

**Final Report**

**UNDERSTANDING THE SURVIVABILITY AND HABITAT USE OF ALLIGATOR  
SNAPPING TURTLES IN EAST TEXAS VIA TELEMETRY STUDIES**



Prepared for the Texas Comptroller of Public Accounts

#21-7336BG

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by

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10 November 2024

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## ACKNOWLEDGEMENTS

We thank Bob Baker, Cody Dunagan, Justin Eddins, and Kelly Norrid, and the staff of Martin Dies Jr. State Park of Texas Parks and Wildlife (TPWD), Floyd Boyett of the United State Army Core of Engineers (USACE), Bill Kirby and Luke Sanders of the Sabine River Authority (SRA), Robert Speight of the Northeast Texas Municipal Water District (NETWMD), Laura Speight of SP8 Ecoservices, Nelson Roach owner of Couch Mountain Ranch, Brett Hortman, Debra Bills, David Stewart, and Jim Steinbaugh of the United States Fish and Wildlife Service (USFWS), and Eric Munscher of SWCA for logistical support and site access. We also thank Jonathan Edwards, Tristan Brownjohn, Sophie Gartenstein, Andy Muhllaney, Will Baxter-Bray, Andy Lara, Marc Moss, Carson Salter, and David Rosenbaum for their assistance in the field. Funding for this study was secured through grants provided by the Texas Comptroller of Public Accounts (CPA), Texas Parks and Wildlife (TPWD), the Sabine River Authority of Texas (SRA), and the Northeast Texas Municipal Water District (NETWMD), and the USDA McIntyre-Stennis program. The handling and use of animals in this study were approved by Stephen F. Austin State University's (SFASU) Institutional Animal Care and Use Committee (IACUC), reference number 2021-002, and Scientific Research Permit No. SPR-0922-127 from TPWD. This paper was written and prepared in part by U.S. Government employees on official time and therefore is in the public domain and not subject to copyright. This research was supported in part by the USDA Forest Service. The findings and conclusions in this publication are those of the author(s) and should not be construed to represent an official USDA, Forest Service, or U.S. Government determination or policy.

## EXECUTIVE SUMMARY

The goal of this project was to assess the feasibility of repatriation efforts for confiscated alligator snapping turtles (*Macrochelys temminckii*) in eastern Texas, USA. Past repatriations have occurred in other parts of *M. temminckii* range, but outcomes have been difficult to assess and efforts with confiscated individuals are rarely evaluated. Here, we conducted two main tasks to answer these questions: 1) compare the responses (i.e., movement and habitat use) of repatriated *M. temminckii* to resident *M. temminckii* at a single release site to understand how these factors may influence survival; and 2) assess the utility of satellite GPS tracking tags for post-release monitoring efforts of *M. temminckii*.

Repatriated turtles (n = 4), previously released in June 2021, were monitored alongside resident turtles (n = 10) within the Angelina/Neches Dam B WMA (AND) at B.A. Steinhagen reservoir in eastern Texas from July 2022 to July 2024. We observed repatriated turtle movements were more sporadic compared to resident turtles across time. These irregular movements were observed even in cooler months when activity may be expected to decrease. Resident turtle movements, in comparison, were more stable across time. Home range metrics of MCPs and KDEs were similar between repatriated turtles and resident turtles. However, the  $wAKDE_C$  metric, which incorporates movement models in home range estimates, revealed that repatriated turtles had slightly larger home range areas compared to resident turtles. We also found substantial variation in repatriated individuals  $wAKDE_C$  estimates than resident individuals. At the macrohabitat scale, repatriated turtles selected sites with more open water, while resident turtles selected emergent herbaceous wetlands and woody wetlands. Repatriated turtles were consistent in their selection of open water macrohabitats across both the active (March – August) and nonactive (September – February) seasons. Resident turtles selected emergent herbaceous wetlands in the active season and woody wetlands in the nonactive season. At the microhabitat scale, both repatriated and resident turtles selected sites with bank undercuts or live trees and roots. However, resident turtles also selected microhabitats that featured abundant emergent or submerged vegetation, corresponding to the patterns observed at the macrohabitat scale.

We used a multi-state approach using Hidden Markov models (HHMs) to estimate survival for both repatriated and resident turtles. In both groups, survival probabilities were influenced by transitions to unknown states. Still, we found that estimated survival of repatriated turtles tended to decrease over time. From the initial release in June 2021, to the start of comparisons with resident turtles, survival of repatriated turtles had declined by almost 50%. When comparisons were made to resident turtles, we continued to see a decline in estimated overall survival until all turtles had either been confirmed dead or were considered lost (i.e.,  $S = 0.07$ ). Conversely, survival estimates of resident turtles were more consistent over the same period, as we did not confirm any mortality events and other losses (i.e., unknown fate) were minimal. Considering the length of time we monitored turtles, resident turtle survival ( $S > 0.75$ ) was similar to what has been reported in other studies of wild populations. Model outputs showed that covariates related to movement had a negative effect on the survival of repatriated turtles, more so than other covariates related to habitat use, suggesting hyperdispersal of

repatriated individuals may have led to decreased survival. Comparatively, we found no relationship between the covariates included in our model and the survival probability of resident turtles. Oddly, movement distances of resident turtles did increase substantially during our monitoring in 2024. However, increased movement distances only influenced unknown state transitions and did not influence overall survival of resident turtles.

As part of a broader effort to assess the feasibility of satellite-linked GPS technologies for future *M. temminckii* monitoring efforts, two additional resident females were captured in March and April of 2024, fitted with low-weight GPS tags with remote download features, and released at AND. We specifically targeted large-bodied females to be monitored during the nesting season to provide some insight into *M. temminckii* nesting ecology (movements, timing, and habitats). We found that the remote download features did not function when turtles were submerged under the surface of the water, which negated our ability to test the fix accuracy of any points that may have been recorded via satellites during monitoring. In addition, we also found that the internal VHF radios built into our smaller loggers were not as effective in determining the location of a tagged turtle as the traditional bolt-on VHF radios. We attempted to recover the two GPS tagged females to manual download data from the GPS loggers. Trapping surveys began May 2024, and in addition to these efforts, we also targeted resident turtles fitted with bolt-on transmitters to evaluate body condition after ~2 years of frequent monitoring. Despite conducting extensive trapping at known monitored turtle locations, neither of the GPS tagged females were recaptured and only one resident turtle was recaptured. Instead, we consistently captured new, previously unknown, *M. temminckii* at those locations. The one turtle we did recapture, a resident male, did not appear to have been negatively impacted by the bolt-on transmitter, and we recorded no changes in body size (i.e., carapace length and body mass) since its initial capture and release.

## CHAPTER 1

### Background Information

#### ALLIGATOR SNAPPING TURTLE

The alligator snapping turtle (*Macrochelys temminckii*), which has been reported to exceed 100 kg in mass, is the largest freshwater turtle in North America (Ernst and Lovich 2009). Historically the species occupied a wide range across the southeastern United States, occurring in river systems draining into the Gulf of Mexico from as far north as Illinois and from western Florida to eastern Texas (Dobie 1971, Pritchard 1989). *Macrochelys temminckii* life-history is characterized by delayed sexual maturity (reproductive maturity at ~11–21 years), high adult survivorship, and low juvenile survivorship (Dobie 1971, Moore et al. 2013, Folt et al. 2016). With such traits, population persistence is reliant on the survival of adults, especially females, and previous studies suggest that an annual removal of just 2% of adult females may lead to population decline (Reed et al. 2002). In the 1960's and 1970's, commercial harvesting of *M. temminckii* for meat resulted in regional population declines (Pritchard 1989), leading all states within their historic range to prohibiting commercial harvesting, imposing protective measures, or regulating recreational harvest (Shipman et al. 1995, Jensen and Birkhead 2003, Shipman and Riedle 2008, Kessler et al. 2017, Huntzinger et al. 2019, 2020). Despite these efforts, habitat loss, mortality associated with incidental bycatch (i.e., hook ingestion or capture on recreational fishing lines), harvest, and illegal take continue to threaten the species and *M. temminckii* has

now been proposed for listing as a federally threatened species under the Endangered Species Act by the U.S. Fish and Wildlife Service (Gibbons 2006, Holcomb and Carr 2013, Steen and Robinson Jr. 2017; Shook et al. 2023; USFWS 2021). Current differences in protection and regulation across the species range may have also contributed to declines of local populations and amplified illegal poaching in protected areas (Howey and Dinkelacker 2013). For example, Texas legislation prohibited the personal and commercial use of this species in 1987, whereas Louisiana permits the collection of one individual turtle per vessel per day (Huntzinger et al. 2019; Rosenbaum et al. 2023). Consequently, law enforcement agencies sometimes confiscate live individuals as part of their efforts to curb *M. temminckii* poaching.

## REPATRIATIONS OF ALLIGATOR SNAPPING TURTLES

With the development of improved reintroduction methods and head-starting programs, repatriation as a strategy to curb global declines in reptiles has continued to garner interest (Germano and Bishop 2009; Ewen et al. 2014). While early evaluations questioned the utility of this strategy (Dodd and Seigel 1991; Reinert 1991), there is growing evidence to suggest success rates of reptile repatriations are higher than initially perceived, stimulating new debate on the utility of translocations in reptile conservation (Dodd and Seigel 1991; Germano and Bishop 2009; Sullivan et al. 2015; Choquette et al. 2023). Given their current global conservation status, turtles are common target taxa for repatriations (Lovich et al. 2018; Rhodin et al. 2018). Most turtles are long-lived, with low juvenile survival, and delayed sexual maturity (Congdon and Gibbons 1990; Congdon et al. 1994). While these traits make turtles especially vulnerable to human exploitation, high natural survival of adults and high fecundity of females with iteroparity also make turtles suitable target species for repatriation (Tuberville et al. 2005; Thompson et al. 2023). In light of such findings, the number and scope of studies implementing repatriation as a conservation tool to reestablish or bolster wild populations of *M. temminckii* has increased (Dreslik et al. 2017). Several previous studies have now investigated the movements (Bogosian 2010; Hyder et al. 2021; Kessler and Dreslik 2024), habitat use (Moore et al. 2014; Voves et al. 2020; Cozad et al. 2023), growth (Bogosian 2010; Moore et al. 2013; Anthony et al. 2015), and survival (Moore et al. 2013; Anthony et al. 2015; Dreslik et al. 2017) of translocated or reintroduced *M. temminckii*. Compared to results from studies of wild populations, reintroduced *M. temminckii* were reported to have larger home ranges and exacerbated movements (Cozad et al. 2023; Kessler and Dreslik 2024) but may utilize similar habitats (Voves et al. 2023). In most reintroduction or translocation studies of *M. temminckii*, individuals were sourced from captive-breeding programs in which measured responses were largely focused on specific age classes (e.g., juveniles or subadults), or releases were localized (i.e., released at a single site) to avoid genetic intermixing (Moore et al. 2004; Townsend 2016; Kessler and Dreslik 2024). Furthermore, most reintroductions and translocations have been carried out at release sites at which *M. temminckii* were thought to have experienced drastic population declines or had been extirpated (Moore et al. 2013, 2014; Kessler and Dresnik 2024).

While these studies have contributed greatly to the development of current *M. temminckii* conservation translocations (Voves et al. 2023), further study is needed to identify what factors influence repatriation success, especially in confiscated individuals (Picardi et al. 2021). Repatriations require thorough pre-release planning to ensure risks to both confiscated individuals and wild populations are limited. Binary assessments of repatriation success or failure are also challenging for long-lived, cryptic species, like *M. temminckii*, because they depend on intensive post-release monitoring and the ability to assess long-term survival. Site-

specific responses may have energetic consequences as repatriated individuals search for suitable habitat, food, and refuge from predation in a novel environment (Roe et al. 2010, Ewen et al. 2014; Picardi et al. 2022). Thus, it may be important to compare repatriated individuals to resident individuals to determine which responses are most likely to contribute to repatriation outcomes (i.e., increased or decreased survival; Rittenhouse et al. 2007, Attum et al. 2013, Moehrenschrager and Lloyd 2016, Rimple et al. 2024).

## **EFFORTS TO MONITOR ALLIGATOR SNAPPING TURTLES**

There is a critical need to further develop and implement new methodologies and techniques to assess *M. temminckii* populations (East et al. 2013; Anthony et al. 2015). Given their longevity and cryptic nature, *M. temminckii* are often difficult to monitor in the aquatic environments they inhabit (Anthony et al. 2015; Munscher et al. 2021). Traditional trapping methodologies used in mark-recapture studies often report low capture per unit effort (CPUE) with few recaptures. However, radiotelemetry data can be incorporated into a mark-recapture framework to provide a more comprehensive view of individual or group responses (Adams et al., *in review*). Monitoring those responses via traditional VHF radiotelemetry can still be an intensive process, and evaluating finer-scale responses may require tracking individuals multiple times a week, across multiple years, while navigating logistically challenging environments (East et al. 2013; Munscher et al. 2021; Trauth et al. 2016).

Satellite-linked GPS technologies have improved our understanding of the spatial ecology of wildlife as they can provide many animal relocation datapoints at fine scales and greater frequency of occurrence (Tomkiewicz et al. 2010; Thomas et al. 2011; Lahoz-Monfort et al. 2021). While costly, these technologies have also proven useful in a wide variety of contexts and are often the preferred method of monitoring organisms that have large home ranges or territories (Finerty et al. 2024), are cryptic or live in hostile environments (Smith et al. 2018), or pose risks with increased human-wildlife interactions (Pekarsky et al. 2021). Most GPS applications have been utilized on terrestrial fauna or marine fauna that surface frequently, because they rely on satellite linkages to the GPS tags fixed on the tracked animal (Fischer et al. 2018; Watanabe and Papastamatiou 2023). While GPS applications for aquatic sea turtles have shown immense value, relatively few studies have attempted to utilize satellite-linked GPS tags on freshwater turtle species (Dall'Antonia et al. 2001; Micheli-Campbell et al. 2017; Gredzens and Shaver 2020; Robinson et al. 2021). Even so, GPS tracking devices have shown promise in semi-aquatic freshwater turtle studies to reveal cryptic behaviors (i.e., nocturnal basking) and nesting ecology (Chow-Fraser 2014; Micheli-Campbell et al. 2017; Hjort Toms et al. 2022). *Macrochelys temminckii* are similar to other freshwater turtles in that juveniles are highly susceptible to mortality and population viability is reliant on the survival of adult females. Knowledge of *M. temminckii* nesting ecology is still severely limited and consists mostly of observational reports (Holcomb and Carr 2013; Jackson and Ewart 2023). While GPS tracking devices are hindered by their inability to relocate a turtle when submerged (Hjort Toms et al. 2022), there is still interest in utilizing GPS tags as a method to monitor *M. temminckii* and reveal cryptic behaviors (i.e., nesting).

## **PROJECT BACKGROUND**

In 2012, U.S Fish and Wildlife Service (USFWS) and Texas Parks and Wildlife Department (TPWD) law enforcement officers initiated a collaboration to investigate and disrupt

the illegal flow of *M. temminckii* from Texas into Louisiana. The joint operation resulted in numerous arrests, including a major case that led to the discovery of ~ 40 turtles that were smuggled out of Texas and into Louisiana in 2016 (Eastern District of Texas 2017). These turtles were eventually confiscated from private property near Sulphur, Louisiana in July 2016 and transferred to the USFWS Natchitoches National Fish Hatchery in Natchitoches, Louisiana. The turtles were retained in holding ponds as evidence while the cases were processed through the courts. The case resulted in multiple Lacey Act violation convictions in December 2017 (USA v. Leger 2017; USA v. Leckelt 2017; USA vs. Simon 2017; USA v. Williams 2018). After the convictions, the USFWS explored establishing a captive propagation colony with the confiscated turtles to supply offspring for potential reintroduction programs in Texas and Louisiana. However, in July 2020, USFWS, TPWD, and Louisiana Department of Wildlife and Fisheries decided that the turtles should be released back into Texas, providing the opportunity for development of repatriation protocols, and subsequently the assessment of repatriation as a potential tool for *M. temminckii* in Texas.

These efforts to develop protocols included genetic analysis to determine the origins of confiscated turtles, site surveys to identify suitable release sites, and health evaluations prior to release (Adams et al., *in review*). Ultimately, confiscated turtles were repatriated at three sites across eastern Texas within the Neches, Sabine, and Cypress River drainages. Post-release monitoring was also conducted at these sites from June 2021 to June 2022 to assess the movement, habitat use, and survival of repatriated turtles across release sites (Adams et al., *in review*). Across all sites, long-distance, irregular movements were observed and survival of repatriated turtles decreased over time (Adams et al., *in review*). This post-release response (i.e., hyperdispersal) is recognized as a major factor influencing the outcome of reptile repatriations (Bilby and Moseby 2024). Since many reptiles are long-lived, repatriations often require intensive post-release monitoring to ascertain long-term success through measures of survival or reproductive success (Germano and Bishop 2009, Sullivan et al. 2015, Germano et al. 2015, Resende et al. 2020). Hyperdispersal may obscure post-release outcomes as repatriated individuals exhibiting such behavior are difficult to monitor and often have lower survival than resident individuals that are more truncated in their movements (Bellis et al. 2020, Morris et al. 2021, Bilby and Moseby 2024). The post-release movements of repatriated aquatic turtles underlie repatriation outcomes (Attum et al. 2013, Attum and Cutshall 2015, Canessa et al. 2016; Otten et al. 2023), yet many freshwater turtle species are known to exhibit low site-fidelity and homing behavior in the wild (Andres and Chambers 2006, Otten et al. 2021, Xiao et al. 2022). For these reasons, repatriations that incorporate individuals from resident populations at recipient sites can have notable value. Direct comparisons of responses (i.e., movement and habitat use) of repatriated and resident individuals provides insights as to how repatriated individuals might adapt to novel environmental conditions and utilize the habitats available at recipient sites. Such comparisons may be indicative of whether repatriated individuals are effectively acquiring resources post-release and inform future repatriation or translocation efforts (Rittenhouse et al. 2007, Attum et al. 2013, Moehrensclager and Lloyd 2016, Rimple et al. 2024).

## **PROJECT SCOPE**

Considering reported population trends and recent range assessments, repatriations will likely continue to be utilized as a tool for *M. temminckii* conservation. It is also likely that demand for turtle meat in illegal markets will result in future confiscations. As part of these



efforts, there is immense value in understanding what factors (i.e., responses) influence repatriation outcomes (i.e. survival). Such evaluations are not only beneficial to repatriation efforts but may also be used to evaluate continued threats to the species across its historic range. The objectives of this research under this project were to:

1. Investigate movement patterns and habitat use as potential factors influencing the survival of repatriated *M. temminckii* by comparing these responses to resident *M. temminckii* at a single release site.
2. Investigate the feasibility of satellite-link GPS tags as a field technique for monitoring responses (e.g., nesting) of *M. temminckii*.

Data associated with this project are available at:

Schalk, Christopher M.; Glasscock, Jessica L.; Adams, Connor S. 2024. Repatriation of alligator snapping turtles in east Texas. Fort Collins, CO: Forest Service Research Data Archive. <https://doi.org/10.2737/RDS-2024-0074>.

Schalk, Christopher M.; Glasscock, Jessica L.; Adams, Connor S. 2024. Monitoring of repatriated and resident alligator snapping turtles in east Texas. Fort Collins, CO: Forest Service Research Data Archive. <https://doi.org/10.2737/RDS-2024-0075>.

These datasets are currently being reviewed for quality control and assurance by personnel at the US Forest Service Data Archive. The DOIs have been assigned early, but currently point to an out of stock page. These DOIs will point to the data publication as soon as it is published.

## **CHAPTER 2**

### **TASK 1. Survival of repatriated and resident *M. temminckii***

#### **OVERVIEW**

Chapter 2 discusses the comparison of movement patterns, habitat use, and survival between repatriated *M. temminckii* and resident *M. temminckii* at one of the original release sites (i.e., AND) from July 2022 – July 2024. This post-release monitoring was conducted approximately one year after the initial release of confiscated turtles in June 2021 (see Chapter 1 for more details). This continued monitoring was performed to identify factors that influence survival probabilities in repatriated and resident *M. temminckii*.

#### **METHODS**

*Study Area*—The Angelina/Neches Dam B Wildlife Management Area (hereafter, AND) in Tyler and Jasper Counties of eastern Texas is jointly operated by the US Army Core of Engineers (USACE) and TPWD and consists of 5,114 hectares of hardwood bottomland and river floodplains. Aquatic habitats within the AND are heavily influenced by the confluence of the Neches and Angelina Rivers, which join to form the impounded B.A. Steinhagen Reservoir. Due to active regulation of both the Town Bluff Dam at B.A. Steinhagen and the Lake Sam Rayburn Dam to the north, there is substantial fluctuation within hydrological regimes across the landscape (Zhang and Wurbs 2018). This has resulted in the formation of a diversity of aquatic

habitats at AND, including large forested oxbow lakes, many low-order streams and bayous, marshy open wetlands, and large stretches of open shallow waters (Moyer 1977).

*Turtle Repatriations and Resident Turtle Captures*—Repatriated turtles were released at AND in June 2021, as part of the larger repatriation effort in 2021 (see Chapter 1). As part of these previous efforts, genetic assignments, site surveys, and health evaluations of confiscated *M. temminckii* led to the repatriation of eight adult turtles (males = 4; females = 4) originating from the Neches River drainage at AND (Apodaca et al. 2023; Adams et al., *in review*; see Chapter 1). Post-release, repatriated turtles were monitored once a week via radiotelemetry until the start of this study in July 2022 (Adams et al. *in review*). Resident *M. temminckii* were sampled from three separate surveys conducted in July, August, and September 2022. We deployed 15 baited 1.2 m diameter commercial hoop nets, baited with frozen *Cyprinus carpio* (Common Carp) suspended in holding canisters, for 3 consecutive nights (i.e., 45 trap-nights) during each survey (Rosenbaum et al. 2023a). Traps were deployed upstream of physical structures (i.e., woody debris, root clumps, undercuts) known to be used as refuge by *M. temminckii*, separated at a minimum distance of 50 m, and checked daily (Rosenbaum et al. 2023). All turtles captured during preliminary surveys were individually marked following the North American Code (Nagle et al. 2017), measured (Iverson and Lewis 2018), and sexed (i.e., male/female and hatchling-subadult/adult; Dobie 1971) prior to release. Morphological measurements included precloacal/total tail length (cm), maximum and midline straight-line plastron length (cm), maximum and midline straight-line carapace length (cm), maximum and midline curved carapace length (cm), maximum straight-line and curved carapace width (cm) from right marginal scute at widest point, body depth (cm) from vertebral scute at highest point, cranial midline length (cm), maximum cranial width (cm), and body mass (kg) (Iverson and Lewis 2018). We selected 10 adult turtles captured from these efforts based on sex and body size. We opted for an even sex distribution (males = 5, females = 5) as males and females may exhibit different movement patterns attributed to differences in their ecology (e.g., mate searching behavior in males; nesting movements in females, and we preferentially selected larger-bodied adults (i.e., > 25 cm straight-midline carapace length) based on minimum body sizes of adults reported in Rostal et al. (2023). Studying adults provides critical demographic parameters in this part of *M. temminckii* range given the sensitivity of populations to decline when adults are lost. Resident turtles selected for monitoring were fitted with Holohil AI-2F radio transmitters (33g) affixed onto the rear marginal scutes (Munscher et al. 2021) and were released at their points of capture.

*Radiotelemetry Efforts*—Repatriated and resident turtles were monitored 2–3 times per week via radiotelemetry to determine the status and location of each turtle from July 2022 to July 2024. Paired random points were also taken with each individual relocation to assess whether repatriated and resident turtles selected certain macro- or microhabitats. Random points were determined using a randomized number generator to select distance and direction metrics at 3–100 m from a turtle locality, which is the minimum and maximum distance considered available to an individual that is not being selected for at the time of the paired relocation point (Fitzgerald and Nelson 2011). For turtle localities in rivers or streams, we selected a random distance upstream/downstream and a random distance from the associated bank. For turtle localities in

oxbow lakes or wetlands we selected a random distance in a random cardinal direction. A Garmin GPSMAP 64Sx handheld GPS (accuracy = 3-m; datum = WGS 84) was used to record GPS coordinates at turtle locations and at paired random points. Mortality events were confirmed by the recovery of deceased individuals or the recovery of transmitters in which shell or bone fragments were also recovered. In some cases, we could not safely confirm mortality by the recovery of radio transmitters or physical specimens. In these cases, the states of individuals that had not moved from their previous location within a 2–3-week period (i.e., 4–9 consecutive relocations) were considered unknown.

*Movement and Home Range Estimation*— To quantify repatriated and resident movement patterns, we reprojected GPS coordinates obtained from telemetry fixes, subset individual localities by telemetry check (i.e., date/time), and calculated straight-line distances between relocations using spatial analyst tools in ArcGIS Pro Version 3.3.2 (Scott and Janikas 2009). Since radiotelemetry data can lead to biases in movement analysis when animals are difficult to locate on regular intervals, we censored calculations of straight-line movement distances at times that a turtle could not be relocated during a previous telemetry check. (Burger et al. 1991; Boback et al. 2020). From those data, a generalized additive mixed model (GAMMs) was constructed to compare movements of repatriated and resident turtles across time (i.e., day of year; Pedersen et al. 2019). To compare differences in home range size between repatriated and resident *M. temminckii*, we calculated 100%, 95%, and 50% MCPs, and 95% and 50% utilization distributions (UD) using a bivariate normal kernel method ( $h_{ref}$  bandwidth; Worton 1989). Because relocations were highly autocorrelated in time and space, and *M. temminckii* movements are inherently limited to freshwater habitats given their aquatic nature, we computed the weighted Autocorrelated Kernel Density Estimates ( $wAKDE_C$ ) that were more appropriate home range estimates (Calenge 2006, 2011a, 2011b; Benhamou 2011; Calabrese et al. 2016; Silva et al. 2022). Distributions of each home range metric produced for repatriated and resident turtle groups were tested Wilcoxon tests.

*Habitat Selection*— Habitat selection of repatriated and resident turtles was quantified within a hierarchical framework, in which macro- and microhabitat data from turtle localities and paired random points were collected under same methodology utilized in initial monitoring efforts (Adams et al., *in review*), and analyzed as a two-step process (Aarts et al. 2008; Beyer et al. 2010; Appendix A). First, we extrapolated the proportions of available and utilized forest, open water, emergent/herbaceous wetland, grassland/herbaceous, and woody wetland cover types from turtle points and random points using compositional analyses (Aebischer et al. 1993; Adams et al., *in review*; Appendix A). A K-select analysis was then used to identify specific characteristics of macrohabitat selected by individual turtles based on what was available on the landscape (i.e., determined from paired random points), assuming habitat availability varied among individuals because of the extensive geographic area in which resident turtles were captured and released (Brunell et al. 2023; Padrón et al. 2023). ANCOVA was used to test if overall macrohabitat utilization differed between repatriated and resident turtle groups. Second, continuous and categorical microhabitat variables characterizing water, bank, canopy, substrate, and structural habitat were collected at turtle points and random points (Appendix A). Then, NMDS was performed on microhabitat data with the Gower's distance metric. To determine if

repatriated and resident turtles selected microhabitats from random, and to test for differences between turtle groups, we performed Permutational Multivariate Analysis of Variance (PERMANOVA). Additionally, each of these analyses were repeated to address seasonal differences in macro- and microhabitat use between repatriated and resident turtles. As ectotherms, *M. temminckii* activity is likely influenced by seasonal shifts in atmospheric conditions and water temperatures (Howey and Dinkelacker 2009). Similar to other reptiles, *M. temminckii* are thought to exhibit predictable patterns of activity (e.g., increased activity in the mating or nesting season) that correspond with changes in seasonal climatic conditions (Rostal et al. 2023; Thompson et al. 2023). For these reasons habitat data were pooled into different active (i.e., July 2022 – August 2022, March 2023 – August 2023, March 2024 – July 2024) and non-active (i.e., September 2022 – February 2023, September 2023 – February 2024) periods and analyzed to interpret seasonal differences between turtle groups.

*Survival*—To compare survival of repatriated and resident turtles, radiotelemetry data was incorporated into a mark-recapture framework (Perry et al. 2012). To account for inconsistency in radiotelemetry data, we used a multi-state modelling approach (Jackson 2011; Fox and Carvalho 2012), in which the calculation of transition probabilities for different ecologically relevant states can strengthen survival estimates (Etterson 2013; Bonilla-Valencia et al. 2022; Labuzzetta et al. 2024). We constructed discrete time hidden Markov models (HMMs) for repatriated and resident turtles using a 4-state model (Rushing 2023). These models included a “release” state representing a one-way transition in which an individual enters the model at a given time, an “alive” state representing a two-way transition which indicates an individual is located alive at a given time, an “unknown” state representing a two-way transition which indicates an individual’s fate is not known at a given time, and a non-reversible “deceased” state based on confirmed mortality events. Since repatriated turtles had initially been released in 2021, we used initial state transition probabilities derived from a previously constructed HMM as a prerequisite for the remaining individuals of this group (Adams et al., *in review*). This methodology also allowed us to estimate survival of resident turtles that were captured and released at different times in 2022. Model outputs were used to compare the overall survival of turtle groups across time (i.e., day of year) and between repatriated and resident groups.

To further evaluate how aspects of movement and habitat use may influence *M. temminckii* survival, we incorporated 9 covariates related to our analyses of movement distances, home range size estimation, and macro- and microhabitat into HMMs. These covariates included sex, distance moved between relocations, whether individuals were outside of core areas (i.e., 50% KDE areas), whether individuals were moving or stationary at the time of relocation, proportions of relevant cover types derived from the first components of macrohabitat ordinations, proportions of relevant variables derived from the first components of microhabitat ordinations, and seasonal period (i.e., active versus non-active). Since repatriated and resident turtles were tagged and released at different times, independent models were built for each group. We selected the model with the lowest Akaike’s Information Criterion (AIC) for the hidden Markov models, indicating the best trade-off in our model set between number of covariates used and explained variance in these datasets. We first tested all the possible combinations of covariates to determine which were relevant to each AST group. Once we

determined that movement influenced repatriated AST survival, we conducted a backward stepwise selection on the first selected repatriated AST model to determine which aspects of movement most affected survival (Venables and Ripley 2002). Using this approach begins with the full model (i.e., first selected model) and removes one variable at a time until AIC cannot be improved further.

## RESULTS

*Movement and Home Range Estimation*— By July 2022, only four of the eight repatriated turtles (3 females and 1 male) released at AND in 2021 were still being monitored, as the other four individuals had died or could not be relocated (Adams et al., *in review*). Carapace lengths of the remaining repatriated turtles at the time of their initial release ranged from 30.46 – 45.72 cm and body mass ranged from 6.2 – 18.05 kg (Table 1). Eighteen resident *M. temminckii* were captured across 405 trap nights (CPUE = 0.04 turtles/trap night). Of those resident turtles selected for monitoring (5 females and 5 males), carapace lengths ranged from 42.1 – 58.7 cm and body mass ranged from 13.9 – 37.9 kg (Table 1). From July 8, 2022, to July 10, 2024, we obtained 320 fixes on repatriated turtles and 997 fixes on resident turtles. Since our increased monitoring in July 2022, we documented two additional mortalities of repatriated turtles (December 2023 and August 2023; Table 2). Two additional repatriated turtles were unknown due to their lack of movement over multiple relocations and failure to recover radio transmitters. No mortality events were documented for resident turtles across the study period. However, one resident turtle could not be relocated after April 2023, despite continued efforts to extensively search for this individual within the study area.

Repatriated turtle movements were more sporadic compared to resident turtles across time (Fig. 1A). Repatriated turtle movements spiked multiple times across the monitoring period ( $F = 0.40$ ,  $p$ -value = 0.67). This pattern was observed even in cooler months when activity may be expected to decrease, while resident turtle movements were more stable during the same period ( $F = 18.38$ ,  $p < 0.001$ ; Fig. 1A). Although movements were significantly different between turtle groups ( $W = 5.45$ ,  $p < 0.01$ ), we did observe resident turtle movements increase substantially after the repatriated turtles could no longer be detected (Fig. 1A). Repatriated turtle MCP's were similar to resident turtle MCP's (Wilcoxon tests; 50% MCP,  $W = 18$ ,  $p$ -value = 0.84; 95% MCP,  $W = 18$ ,  $p$ -value = 0.84; 100% MCP,  $W = 13$ ,  $p$ -value = 0.37; 50% KDE,  $W = 25$ ,  $p$ -value = 0.64, 95% KDE,  $W = 23$ ,  $p$ -value = 0.73; Table 3). Home range estimates from KDE's were also similar between groups, as the mean home range area was  $6.93 \pm 5.62 \text{ km}^2$  for repatriated turtles and  $5.17 \pm 3.33 \text{ km}^2$  for resident turtles (Wilcoxon test; 95% KDE,  $W = 23$ ,  $p$ -value = 0.73), and the mean core site area was  $1.06 \pm 0.94 \text{ km}^2$  for repatriated turtles and  $0.73 \pm 0.40 \text{ km}^2$  for resident turtles (Wilcoxon test; 50% KDE,  $W = 25$ ,  $p$ -value = 0.64; Table 3). Incorporating movement models to produce  ${}_w\text{AKDE}_C$  home range estimates showed repatriated turtles had slightly greater mean diffusion rates (0.12 km/day) than resident turtles (0.09 km/day), and slightly larger  ${}_w\text{AKDE}_C$  home range areas than resident turtles (repatriated 95%  ${}_w\text{AKDE}_C$  range =  $0.66 \text{ km}^2 - 15.02 \text{ km}^2$ , resident 95%  ${}_w\text{AKDE}_C$  range =  $0.31 \text{ km}^2 - 9.34 \text{ km}^2$ ; Wilcoxon test,  $W = 7$ ,  $p$ -value < 0.1; Fig. 2). Individual assessments of  ${}_w\text{AKDE}_C$  home range estimates revealed substantial variation within repatriated individuals, and more consistency in

home range estimates among resident individuals (Fig. 3). For example, the largest and smallest  $wAKDE_C$  home range estimates across all monitored individuals with >30 relocations belonged to repatriated females (i.e., AND4 and AND5 respectively; Fig. 2).

*Habitat Selection*– At the macrohabitat scale, repatriated turtles’ use of open water (i.e., the river channel) was comparable to its availability on the landscape (ANCOVA,  $p = 0.13$ ; Table 4). Resident turtles selected emergent herbaceous wetlands and woody wetlands macrohabitats in greater proportions than what was available on the landscape (ANCOVA,  $p < 0.05$ ; Table 4). The occurrence of repatriated turtles in open water macrohabitats did not vary across active and nonactive seasonal periods, whereas resident turtles tended to select for emergent herbaceous wetlands (i.e., open wetlands) in the active season and woody wetlands (i.e., forested oxbow lakes) in the nonactive season (Table 4). Although both repatriated and resident turtles selected microhabitats that differed from random (PERMANOVA, repatriated,  $p < 0.05$ ; wild,  $p < 0.05$ ), we did not see strong differences in microhabitat preferences between groups (PERMANOVA,  $p < 0.11$ ). The presence of bank undercuts and live trees/roots were important structural microhabitat features for both groups (Fig. 3; Table 5). Such features were abundant across the study area, regardless of macrohabitat. At least one repatriated turtle (i.e., AND 2) did show an affinity for a microhabitat feature not used by other turtles (i.e., artificial structure), utilizing the overhang from a retaining wall within its core site area. This may be why artificial structure was considered an important variable defining the microhabitat gradient at our study site (Table 6). Even though we observed that repatriated and resident microhabitat use overlapped substantially across seasons, we also observed that resident turtles tended to use more microhabitats featuring abundant cover of emerged/submerged vegetation compared to repatriated turtles (Fig. 3; Table 5). Since this type of vegetation is more likely to proliferate in open, more productive, habitats (i.e., emergent herbaceous wetlands) than flowing rivers/streams (i.e., open water), this likely corresponds with resident turtle macrohabitat selection.

*Survival*–The initial state matrix adopted from the previous HMM (Adams et al., *in review*) showed that repatriated turtles were more likely to transition into “unknown” or “deceased” states compared to resident turtles, in which the initial state matrix estimated from radiotelemetry data showed a high likelihood to stay in the “Alive” state (Table 6). Overall survival estimations for repatriated turtles were significantly lower than resident turtles (repatriated  $R^2 = -0.71$ ,  $p < 0.01$ ; resident  $R^2 = 0.14$ ,  $p < 0.001$ ; Fig. 1B). Estimated survival of repatriated turtles decreased over time, whereas survival estimated from resident turtles was only influenced by “unknown” state transitions (Fig. 1B). Modelling of covariates effects on survival revealed that distance moved between relocations, activity (moving vs. stationary), and season influenced state transition probabilities of repatriated and resident turtles, whereas habitat (i.e., macro- and microhabitat) had minimal influence (Table 7). Movement distance greatly influenced the survival of repatriated turtles compared to resident turtles (Table 7). Specifically, movement distance was more likely to result in a state transition shift resulting in a mortality event for repatriated turtles compared to resident turtles (Table 7; Fig. 1C).

## DISCUSSION

We found evidence suggesting hyperdispersal, or irregular long-distance movements, led to lower survival in repatriated turtles. Even though resident turtles moved longer overall distances than repatriated turtles, we observed differences in seasonality, home range size, and habitat selection coincided with differences in survival between repatriated and resident turtles. When incorporated into our survival models, several metrics indicative of hyperdispersal correlated with lower survival of repatriated turtles, but apparently had no relationship with resident turtle survival. Below we highlight the potential of hyperdispersal to influence repatriation outcomes of confiscated *M. temminckii* and underline the importance of comparing responses of repatriated individuals to resident individuals.

In most cases, resident turtles did not have to move long distances to access a different macrohabitat, and having a familiarity with the study area is also expected to result in more consistent home range estimates as less energy (i.e. decreased movement) is prioritized to access potential resources (Roe et al. 2010). Despite this, we found most home range metrics (i.e., MCP and KDE) were similar between repatriated and resident turtles. When incorporating movement models into home range estimation (i.e.,  $wAKDE_C$ ), we estimated repatriated turtles to have slightly larger home ranges than resident turtles. Estimates of this metric varied greatly within repatriated individuals compared to resident individuals. This variation may be because only a small number of repatriated individuals survived long enough to estimate comparisons with resident turtles. Still, estimated areas were like those reported in Cozad et al. (2023), which reported estimates of  $12,882.8 \pm 8781.5 \text{ m}^2$  for males and  $10,621.6 \pm 6020.4 \text{ m}^2$  for females in a study that monitored 9 adult repatriated *M. temminckii* in Florida. Resident turtle home ranges may be more contiguous than repatriated turtles that might have to travel more frequently between cores sites within their home ranges. Increased movement of repatriated individuals across the landscape, and within their home range area may then be viewed in the same light as the irregular movement patterns that describe hyperdispersal (Bilby and Moseby 2024). These responses may scale up and have an additive effect on repatriated turtles, with consequences to fitness, and ultimately survival at recipient sites (Attum et al. 2013; Anthony et al. 2015).

Several previous studies have acknowledged the potential for hyperdispersal to influence the outcomes of reptile repatriations (Bilby and Moseby 2024). Freshwater turtles are known to vary in site fidelity and homing behavior in the wild, which may make them more susceptible to hyperdispersal in repatriations, especially those that employ hard releases where individuals are unfamiliar with the novel aquatic environment compared to resident conspecifics (Selman 2024; Otten et al. 2021; Xiao et al. 2021). Since soft-release strategies are unlikely to be implemented in repatriations of confiscated *M. temminckii*, we may expect hyperdispersal to occur immediately following releases (Adams et al., *in review*). However, compared to residents, we found that repatriated individuals continued to make irregular movements years after their initial release. Resident movements were found to follow similar seasonal patterns reported in other regional resident populations, as we observed activity (i.e., movement) generally decreased in cooler months and increased in the warmer months when *M. temminckii* are more likely to mate or nest (Harrel et al. 1996; Munscher et al. 2021). Compared to the results in this study, other studies have reported greater stability in movement and dispersal of reintroduced *M. temminckii*. For example, Kessler and Dreslik (2023) found that repatriated turtle movements were mostly

influenced by passive dispersal, and Hyder et al. (2021) found that repatriated turtles exhibited similar movements to turtles in other wild populations ~12 years after initial release. However, we found that repatriated turtles would sporadically move longer distances during times when resident movements were truncated. Still, most studies have been conducted on captive-propagated juveniles and subadults that investigate short-term responses (Dreslik et al. 2017; Hyder et al. 2021; Kessler and Dreslik 2023), whereas adult *M. temminckii* may have to move longer distances over time to find suitable habitat, food, or to avoid intraspecific antagonistic interactions at recipient sites (Harrel and Douglas 1996; Enge et al. 2023; Thompson et al. 2023).

We observed differences in macrohabitat selection between repatriated and resident turtles that may be explained by movement. Repatriated turtles had strong affinities for open water habitats (i.e., main river channels) within the study area, whereas resident turtles were more likely to utilize wetlands, oxbows, and bayous off the main river channel. Other studies comparing the responses of repatriated and resident freshwater turtles have attempted to link such responses. For example, Attum and Cutshall (2015) found that longer-dispersal distances in translocated *Sternotherus carinatus* led to differences in habitat utilization between released individuals and residents. Long-distance movements of repatriated *M. temminckii* may have been mostly facilitated by traversing large river channels, which would also explain why repatriated turtles were more likely to be observed actively moving during relocations compared to residents. Longer-distance dispersal that results in the prevalent selection of certain macrohabitat could also reflect unfamiliarity with those habitats on the landscape as Attum et al. (2013) also found that dispersal distance was dependent on habitat heterogeneity. AND has a high diversity of macrohabitats and abundant structural features at the microhabitat scale that are important for *M. temminckii* (Riedle et al. 2006; Lescher et al. 2013; Adams et al. 2024). However, seasonal pulsing events (i.e., floods, dam releases) within the two large rivers regulate the connectivity of these habitats. Resident turtles may be more adaptable to fluctuations in available macrohabitats than repatriated turtles (*sensu* Piper 2011), which could explain why we observed differences in spatial and temporal (i.e., seasonal) macrohabitat selection but similar microhabitat selection. Being able to exploit different macrohabitats may have some advantages for turtles (Brown et al. 1994; Dubois et al. 2009). As ectotherms using shallower, productive wetlands where water temperatures tend to be higher in warmer months may help facilitate the energy acquisition necessary for mate searching or food resources (Dubois et al. 2009; Fitzgerald and Nelson 2011). Alternatively, forested oxbows that are semi-isolated from the main river may provide refuge from predators or negative intraspecific interactions during colder months when activity slows down and energy expenditure must be reduced (Bodie and Semlitsch 2000; Roe et al. 2010).

Because of their longevity and cryptic nature, monitoring efforts of *M. temminckii* are logistically challenging. Including repatriated individuals that may hyperdisperse, becomes even more difficult as fates of individuals become harder to determine, and population estimates less reliable. Using multi-state modelling with Hidden Markov Models to help account for these pitfalls, we found that survival of repatriated confiscated turtles was lower than what has been reported in other *M. temminckii* repatriations, and markedly lower than that of resident turtles monitored simultaneously. Other repatriations have suggested that survival of repatriated individuals increases with growth and age (see Dreslik et al. 2017), yet survival estimates of



confiscated adults we released at AND gradually declined until all repatriated individuals had either died or were lost (Adams et al., *in review*; Moore et al. 2013). Again, the majority of *M. temminckii* repatriations have focused on the survival of juvenile or subadult life stages that were captively propagated (Moore et al. 2013; Anthony et al. 2015; Spangler et al. 2021; Kessler and Dreslik 2023), whereas the survival of confiscated adults may be influenced by factors that are not easily quantified (e.g., resource acquisition, nesting ecology, and intraspecific interactions). Many past studies have also relied on traditional mark-recapture techniques that rely on the recapture of turtles years after their release. In such cases, survival estimates for repatriated *M. temminckii* may be influenced by low recapture rates and emigration in addition to mortality (Anthony et al. 2015). Despite reporting lower survival of repatriated individuals compared to other *M. temminckii* repatriations, survival of resident turtles may be similar to that expected in wild adults (Reed et al. 2002). Survival estimates for wild populations are few and vary substantially across systems and in methodology (Howey and Dinkelacker 2013; Trauth et al. 2016), but natural adult survivorship is assumed to be high (i.e., >95%) as *M. temminckii* display a Type III survivorship curve (Reed et al. 2002). Our overall estimated survival of resident turtles (i.e., 0.89) was ultimately lower than adult threshold survival reported in Reed et al. (2002). This was due to one individual that could not be accounted for (i.e., unknown fate). This may have been the result of a failed VHF tag rather than an emigration or mortality event, but we could not verify fate because we failed to detect a signal despite efforts to relocate this individual across the study area.

Our multi-state modelling of radiotelemetry data, incorporated into a mark-recapture framework, showed that there is a degree of uncertainty that may persist and obscure post-release monitoring evaluations when repatriated individuals are capable of moving great distances across the landscape. However, several aspects of movement that collectively describe hyperdispersal (i.e., actively moving, moving long distances between relocation, moving more frequently in and out of core areas) were correlated with low survival. Hyperdispersal may be a common issue in repatriations of large-bodied aquatic reptiles that are assumed to have high natural survival, and this behavioral response is widely reported in sea turtles and crocodilians (Shimada et al. 2016; Brunell et al. 2023). Our findings suggest that reducing hyperdispersal is an important step to ensuring the success of future repatriations of confiscated adult *M. temminckii*. Although the spatial ecology and habitat use of wild *M. temminckii* is still not fully understood, such efforts will be increasingly valuable to future repatriation efforts. If there is plasticity in *M. temminckii* movement and habitat use between systems, repatriations may be able to take advantage of these differences to mitigate hyperdispersal or increase certainty in post-release monitoring applications. For example, several studies have reported truncated movements of adults in smaller stream systems (Riedle et al. 2006; Munscher et al. 2021; Adams et al. 2024). In some cases, smaller forested streams may contain abundant resources, while also limiting the dispersal of repatriated individuals (Adams et al. 2024). In any case, there is a critical need to further understand the nature of threats to *M. temminckii* and their potential effect on adult survivorship. A comprehensive understanding of the impacts of threats (e.g., incidental bycatch, nest predation) to resident populations, alongside the responses of repatriated individuals, at recipient sites will better inform future repatriations that attempt to bolster wild populations.

**Table 1.** Demographics of repatriated and resident *M. temminckii* monitored from July 8, 2022 to July 10, 2024 at Angelina/Neches Dam B WMA. Morphological measurements were collected immediately prior to release and included maximum and midline straight-line carapace length (SLCL), maximum and midline curved carapace length (CCL), maximum straight-line width (SLCW), maximum curved width (CCW), maximum straight-line plastron length (SLPL), precloacal tail length (PTL), total tail length (TTL), cranial length (CL), cranial width (CW), body depth (BD), and mass.

ID	Group	Notch code	Sex	Max SLCL (cm)	Mid SLCL (cm)	Max CCL (cm)	Mid CCL (cm)	Max SLCW (cm)	Max CCW (cm)	Max SLPL (cm)	PTL (cm)	TTL (cm)	CL (cm)	CW (cm)	BD (cm)	Mass (kg)
AND2	Repatriated	CIV	Male	48.3	45.0	54.6	52.6	48.3	56.2	31.8	17.8	46.0	13.0	13.2	23.6	19.1
AND4	Repatriated	CIY	Female	30.5	29.0	34.2	35.0	25.7	38.2	21.6	7.6	25.3	9.4	10.2	12.7	6.2
AND5	Repatriated	CSK	Female	32.5	30.7	35.2	35.8	26.9	38.4	23.4	6.1	24.1	8.4	9.4	12.7	7.1
AND8	Repatriated	CJV	Female	43.9	41.2	48.2	47.4	35.6	53.0	33.0	6.4	38.4	13.5	12.7	15.5	17.2
AND11	Resident	CVW	Female	47.4	43.5	48.8	47.3	38.2	49.9	34.8	9.4	39.6	15.2	14.0	16.3	15.9
AND12	Resident	DIJ	Female	42.6	39.9	42.8	43.0	34.3	47.0	28.8	7.5	36.4	13.3	12.2	16.3	13.9
AND13	Resident	DIK	Male	29.2	34.4	32.6	34.4	28.1	39.2	23.0	5.4	26.3	18.8	9.7	27.9	5.1
AND14	Resident	DIP	Female	47.0	48.8	50.4	48.8	39.1	54.4	33.3	8.4	35.4	14.4	13.1	18.1	19.7
AND15	Resident	DIV	Male	51.2	49.3	53.7	53.3	43.4	57.1	35.5	13.0	39.5	17.5	16.3	17.7	27.1
AND16	Resident	DIX	Male	54.2	51.3	59.3	58.0	43.2	60.2	38.3	15.5	48.0	17.9	15.6	19.2	31.0
AND17	Resident	HIJ	Male	57.2	52.7	64.5	56.4	46.7	65.4	38.1	16.7	37.5	20.0	17.5	20.7	31.8
AND18	Resident	HIK	Female	42.1	39.9	45.2	43.7	35.2	48.0	30.4	7.0	31.6	15.7	13.2	16.5	14.4
AND19	Resident	HIL	Male	59.9	56.4	61.1	55.1	48.0	58.2	41.9	18.3	46.0	15.2	17.5	23.4	38.2
AND20	Resident	DIW	Female	46.0	43.4	48.5	48.3	46.5	51.2	31.5	7.7	41.0	14.0	13.4	19.4	17.2

**Table 2.** States of resident and repatriated alligator snapping turtles monitored from July 8, 2022 to July 10, 2024 at Angelina/Neches Dam B WMA States (i.e., Alive, Unknown, Deceased) indicate the last known state for each individual and are included alongside the dates of state confirmation. Individuals classified as Alive survived from their initial release date to the end of monitoring on July 10, 2024.

ID	Relocations	Group	Release Date	State	State confirmation date	Sex
AND2	n = 98	Repatriated	6/22/2021	Deceased	12/20/2023	Male
AND4	n = 83	Repatriated	6/22/2021	Unknown	8/9/2023	Female
AND5	n = 71	Repatriated	6/22/2021	Unknown	7/12/2023	Female
AND8	n = 68	Repatriated	6/22/2021	Deceased	8/31/2023	Female
AND11	n = 123	Resident	5/11/2022	Alive	7/10/2024	Female
AND12	n = 113	Resident	5/22/2022	Alive	7/10/2024	Female
AND13	n = 30	Resident	9/28/2022	Unknown	4/3/2023	Male
AND14	n = 117	Resident	9/28/2022	Alive	7/10/2024	Female
AND15	n = 98	Resident	9/28/2022	Alive	7/10/2024	Male
AND16	n = 103	Resident	9/22/2022	Alive	7/10/2024	Male
AND17	n = 103	Resident	10/12/2022	Alive	7/10/2024	Male
AND18	n = 102	Resident	10/12/2022	Alive	7/10/2024	Female
AND19	n = 108	Resident	10/12/2022	Alive	7/10/2024	Male
AND20	n = 100	Resident	10/12/2022	Alive	7/10/2024	Female

**Table 3.** Home range area estimates (km<sup>2</sup>) of repatriated and resident *M. temminckii* monitored at Angelina/Neches Dam B WMA from July 8, 2022, to July 10, 2024. Estimates include 50%, 95%, and %100 minimum convex polygons (MCP), and 50% and 95% Kernel Density Estimates (KDE).

ID	Sex	Group	50% MCP	95% MCP	100% MCP	50% KDE	95% KDE
AND2	Male	Repatriated	0.53	3.79	8.65	1.97	10.71
AND4	Female	Repatriated	0.29	4.15	10.51	1.76	12.59
AND5	Female	Repatriated	0.02	0.29	1.48	0.10	0.82
AND8	Female	Repatriated	0.00	0.61	4.38	0.42	3.60
AND11	Female	Resident	0.28	1.28	8.32	0.94	4.49
AND12	Female	Resident	0.21	0.87	8.46	0.45	2.54
AND13	Male	Resident	0.00	0.01	0.42	0.05	0.33
AND14	Female	Resident	0.71	4.20	10.81	1.20	8.44
AND15	Male	Resident	0.24	8.44	10.15	1.08	9.66
AND16	Male	Resident	0.48	3.33	11.47	1.32	10.62
AND17	Male	Resident	0.30	1.48	6.55	0.72	4.90
AND18	Female	Resident	0.11	1.09	13.36	0.40	3.47
AND19	Male	Resident	0.22	0.92	9.74	0.49	2.98
AND20	Female	Resident	0.13	1.05	9.82	0.63	4.26

**Table 4.** Results from K-select analyses (PCA 1) showing macrohabitat selection (Bonferroni  $\alpha$  level =  $0.05/99 = 0.0005$ , two-tailed test) of repatriated and resident *M. temminckii* based on compositional analyses of available and utilized NLCD cover types. Turtles were monitored at Angelina/Neches Dam B from July 8, 2022 to July 10, 2024 across active (March – August) and nonactive (September – February) seasonal periods. Significance ( $\alpha < 0.05$ ) of the marginality for each group is noted in bold.

Analysis	habitat variable	Overall		Active		Non-active	
		repatriated	resident	repatriated	resident	repatriated	resident
Macrohabitat (K-select Analysis)	forest cover	0.09	11.24	27.9	0.97	0.07	0.13
	open water	<b>-0.94</b>	-0.63	<b>-0.88</b>	-0.27	<b>-0.91</b>	-0.41
	emergent herbaceous wetland	-0.65	<b>-0.74</b>	-0.19	<b>-0.87</b>	<b>-0.66</b>	0.24
	grassland/herbaceous	0.04	0.03	0.07	0.01	0.03	0.01
	woody wetland	-0.16	<b>-0.69</b>	0.33	-0.45	-0.56	<b>-0.97</b>

**Table 5.** Scores for measured habitat variables from the Nonmetric Multidimensional Scaling (NMDS) ordination of microhabitats utilized by repatriated and resident *M. temminckii* at Angelina/Neches Dam B WMA.

Microhabitat variable	NMDS 1	NMDS 2
flow rate (m/s <sup>2</sup> )	0.0404	-0.0467
surface temperature C	0.0613	-0.0061
water depth (m)	0.0894	-0.1147
sand substrate (% cover)	0.0174	-0.1460
mud/silt substrate (% cover)	0.0803	0.0917
detritus substrate (% cover)	0.0655	0.0782
undercut (presence/absence)	-0.5146	-0.4606
canopy (% cover)	-0.2409	0.0822
large woody debris (presence/absence)	0.0229	-0.0435
small woody debris (presence/absence)	0.0025	-0.0364
live trees/roots (presence/absence)	-0.3298	0.1381
artificial structure (presence/absence)	-0.5378	0.0173
overhanging vegetation (presence/absence)	-0.3913	0.0293
emergent/submerged vegetation (% cover)	0.0824	0.0566
floating vegetation (% cover)	0.0318	0.0751

**Table 6.** Initial state transition matrices depicting initial probabilities for state shifts of repatriated and resident *M. temminckii* at Angelina/Neches Dam B WMA. The initial state transition matrix for repatriated turtles was estimated from multi-state survival models produced from their release in June 2021 to June 2022 (see Adams et al. *in review*) while the initial state transition matrix for resident turtles was estimated from July 8, 2022 to July 10, 2024.

		Alive	Unknown	Deceased
Repatriated	Alive	0.95	0.04	0.01
	Unknown	0.08	0.92	0.00
	Deceased	0.00	0.00	1.00
		Alive	Unknown	Deceased
Resident	Alive	0.99	0.01	0.00
	Unknown	0.89	0.11	0.00
	Deceased	0.00	0.00	1.00

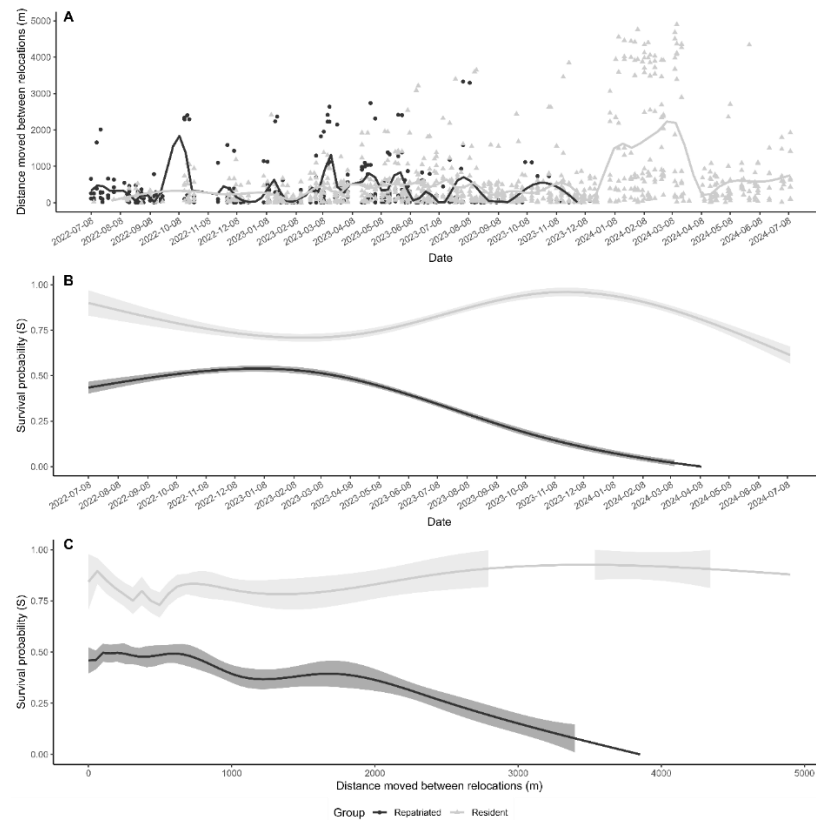
**Table 7.** Regression coefficients for the transition probabilities between the states (S) of alive (S1), unknown (S2), and deceased (S3) for repatriated and resident *M. temminckii* tracked via radiotelemetry from July 8, 2022 to July 10, 2024 at Angelina/Neches Dam B WMA. Positive values indicate that the included covariate tends to indicate a shift from one state to the other, whereas negative values indicate a tendency to stay in the initial state and limit transition to the other state. Note that S3 (deceased) indicates mortalities have occurred and is therefore an irreversible state dynamic. Confidence intervals at 95% are indicated in parentheses.

Covariate	Conditions	Repatriated			Resident		
		S1→S2	S1→S3	S2→S1	S1→S2	S3→S1	S2→S1
Sex	male	0.54 (0.41)	0.13 (0.08)	0.08 (0.05)	0.33 (0.29)	–	0.79 (0.11)
	female	0.27 (0.11)	0.11 (0.19)	0.16 (0.21)	–0.41 (0.23)	–	0.95 (0.21)
Movement	distance moved between relocations (m)	0.72 (0.53)	0.66 (0.24)	0.48 (0.36)	0.86 (0.45)	–	–0.37 (0.14)
Activity	moving	0.83 (0.56)	0.39 (0.43)	–0.42 (0.22)	0.22 (0.19)	–	–0.16 (0.07)
	stationary	–0.37 (0.15)	–0.21 (0.17)	0.61 (0.55)	–0.68 (0.52)	–	0.15 (0.01)
Macrohabitat	PCA 1	–0.47 (0.21)	–0.63 (0.31)	–0.67 (0.43)	–0.18 (0.24)	–	–0.24 (0.13)
Microhabitat	NMDS 1	–0.68 (0.36)	–0.76 (0.49)	–0.71 (0.52)	–0.59 (0.41)	–	–0.82 (0.16)
Temperature	sensor C	–0.22 (0.17)	–0.37 (0.34)	–0.62 (0.37)	–0.17 (0.08)	–	–0.77 (0.13)
Season	active	0.25 (0.12)	–0.08 (0.13)	0.13 (0.21)	0.57 (0.39)	–	0.68 (0.41)

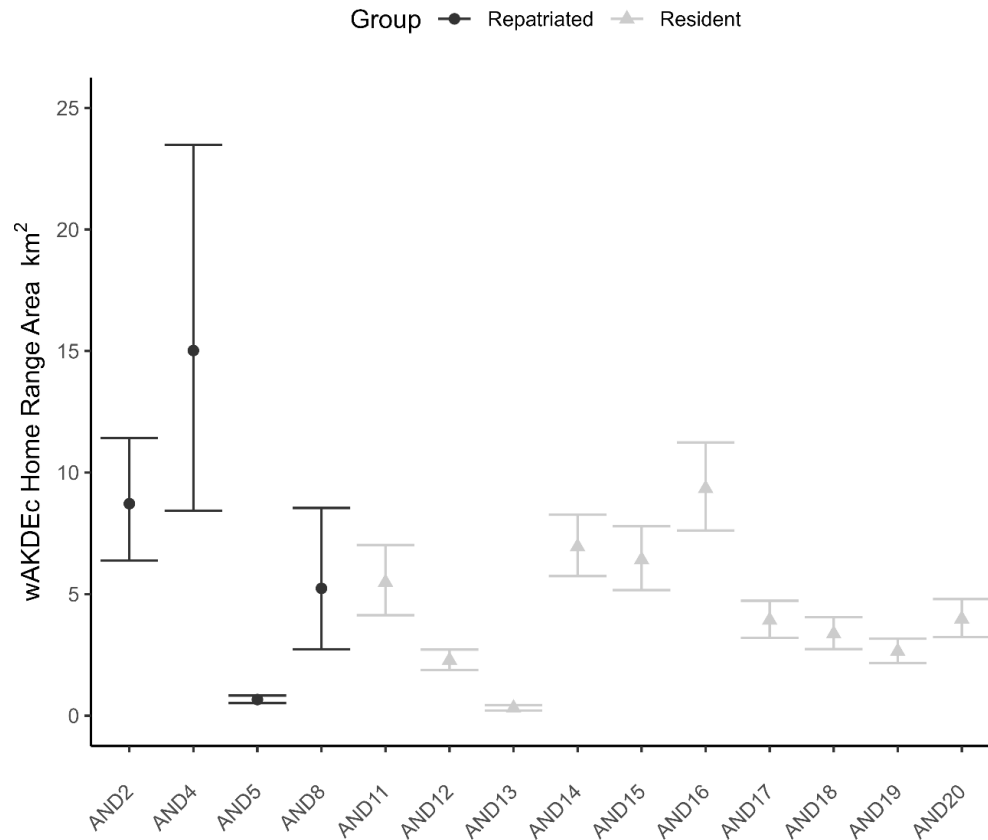


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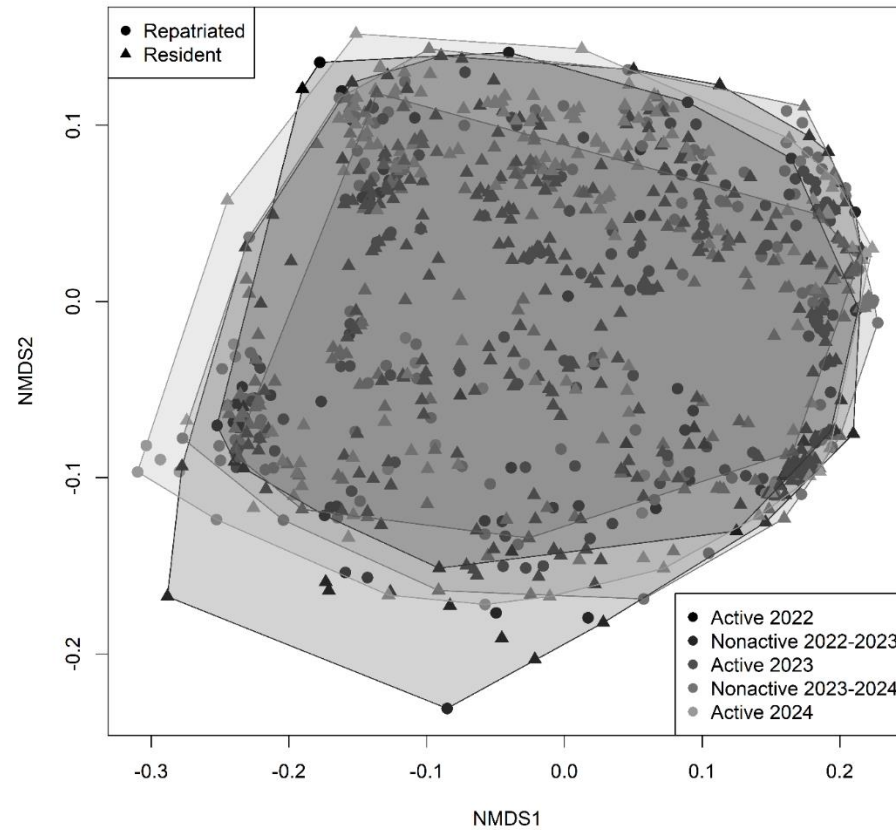
nonactive	-0.38 (0.28)	0.44 (0.38)	-0.11 (0.04)	-0.81 (0.54)	-	-0.35 (0.11)
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**Figure 1.** Movement and survival of *M. temminckii* monitored from July 8, 2022, to July 10, 2024 at Angelina/ Neches Dam B WMA, Texas, USA. Results include comparisons of **A)** generalized additive models (GAMs) and adaptive spline regression analyses of movement distances between relocations (m) across time, **B)** overall survival estimates from multi-state Hidden Markov Models, and **C)** relationship between movement distances (m) and estimated survival for repatriated (i.e., black circles and lines) and resident (i.e., grey triangles and lines). Confidence intervals could not be calculated for times when sample sizes were low or when metrics could not be quantified for individuals being in unknown or deceased states. All repatriated turtles were confirmed either in deceased or unknown states by September 2023, whereas monitoring continued for resident turtles until July 10, 2024.



**Figure 2.** Home range areas (km<sup>2</sup>) of repatriated and resident *M. temminckii* individuals at Angelina/Neches Dam B WMA based on 95% weighted, Autocorrelated Kernel Density Estimates (<sub>w</sub>AKDE<sub>C</sub>). For individuals with ≤ 30 relocations (i.e., AND13), AKDE estimates were corrected for small sample sizes (AKDE<sub>C</sub>). Bars represent low and high confidence intervals (CI) for individual <sub>w</sub>AKDE<sub>C</sub> home range areas, with non-overlapping CI's indicating differences between individuals.



**Figure 3.** Nonmetric Multidimensional Scaling (NMDS) depicting microhabitat use of repatriated and resident *M. temminckii* from Active 2022 (July 2022 – August 2022), Nonactive 2022-2023 (September 2022 – February 2023), Active 2023 (March 2023 – August 2023), Nonactive 2023-2024 (September 2023 – February 2024), and Active 2024 (March 2024 – July 2024).

## CHAPTER 3

### TASK 2. Utility of GPS Satellite Transmitters as a Monitoring Technique

#### OVERVIEW

Chapter 2 discusses the utility of satellite-link GPS technology as a potential method for monitoring *M. temminckii*. Here we provide details on the GPS tags used, attachment of those tags, and our findings on the functionality of GPS tags deployed on two adult females at AND. We also discuss these efforts, in the context of previous monitoring efforts, and provide a general comparison to traditional methodologies.

#### METHODS

*Satellite-link GPS Tags*—To assess the utility of satellite-link GPS technology to monitor *M. temminckii*, we used two Advanced Telemetry Services 64 g W510 model (AA battery) GPS loggers with the ATS WildLink receiver and antennae apparatus. This moderately sized unit can be programmed to attempt satellite linking at a minimum interval of 15 minutes and has an estimated battery life of 2–3 months depending on the programmed schedule. We opted to use this model because of its low cost relative to other GPS tags on the market, and its built-in VHF radio that enables tagged individuals to be manually radiotracked and datapoints obtained from satellite linking to be remotely downloaded.

*GPS Tag Deployment*—We opportunistically trapped for adult female turtles using the same standardized methodology used to capture other resident turtles at AND (see Chapter 2 for more details) in March and April of 2024. When a female turtle was captured and morphological measurements were collected, we cleaned and scrubbed the vertebral scutes of the carapace with water and a heavy-duty polyester brush to remove mud and algae. We then dried the cleaned surface, placing the GPS logger as flush as possible on the vertebral scutes, slightly towards the posterior end of the carapace to reduce entanglement (Fig. 4). Once the best position was confirmed we used LOCTITE Ultra Gel 5-g industrial grade superglue to tac the GPS tag in place. We then constructed a wall of electric tape around the GPS tag, leaving an approximately 3 cm gap on each side of the tag, and layered marine-grade J-B Weld Fiberglass Resin epoxy over the transmitter gradually sealing the edges and allowing the epoxy to dry between layering. Once completely dried, we removed the electrical tape and applied JB Waterweld epoxy putting over the top of the transmitter for additional security (Adams et al., *in review*). These females were then released back at their original points of capture. The first female was lost soon after her release (see additional details below), so the second female we captured was also fitted with a traditional Holohil AI-2F transmitter, affixed with nuts and bolts to the rear marginal scutes and covered in J-B Waterweld epoxy putty (Fig. 4).

GPS tag programming schedules, VHF radios, and remote downloading were tested before and after each tag was attached to a female turtle. We programmed the GPS tags to record fixes on 15-minute intervals between sunrise and sunset each day to maximize the number of fixes that could be evaluated for fix accuracy, assuming the tags would not be able to link with

satellites when underwater (Quaglietta et al. 2012). We then released the two females at their initial locations of capture and again tested the built-in VHF radio transmitter. We monitored each female 2–3 times each week via radiotelemetry from the time GPS tags were deployed until June 2024, corresponding with the tail end of the expected regional nesting season for *M. temminckii* (Dobie 1971; Holcomb and Carr 2013; Thompson et al. 2023). At each telemetry check we attempted to remotely download data from the GPS tag. Because the first female fitted with a GPS tag was lost soon after her release, the second female we captured was also fitted with a traditional Holohil AI-2F transmitter, affixed with nuts and bolts to the rear marginal scutes and covered in J-B Waterweld epoxy putty (Fig. 4). In this way, we could provide an insurance for relocating this individual in the hopes of still recovering data from the satellite-link GPS tags.

*GPS Tag and VHF Radio Recovery Efforts*—Given the low estimated battery life of our programmed GPS tags, and the length of time other resident turtles had been monitored (~2 years), we conducted additional trapping surveys from May 2024 to October 2024 to recapture monitored individuals. Recapturing these individuals would also allow us to examine the durability of GPS satellite tags and bolt-on VHF radios and evaluate any potential risks these transmitters may have on *M. temminckii* health. Trapping surveys consisted of tracking monitored individuals to their known locations (via radiotelemetry), deploying a minimum of 15 baited hoop net traps in the vicinity of a known turtle location for 1–4 consecutive nights. We checked traps daily and rebaited each trap with fresh fish. In some cases, inclement weather prevented us from trapping for consecutive nights. In other cases, the targeted turtle left the area and traps had to be relocated or pulled.

## RESULTS

*GPS Tag Functionality*—The first GPS tagged female turtle (AND 21) was captured and released on March 21, 2024 (Table 8). Interestingly, this female was a recapture from previous trapping efforts conducted in May 2021 to assess the demographics of resident *M. temminckii* prior to the repatriation of confiscated turtles in June 2021 (Adams et al., *in review*). Within a week of the release (i.e., < 3 relocations), we were unable to locate AND 21. Since, AND 21 was recaptured in the same location as years prior, we assumed that the failure to relocate was likely due to the failure of the internal VHF radio within the GPS tag (i.e., no signal). The second female (AND 22) was hand captured at Martin Dies Jr. State Park after observing this individual on land next to a small bayou while on the way to conduct trapping surveys on April 15, 2024. Since we failed to relocate the first GPS-tagged female, and we assumed this female may have been attempting to nest when found, we attached a bolt-on transmitter as an additional method for relocation. We noted that the remote download functioned before her release but would not work as soon as this turtle returned to the water. Although the internal VHF on AND 22 functioned until the end of monitoring in October 2024, we found this device was more unreliable than the bolt-on VHF transmitter in determining an accurate relocation. In most cases, this female could only be triangulated to a general area via the internal VHF transmitter. The internal VHF was only effective in determining the exact location of this turtle in 6 out of 27 relocation attempts, whereas the bolt-on VHF transmitter was effective in determining the exact location of this turtle

in 23 of 27 relocation attempts. We were unable to remotely download any data off the deployed GPS tags after releases despite attempting to during every relocation, and being within the necessary proximity for connection (i.e., < 100m necessary for connection according to Wildlink specifications). This was surprising considering the remote download feature is not dependent on satellite linkage, which is more likely to be hindered by the submergence of the GPS in aquatic environments (Quaglietta et al. 2012).

*GPS Tag and VHF Radio Recovery Efforts*—Considering our inability to remotely download data from the GPS tags, we conducted 16 trapping surveys targeting GPS tagged females and other monitored resident turtles. A total of 1360 trap nights resulted in 13 *M. temminckii* captures and an overall capture per unit effort of 0.01. However, neither of the GPS tagged females were recaptured, and only one resident turtle was recaptured during these efforts. The recaptured resident turtle (AND 19), which had not changed in body mass (38.2 kg) or carapace length (59.9 cm) since its original capture, showed no damage from the bolt-on transmitter (Table 8). The transmitter had become loose and was only partially attached to the carapace by one bolt and some remaining epoxy putty, suggesting it would have eventually fallen off (Fig. 5).

## DISCUSSION

Monitoring animals via satellite, with the use of satellite-linked GPS tags, has revolutionized how we study the spatial ecology of animals (Recio et al. 2011; Marrant et al. 2022; Wild et al. 2022). Since its early implementation, GPS tags have been used to answer a variety of questions for a wide variety of taxa and have proved to be a cost-effective and less invasive technology for obtaining finer-scale relocations for some target taxa (Marrant et al. 2022; Ronoh et al. 2022; Finerty et al. 2024). Despite these gains, GPS tags are not widely used in studies of freshwater turtles because of the inability to obtain fixes when antennas are submerged underwater, generally becoming a less cost-effective methodology with increasingly aquatic target taxa (Quaglietta et al. 2012; Christensen and Chow-Fraser 2014). We found that GPS tags we tested were not an effective method to monitor the two females deployed at AND. This was attributed to the inability to remotely download any data that may have been collected via satellite, the failure of internal VHF radios to accurately relocate tagged females, and the inability to physically recover GPS tags and manually download GPS tag data. While discouraging, these results further contribute to our knowledge of the risks associated with GPS tracking technologies to monitor cryptic, aquatic species. Our findings also highlight the need for the further development of methodologies that can take advantage of these newer technologies to investigate unknown aspects of *M. temminckii* ecology.

We specifically targeted large-bodied female *M. temminckii*, during the nesting season, to assess the feasibility of our GPS tags. Similar applications have been used in other freshwater turtles with mixed results (Cochrane et al. 2019). Dall’Antonia et al. (2010) found GPS dataloggers modified specifically for European pond turtles (*Emys orbicularis*) were an effective way to quantify diel activity patterns, while Hjort Toms et al. (2022) used GPS tags to reveal previously unrecorded nocturnal behaviors in spotted turtles (*Clemmys guttata*) and Blanding’s turtles (*Emydoidea blandingii*). In these cases, GPS tags were effective because the target taxa basked frequently to thermoregulate (Ribiero et al. 2024). Although they have occasionally been

reported to bask, *M. temminckii* likely do not bask as frequently as other freshwater turtles (Carr et al. 2011). Instead, diurnal activity is mostly confined to the aquatic environment apart from nesting females (Franklin et al. 2023).

For monitoring nesting behavior or nest success, GPS tags may eventually prove to be a cost-effective alternative to traditional methodologies. Nesting behaviors are difficult to observe in *M. temminckii* and very few studies have been able to consistently identify nest sites (Carr et al. 2023). Given their large body size, *M. temminckii* can be fitted with larger GPS tags that have a longer battery life, and thus deployed for longer periods of time. However, obtaining adequate relocations to answer questions on nest-site selection or nest-site fidelity will likely depend on the ability to release more individuals that can be consistently monitored long-term. Given the high cost of services to provide real-time satellite-linked data, and the environments which they live (i.e., aquatic habitats with dense canopy cover), it is likely that most of these applications will still require the recapture of GPS tagged individuals. For example, Hulbert et al. (2024) compared data obtained from GPS tags to traditional radiotelemetry on semi-aquatic turtles and found that dense canopies and dense understories greatly limited the ability to accurately relocate turtles when on land compared to traditional radiotelemetry efforts. The GPS tagged used were also unable to obtain points when turtles were in the water, and most turtles had to be recaptured to obtain GPS tag data (Hulbert et al. 2024). Similarly, our efforts to test the utility of smaller GPS tags on *M. temminckii* required us to also use traditional VHF radios to keep track of a turtle for remote download attempts.

Even so, we still had to put considerable effort into attempts to recapture these turtles and obtain GPS satellite tag data. Despite knowing the location of individuals during our recovery efforts, neither of the GPS tagged females, and only one of the resident turtles, were recaptured across 1380 trap nights. Instead, we captured 13 new, unmarked individuals. If the implementation of GPS technologies to monitor *M. temminckii* ultimately relies on the physical recovery of GPS tags, such applications may only benefit studies conducted in smaller, closed systems where less effort is required to capture-recapture individuals (Trauth et al. 2016; East et al. 2013).





**Figure 4.** Attachment location of an ATS W510 GPS tag on the vertebral scutes of a resident female *M. temminckii* at Angelina/Neches Dam B WMA. Also depicted in the photograph, a Holohil AI-2F VHF transmitter attached to the posterior marginal scutes

**Table 8.** Morphological measurements of *M. temminckii* captured during GPS tag deployment and GPS tag/VHF radio recovery efforts from March 2024 to October 2024. Morphological measurements include maximum and midline straight-line carapace length (SLCL; cm), maximum and midline curved carapace length (CCL; cm), maximum straight-line carapace width (SLCW; cm), maximum curved carapace width (CCW; cm), maximum straight-line plastron length (SLPL; cm), pre-cloacal tail length (PTL; cm), total tail length (TTL; cm), cranial length (CL; cm), cranial width (CW; cm), body depth (cm), and mass (kg). AND 21 and AND 21 were females fitted with GPS tags. Only AND 19, a male resident from our previous tracking efforts, was recaptured during these efforts. The morphological measurements of AND 19 from initial release can be found in Chapter 2.

Turtle ID	Notch Code	Initial Capture/Release Date	Recapture Date	Sex	Max SLCL	Mid SLCL	Max CCL	Mid CCL	Max SLCW	Max CCW	Max SLPL	PTL	TTL	CL	CW	BD	Mass
AND19	HIL	10/12/2022	7/31/2024	M	59.9	56.4	61.1	55.1	48	58.2	41.9	18	46	15.2	17.5	23.4	38.2
AND21	HPS	3/21/2024	N/A	F	32.8	31.7	35.2	33	29.4	31.4	19.2	8.3	27.7	11.3	10.1	12.2	11.4
AND22	ART	4/15/2024	N/A	F	48.5	46.2	71.3	68.8	40.3	63.4	55	7.1	39.8	14.8	14.3	17.8	18.5
N/A	HIJ	3/5/2024	N/A	F	27	25	38.2	37	21.2	39.2	19	6	37.3	9.2	7.7	9.6	3.6
N/A	BCT	3/12/2024	N/A	M	52.7	51.4	54.1	53.7	40.6	57.2	52.7	14	37	20.7	21	20.4	30.1
N/A	DHQ	3/28/2024	N/A	F	35.2	34	37.2	34.1	29	37.5	25.1	5	28.4	10.9	10.2	13.3	18.1
N/A	GST	4/2/2024	N/A	F	29.4	28.1	37.2	34.4	25	34.4	20.9	5	22.6	8.7	9.5	28.2	4.6
N/A	KNR	4/3/2024	N/A	M	50.4	48.2	53.8	43.8	57.1	54.2	34.4	12	36.2	18.3	16.4	18.2	26.2
N/A	KMR	4/9/2024	N/A	M	–	–	69.9	65.3	40.3	82.2	46	25	56.1	–	–	28.5	50.1
N/A	DEF	5/22/2024	N/A	F	26.5	26	28	26.9	22.4	28.4	18.6	5.4	26.3	8.4	8.3	10.6	4.3
N/A	KLW	6/6/2024	N/A	F	32.4	31	34.1	33.2	26.6	32.6	22.8	5.1	20.5	10.3	9.8	12.5	6.2
N/A	BCL	6/18/2024	N/A	F	36.8	35	38.1	36.2	31.7	40	25.3	8	28.2	12.8	11.2	14.1	20.33
N/A	DGV	7/23/2024	N/A	F	29.9	31.5	34.2	29.9	26.3	37.3	22.7	7.4	25.3	8.8	8.4	11.3	15.6
N/A	BCN	8/13/2024	N/A	M	56.6	54.4	68	67.1	44.9	66.2	38.5	11	38.9	17.2	16.1	19.6	36.11
N/A	BET	9/5/2024	N/A	F	35.2	33.4	36.1	34.1	29.9	30	23.5	6.7	25.8	12.1	10.9	13.7	19.39
N/A	CDE	10/30/2024	N/A	J	29.7	28.9	33.9	32.6	28.2	29.1	16.3	7.9	25.4	11.8	11.3	12.5	9.4



**Figure 5.** Close-up depicting the condition of a Holohil AI-2F VHF transmitter recovered from an adult male resident turtle. This turtle was initially tagged and released on October 12, 2022 and recaptured on July 31, 2024. A total of 658 days were between initial release and recapture.



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