari et al. 2021) and by visually inspecting trace plots (Gelman and Hill 2007). We used the ‘MCMCvis’ package (v. 0.16.3; Youngflesh 2018) to summarize MCMC results, the ‘ggda’g (v. 0. 2.13; Barrett 2024) and ‘dagitty’ (v. 0.3.4; Textor et al. 2016) packages to build a directed acyclic graph (DAG), and the ‘tidyverse’ package (v. 2.0.0; Wickham et al. 2019) for plotting and data management.

Results

We captured 18 individual alligator snapping turtles during our 4 seasonal capture surveys in Pepper Creek from West Halls River Road downstream to the weir (Table 1). During our first trapping session on 12 April 2023, we held overnight a hand-captured 31-kg male and a 41-kg male caught in the first trap we had set 2

Table 1. Number of captures and recaptures of Suwannee Alligator Snapping Turtles in Pepper Creek, Citrus County, FL. The turtle trapped on the first date was removed from the trap soon after setting the trap and was held overnight. F = female, M = male.

| Date     | No. trap nights | No. trapped | No. hand captured | No. recaptures |
|----------|-----------------|-------------|-------------------|----------------|
| 4/12/23  |                 | 1 M         | 1 M               |                |
| 4/13/23  | 14              | 4 M, 2 F    | 1 M               |                |
| 6/27/23  |                 |             | 2 M               | 1 M            |
| 6/28/23  | 16              | 2 M         | 1 M               | 1 M            |
| 10/11/23 |                 |             | 1 M, 1F           |                |
| 10/12/23 | 14              | 3 M, 1 F    |                   | 2 M            |
| 3/15/24  | 16              | 2 M         |                   | 2 M            |

hours earlier. In subsequent trapping sessions, we released turtles at the boat house that were hand-captured while setting traps but did not count these individuals as recaptures if caught the following day (Table 1). Our sample consisted only of adults, and we did not encounter any juveniles. The 14 males measured 369–572 mm CL and weighed 11–41 kg, and the 4 females measured 381–466 mm CL and weighed 12–25 kg (Fig. 3). While setting traps on 12 April 2023, we saw a larger turtle likely weighing >45 kg (presumably the individual known to Park staff as “Bigfoot”) with a smaller turtle, presumably a female. The mean CPUE was 0.25, but turtles frequently escaped from traps, as evidenced by crushed sardine tins in empty traps. We also observed turtles unsuccessfully trying to enter traps. Two females radiographed on 13 April 2023 did not contain eggs.

We successfully sequenced 3RAD libraries for 16 of the 18 Homosassa turtles. The sequences for 2 individuals that returned fewer than 1 million reads were excluded from the assembly. We combined the sequences for these 16 turtles and 105 reference turtles. The final ipyrad assembly contained a total of 133,992 loci. As each analysis varies in its sensitivity to missing data, we filtered the SNPs

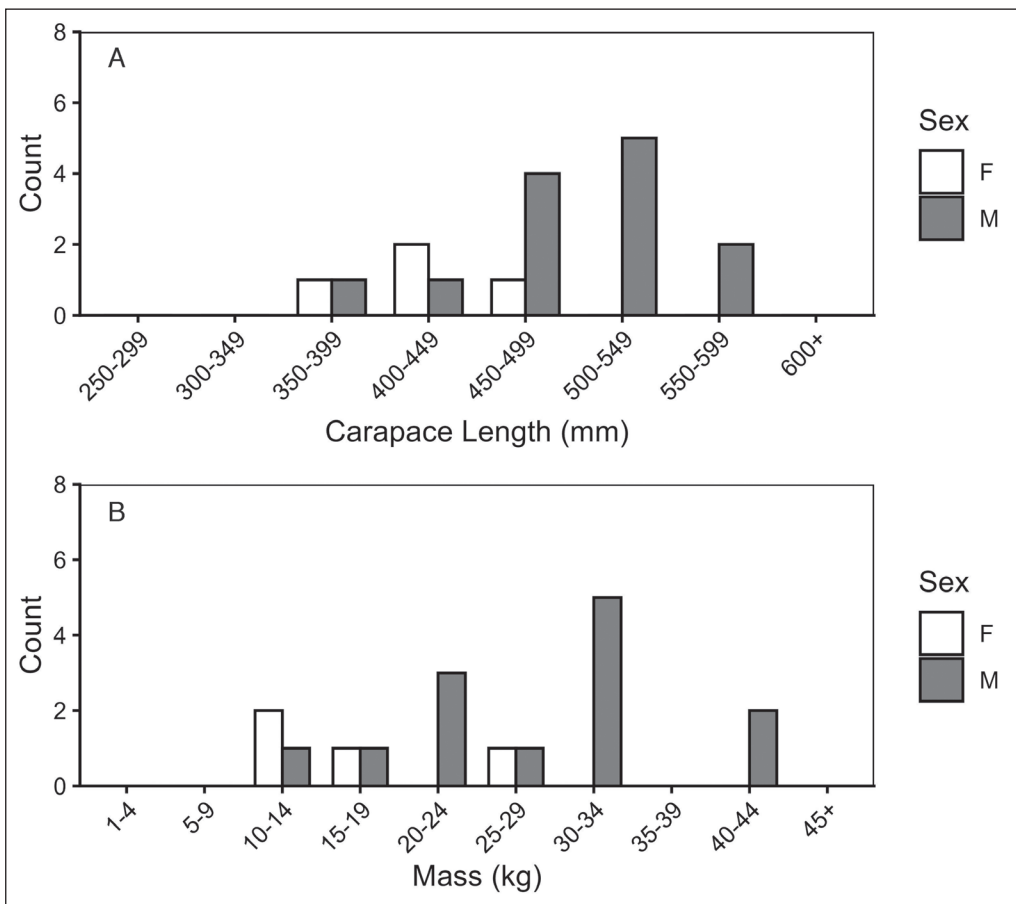


Figure 3. Bar plots for (A) carapace length and (B) mass for male and female Suwannee Alligator Snapping Turtles captured in 2023–2024 in Pepper Creek, Citrus County, FL.

depending on the analysis. The PCA of the genetic data included all 121 individuals and 24,153 SNPs. The PCA showed that the Homosassa turtles genetically resembled other Suwannee Alligator Snapping Turtles (Fig. 4A). For Locator analyses, we used a subset of 11,005 SNPs for the 119 turtles with precise locality information. Locator analyses consistently showed the Homosassa turtles originated either in the Suwannee River near its confluence with the Santa Fe River, in the lower Santa Fe River, or north in the Withlacoochee River tributary. Plotting all the bootstrapped location assignments for all 16 turtles showed a heatmap centered in the lower Santa Fe River near its junction with the Suwannee River (Fig. 4B), which is ~175 km by water from the mouth of the Homosassa River. We calculated kinship coefficients for all pairwise comparisons of Suwannee Alligator Snapping Turtles ( $n = 45$  turtles, 990 pairwise comparisons) using 5566 polymorphic SNPs. The kinship coefficient for every pairwise comparison of the Homosassa turtles was greater than 0.25, indicating that all 16 turtles analyzed were either parent–offspring or siblings.

Our Bayesian population model converged successfully and showed solid mixing across all parameters ( $R = 1.0$ ;  $ESS_{\text{bulk}} > 23,000$ ;  $ESS_{\text{tail}} > 22,000$ ). The model estimated the population consists of ~33 individuals (posterior median; SD: 8.21; 95% CRI: 22–35), which yields ~19 (min–max = 14–21) turtles/km for this part of Pepper Creek. The inclusion probability was estimated at  $\psi = 0.241$  (SD = 0.067; 95% CRI: 0.133–0.395), which revealed that the data-augmentation ceiling was

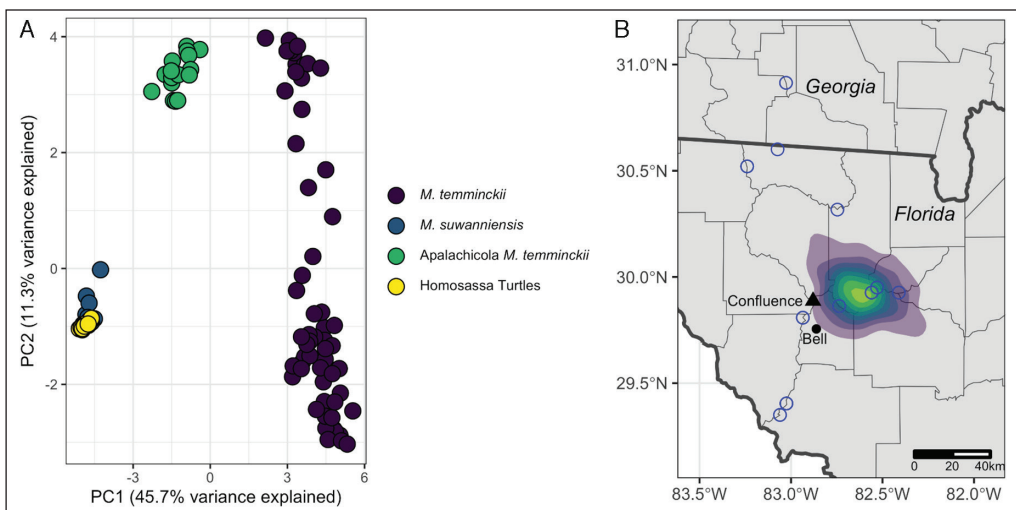


Figure 4. Principal component analysis and program Locator results for Suwannee Alligator Snapping Turtles captured in Pepper Creek, a tributary of the Homosassa River, Citrus County, FL. (A) Principal component analysis of 24,153 SNPs from 121 turtles, showing that Homosassa turtles cluster with Suwannee Alligator Snapping Turtles. (B) Heat map showing the assignments made by the program Locator for all 16 Homosassa turtles, with bluer and yellower colors indicating more locations assigned to those areas in 50 bootstrap runs for each turtle. Locator analysis indicates that turtles originated near the confluence (triangle) of the Santa Fe and Suwannee rivers near the town of Bell (circle). Blue unfilled circles are reference samples in the vicinity used in the Locator analysis.

sufficient, as the upper credible interval was not constrained. Our median detection probability was  $\sim 0.15$  (SD = 0.047; 0.081–0.271), which is consistent with lower capture rates reported here and in other studies.

## Discussion

The discovery of Alligator Snapping Turtles in the Homosassa River led to the question of whether this was a natural population that had gone undetected by scientists or an introduced population. Based on carapace and skull morphology, scutellation, and head coloration (Fig. 1D), we believed that the Homosassa River population consisted of the federally threatened (US Fish and Wildlife Service 2024) Suwannee Alligator Snapping Turtle, which we later confirmed genetically. Suwannee Alligator Snapping Turtles are apparently restricted to the Suwannee drainage (Enge et al. 2021b, Thomas et al. 2014), and the mouth of the Homosassa River empties into the Gulf  $\sim 70$  km southeast of the mouth of the Suwannee River. Western Alligator Snapping Turtles enter brackish or even salt water (Enge et al. 2021a, Ewert et al. 2006, Jackson and Ross 1971), suggesting the possibility of long-distance movements between river mouths. *Pseudemys concinna suwanniensis* Carr (Suwannee Cooter) also enters brackish water and occurs from the Ochlockonee River in the Florida panhandle south to the Alafia River in Hillsborough County (Heinrich et al. 2021), suggesting that Suwannee Alligator Snapping Turtles could also occur south of the Suwannee drainage. However, a turtle captured in the Alafia River near Mullberry, Polk County, in 1997 (UF 201848) appeared to be an introduced Western Alligator Snapping Turtle (Enge et al. 2025). Genetic analyses of 16 individuals from Pepper Creek showed that they likely originated from near the junction of the Santa Fe and Suwannee Rivers, far from the Homosassa River. Moreover, genetic evidence indicated that they were likely either parent–offspring or siblings, suggesting that they either originated from a founding event of related individuals or that only related individuals survived.

The 14.5-km Homosassa River and similar short, spring-fed streams in the area—Crystal, Chassahowitzka, and Weeki Wachee rivers—exhibit distinct salinity gradients between their headwater areas and outfalls into the Gulf (Champion and Starks 2001) and would appear to be unlikely candidates for natural, extralimital populations of Suwannee Alligator Snapping Turtles. Conversations with area residents yielded reports of large snapping turtles in these rivers and farther north in the Withlacoochee River (Marion County; not to be confused with the Withlacoochee tributary of the Suwannee River in Madison and Hamilton counties), but we had no photographic evidence that these observations were not large *Chelydra serpentina* (L.) (North American Snapping Turtle). The Withlacoochee River, which is 227 km long and whose mouth is  $\sim 53$  km southeast of the mouth of the Suwannee River by water, would appear to be a more likely candidate to have a Suwannee Alligator Snapping Turtle population. Limited trapping of the Withlacoochee River in Marion County (11 traps set on 23 August 2024) and the Chassahowitzka River (6 traps plus a snorkel survey on 28 June 2023) failed to detect alligator snapping turtles, but 4 traps plus a snorkel survey on 27 June 2023 also failed in the Southeast Fork

of the Homosassa River, where alligator snapping turtles were photographed by K. Spratt. Trapping in the Waccasassa River south of the Suwannee River also failed to detect alligator snapping turtles (Enge et al. 2021b). Two zooarchaeological sites on the Crystal River, the next river north of the Homosassa River, yielded at least 11 turtle species, including the North American Snapping Turtle (Duke et al. 2020). The absence of alligator snapping turtle remains in shell middens ca. 1200–1800 years ago suggests it is not native to this area, although this highly aquatic species may not have been readily harvested.

Although we did not capture alligator snapping turtles in the linear sections of Pepper Creek north of West Halls River Road, we received credible reports from a resident who observed a large, light-headed turtle behind the mobile home park and another resident who regularly feeds a large turtle behind her trailer. We do not know whether turtles regularly move through the culvert beneath the road, but turtles readily traverse the entire 1.75-km section of Pepper Creek south of the road in the Park, as evidenced by a turtle (#8) that was first trapped at the weir near the mouth of the creek and was recaptured close to the visitor center 1.2 km upstream (Fig. 2). A hand-captured turtle (#15) released at the boat house was trapped 880 m away the following morning (Fig. 2).

Interviews with former and present staff of the wildlife attraction regarding the provenance of the Suwannee Alligator Snapping Turtle population were inconclusive. Ross Allen's Reptile Institute in Silver Springs, Marion County, had several Suwannee Alligator Snapping Turtles on display (Allen and Neill 1950), but these animals were not sent to Homosassa when Ross Allen left in 1975 and the attraction later closed (J. Dambach, Crystal River, FL, pers. comm.). J. Dambach was the reptile manager at Nature World, which was purchased by Citrus County in 1984 to protect the environmentally sensitive area until the State could purchase it 5 years later (FDEP 2019). K. Alfieri (Eastham, MA, pers. comm.), who worked for Nature World and was the first biological scientist for the FDEP in 1989, extensively dove the Homosassa River outside the Park but saw only 1 large turtle in 1986 or 1987 that might have been an alligator snapping turtle. According to a newspaper article by Barbara Behrendt in the Tampa Bay Times on 19 October 1984, 4 Alligator Snapping Turtles, including a 57-kg animal, were donated to Nature World by Joel Smith's Alligator Farm in Trenton, Gilchrist County, and put in a spring-fed pool along the boardwalk (Fig. 1A). This "blue hole" is located 280 m by river from the weir at the entrance to Pepper Creek (Fig. 2), and at the time, was separated from the Homosassa River by a mesh fence (now gone) constructed by a volunteer group, the Friends of Nature World. Several employees (P. Dillard, J. James, and E. Toney, Homosassa, FL, pers. comm.) remember seeing alligator snapping turtles in this pool, and according to J. Dambach (pers. comm.), a pair escaped when the river flooded in March 1993 during the No Name Storm (i.e., Storm of the Century). However, K. Alfieri (pers. comm.) was unaware of alligator snapping turtles still being present when the FDEP purchased the property in December 1989. R. Poppe (FDEP, Homosassa, FL, pers. comm.) remembers seeing alligator snapping turtles in Pepper Creek since at least 2006 and said that the Park manager, A. Yerin,

removed a large turtle from Pepper Creek to put on display in the Discovery Center. This turtle was later returned to Pepper Creek (M. Langione, FDEP, Homosassa, FL, pers. comm.). In 2008, P. Moler (FWC, Gainesville, FL, pers. comm.) provided the Park with a Western Alligator Snapping Turtle from Telogia Creek, Liberty County, FL, to display in the Discovery Center, but this turtle was returned to Telogia Creek in 2014.

The best available information indicates that the Suwannee Alligator Snapping Turtle population in the Homosassa River originated from 4 turtles donated by Joel Smith in 1984 after draining a pond on his alligator farm. We do not know how Joel Smith obtained these turtles, but he lived near Bell on the Suwannee River in Gilchrist County and could have caught them himself or got them from people running bush hooks for catfish. Our program Locator assignments indicated the Homosassa turtles originated near the confluence of the Suwannee and Santa Fe rivers within 40 km of Bell (Fig. 4B). In the ensuing 5–9 years, all captive adult turtles apparently escaped from their pool along the Homosassa River; however, hatchlings could have escaped through the mesh fence since 1985 and populated the river and nearby Pepper Creek. The weir on Pepper Creek and the underwater summertime barrier at Long River Bridge present barriers to aquatic movement, but Alligator Snapping Turtles could circumvent these barriers by moving over land or during flood events. Typically, there is insufficient water for turtle movements in the channel downstream of the weir. Alligator Snapping Turtles occasionally make terrestrial movements not associated with nesting (Carr et al. 2023b), and a large turtle (probably a male, based on its size) was observed on the boardwalk near the Pepper Creek weir (K. Spratt, pers. observ.). Alligator snapping turtles generally show strong genetic differentiation between river drainages, likely owing to their rare overland and marine dispersal (Apodaca et al. 2023). Thus, if the Homosassa turtles were a native population, we would expect them to show more genetic differentiation from the Suwannee River populations.

Our estimated density of 19 turtles/km in Pepper Creek is higher than estimates of 14.4 turtles/km in the Suwannee River (T.M. Thomas, unpubl. data) and similar to 18 Western Alligator Snapping Turtles/km in an Arkansas stream that had been commercially harvested in the past (Howey and Dinkelacker 2013). However, our density is lower than the 28–34 Western Alligator Snapping Turtles/km in 2 small streams in Oklahoma (Riedle et al. 2008), but our turtles were all adults, whereas juveniles predominated in the Oklahoma streams. In the Suwannee River in Florida, which is a much larger stream than Pepper Creek, identical traps captured 21% juveniles (Thomas et al. 2023b). The portion of Pepper Creek in the Park had a closed canopy that may have been unsuitable for nesting, and the sparse aquatic vegetation may have provided little protective cover for juveniles. Females may have nested in the more open portion of Pepper Creek north of West Halls River Road, which had dense submerged aquatic vegetation and small, shallow channels more suitable for juveniles. Another possible reason for our lack of success in trapping juveniles is that they were less successful than adults in finding trap openings because of the lack of a current and their greater reliance on lingual luring than on

opportunistic scavenging to obtain food (Elsey 2006, Pritchard 1989). Our CPUE of 0.25 was identical to the mean CPUE found in the Suwannee River in Florida (Enge et al. 2021b). The Homosassa sex ratio was heavily skewed towards males (3.5:1), which was also the case in the Suwannee River (Thomas et al. 2023b). In contrast, Suwannee Alligator Snapping Turtles in the Santa Fe River had an equal sex ratio (Johnston et al. 2015). Our finding that a translocated individual moved at least 880 m overnight in Pepper Creek is not surprising. In the Suwannee River, turtles had linear home ranges 1.1–8.1 km long, and their 2–8 core activity areas were located ~300 m apart (Enge et al. 2014).

Adult alligator snapping turtles are opportunistic scavengers that consume a wide variety of aquatic invertebrates, fish, and crayfish (Elsey 2006). They also prey upon water birds, small mammals, small *Alligator mississippiensis* (Daudin) (American Alligator), and small turtles (Sloan et al. 1996). In a spring-influenced section of the Santa Fe River, Suwannee Alligator Snapping Turtles tended to eat mostly larger fish species and fewer crayfish and snails than North American Snapping Turtles (Denton et al. 2023). Suwannee Alligator Snapping Turtles eat snails and bivalve mollusks (Allen and Neill 1950), and we frequently observed scarified areas in Pepper Creek where, presumably, turtles had foraged for mollusks by raking with their front feet. Adult turtles in Pepper Creek likely eat fish and the dense populations of snails and clams, which benefit from the high calcium carbonate load in the water due to the underlying limestone (Wolfe et al. 1990). Radiographs revealed large quantities of crushed mollusks in some stomachs. Nonnative *Corbicula fluminea* (Müller) (Asian Clam) and the native mussels, *Utterbackia peninsularis* Bogan and Hoch (Peninsular Floater) and *Mytilopsis leucophaeata* (Conrad) (Dark Falsemussel), are present in Pepper Creek. However, downstream of the main spring in the Park, Walsh and Williams (2003) failed to find freshwater mussels, possibly due to tidal influence and associated salinity effects (SWFWMD 2017). We suspect the alligator snapping turtle population elsewhere in the Homosassa system is not as dense as in Pepper Creek, possibly because of fewer mollusks and less protective cover. Native submerged aquatic vegetation, such as *Vallisneria americana* Michx. (Eelgrass), in the Homosassa River has become much reduced because of increased nitrate concentrations, salinity, and foraging by Florida Manatees (SWFWMD 2017).

Alligator snapping turtles in the Suwannee River preferred areas of shallow water with underwater structure, such as large woody debris, or undercut banks (Thomas et al. 2023a). The winding portion of Pepper Creek in the Park has some cover in the form of limestone, shoreline tree roots and vegetation, and a deep detrital layer, but fallen trees are removed to keep the channel navigable by pontoon boats. The canopy cover shades out submerged aquatic vegetation, and there is insufficient current to create undercut banks. Turtles in Pepper Creek have become accustomed to the electric-powered pontoon boats and are often diurnally active. Boat operators often mention their presence to Park visitors, who can sometimes observe them because of the shallow, relatively clear water and sparse vegetative cover.

According to Nerozzi et al. (2024), alligator snapping turtles have a low “invasiveness risk,” and Suwannee Alligator Snapping Turtles in the Homosassa River represent the first published report of an introduced population established outside its native range. However, a large population of Western Alligator Snapping Turtles is reported to be established in Lake Wittsee, Germany, after pets were released in the 1990s (Crossland 2020). Populations may also be established in China (Liu et al. 2021). The survival of an introduced population in Citrus County is not surprising considering that presumably released turtles have been found even farther south in the peninsula (Enge et al. 2021b, 2025), and fossil records exist in Pinellas County, which is further south, as recently as 300,000 years ago (Meylan 1995, Thomas et al. 2014). At least 5 states have reintroduced or transplanted Western Alligator Snapping Turtles to augment natural populations, with mixed results (Adams et al., in press; Carr et al. 2023a); however, a founder group of only 4 turtles was sufficient to establish a population in the Homosassa drainage.

Throughout the range of alligator snapping turtles, the primary threat is incidental bycatch by fishing gear (Shook et al. 2023). Despite our study population being in a state park where fishing is prohibited and all wildlife is protected, the turtles are still not safe from anthropogenic threats. While trapping, we observed a few illegal anglers along Pepper Creek, and poachers are suspected of shooting the large turtle in 2022 and killing a marked, 27-kg male by bludgeoning and stabbing after our study was completed.

There are no plans to remove this population of a federally threatened species, and any attempts would probably be futile. We had variable success trapping the population in 1.75 km of Pepper Creek south of West Halls River Road, and we have reports of turtles in Pepper Creek north of the road and elsewhere in the Homosassa system. Trapped turtles could not be released in the Suwannee system without possibly impacting resident turtles, and the FWC already has difficulty finding qualified adopters of confiscated alligator snapping turtles. A dietary study might help determine whether this introduced, high trophic-level predator is significantly impacting native wildlife species, though the population has already been present for 40 years. In September 2024, Hurricane Helene produced storm surges of 3 m in parts of Citrus County, and the Homosassa River flooded up to West Halls River Road. We do not know how this influx of saline water impacted the Alligator Snapping Turtle population and its prey. This study provides baseline data for monitoring the health and conservation status of this population in the future.

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