

MOVEMENT PATTERNS, HOME RANGE, AND MICROHABITAT
USE OF ALLIGATOR SNAPPING TURTLES (*MACROCHELYS*
TEMMINCKII) IN A SMALL EAST TEXAS STREAM SYSTEM

Connor S. Adams¹, Sophia Gartenstein¹, Josh B. Pierce²,
Jessica L. Glasscock¹ and Christopher M. Schalk^{2*}

¹Arthur Temple College of Forestry and Agriculture, Stephen F. Austin State University,
Nacogdoches, TX 75962

² Southern Research Station, U.S.D.A. Forest Service, Nacogdoches, TX 75965

*Corresponding author; Email: Christopher.Schalk@usda.gov

Abstract.—The alligator snapping turtle (*Macrochelys temminckii*), the largest freshwater turtle in North America, faces numerous threats, with population declines and range contractions suspected to have occurred across its historic range. Previous research studying movement patterns and microhabitat use of *M. temminckii* has mostly been conducted in large, open, lentic environments and few studies have been conducted in small, lotic habitats. We investigated the movement and microhabitat use of adult female and juvenile *M. temminckii* within Bonaldo Creek, a small tributary of the Angelina River in eastern Texas. Six *M. temminckii* were monitored (two or three relocations per week) via radiotelemetry from July 2008 to September 2009. We found that the linear home range for adult females (405.1–1395.5 m) was longer than that of the unsexed juveniles (439.7–996.9 m), although movement frequency was similar between groups. Juveniles utilized a smaller subset of microhabitats compared to adult females. Adult females utilized microhabitats with abundant submerged structure, while overhanging vegetation was an important microhabitat feature for juveniles. The broader microhabitat use we observed in adult females may have been influenced by seasonal factors, highlighting the need for more long-term, seasonal assessments of *M. temminckii* movement and microhabitat. Such investigations will bolster our understanding of the spatial and temporal factors that influence *M. temminckii* populations in different systems.

Keywords: range edge; lotic ecosystems; long-lived organism; first-order stream; habitat heterogeneity; seasonal variation

Despite being one of the largest freshwater turtles in the world, the alligator snapping turtle (*Macrochelys temminckii*) is difficult to study due to its aquatic and highly secretive nature (Ernst & Lovich 2009; Rosenbaum et al. 2023a). Once widespread throughout the southern

United States, from Florida to Texas and as far north as Illinois and Kansas, this bottom-dwelling predator-scavenger faces numerous threats and is listed as threatened in several states (Pritchard 1989; Moll & Moll 2000; Jensen & Birkhead 2003; Riedle et al 2005; Folt & Godwin 2013; Baxley et al. 2014; Munscher et al. 2023). Overharvesting and habitat alteration have caused populations of *M. temminckii* to decline, with prominent range contractions now documented in the northern and western reaches of its historical range (Reed et al. 2002; Riedle et al. 2008; Howey & Dinkelacker 2013; Huntzinger et al. 2019; Kessler et al. 2017; Shook et al. 2023). Despite having protection in several states, including Texas, *M. temminckii* are currently proposed for federal listing as a threatened species and knowledge on its status, distribution, and ecology is still lacking in many areas (USFWS 2021). This lack of knowledge persists partly because of the species cryptic behavior and limited accessibility to their habitats, especially in Texas where the large majority of land is privately owned.

Macrochelys temminckii often utilize core sites, characterized by specific microhabitat features such as an abundance of structural cover such as cut banks, root balls, and submerged trees and dense canopy cover (Bogosian III 2010; Lescher et al. 2013; Howey & Dinkelacker 2009; Munscher et al. 2021; Rosenbaum et al. 2023b). However, over longer periods of time, *M. temminckii* move extensively throughout their aquatic habitats (Table 1). Moreover, the majority of studies on *M. temminckii* movement patterns and habitat use were conducted in open, lentic environments and larger rivers or bayous, with fewer studies conducted in low-order, lotic environments. In most studies, these investigations were conducted only during the spring and summer months when *M. temminckii* are known to be more active, or sampling was conducted sporadically throughout the length of the study (Table 1).

Understanding how species utilize resources within their environment is crucial to predicting how changes to resource gradients will affect reproduction, gene flow, and metapopulation dynamics (Holyoak et al. 2008). Despite *M. temminckii* occurring in a variety of aquatic habitats, only a few studies have been conducted at the south-

Table 1. Summary of prior studies investigating the home range and movement of Alligator Snapping Turtles (*Macrochelys temminckii*) using radiotelemetry. The sample size (n) for each demographic group is listed in parentheses. All units for home range size are in meters (m) and refer to linear home range size, unless otherwise reported (e.g., BBKE = Brownian bridge kernel estimation). All movement distance metrics are in meters (m). Note: Riedle et al. (2006) reported distance moved between core sites and Moore et al. (2014) reported dispersal distance from release sites. Ref=reference; ST=state; Mo=duration (number of months; Surv Freq=survey frequency; Source=source population; n=study sample size (total (T), male (M), female (F), unsexed (U)); HR=mean home range \pm SD; MD=mean move distance \pm SD; N/R=not reported in the study.

Ref	ST	System	Mo	Surv Freq	Source	n	HR	MD
Sloan & Taylor (1987)	LA	Large lake system large impounded bayou	15	Daily	Natural and Introduced	T (11) M (5) F (4) U(3)	N/R	N/R
Shipman (1993)	KS	Third-order stream	12	Weekly	Natural	F (1)	N/R	F: 719.0
Harrel et al. (1996)	LA	Large bayou	15	Irregular	Natural	M (3) F (9)	M: 886.3 \pm 243.9 F: 388.9 \pm 220.8	M: 3 52.2 F: 160.3
Riedle et al. (2006)	OK	Low-order streams	14	Two/three relocations per week (active season)	Natural	T (19)	777.8	N/R
Ream (2008)	TN	Riverine backwater lentic	14	Daily (active season) Monthly (dormant season)	Trans-located	U juvenile (6)	0.044 \pm 0.021 ha	N/R
Shipman & Riedle (2008)	MO	River channel	7	N/R	Natural	M (5) F (4)	M: 1309.5 \pm 566.8 F: 2207.4 \pm 980.5	M: 232 \pm 108.4 F: 361.7 \pm 87.6
Howey & Dinkelacker (2009)	LA	Large bayou	13	Weekly	Natural	M (3) F (9)	N/R	N/R

Table 1 (continued)

Ref	ST	System	Mo	Surv Freq	Source	n	HR	MD
Bogosian III (2010)	LA	Large oxbow lake	12	Weekly (active season) Biweekly (dormant season)	Natural and Trans-located	M (4) F (3) U subadult (3)	N/R	Natural: 56.7±7.7 Trans-located: 60.3±11.9
Fitzgerald & Nelson (2011)	TX	Large oxbow lake	15	Irregular	Natural	Not provided	N/R	N/R
Moore et al. (2014)	OK	Impounded river channel	17	Weekly (active season)	Trans-located	M (6) F (6) U juvenile (15)	M: 2175.7±1817.8 F: 1402.2±1651.6 U juvenile: 730.3±889.1	M: 495.5±924.5 F: 1042.8±1615.6 U juvenile: 765.0±1332.6
Spangler et al. (2021)	OK	Spring fed tributary	6	Daily	Captive Bred	U hatchlings (12)	N/R	N/R
Munscher et al. (2021)	TX	Urbanized bayou	30	Biweekly	Natural	M (6) F (4)	M: 1613.0±1132.5 F: 2301.3±1992.4	M: 237.1±191.8 F: 2301.3±1992.4
Kessler & Dreslik (2023)	IL	Fifth-order stream	18	Daily	Trans-located	T (183)	N/R	N/R
Cozad et al. (2023)	FL	Large river system	9	Daily (first year) Weekly and Biweekly (after first year)	Trans-located	M (4) F (4)	M: 12882.8±8781.5 F: 10621.6±6020.4 M (50% (BBKE): 65.8±37.5 ha F (50% (BBKE): 44.6±28.9 ha	

western extent of the species range (Munscher et al. 2020, 2021, 2023; Gordon et al. 2023; Rosenbaum et al. 2023a). Given that this species has exhibited contractions at the periphery of its range, its particularly important to understand its resource use at range edges (Rosenbaum et al. 2023b). Investigating the movement and habitat use of *M. temminckii* across an understudied habitat type (i.e., small lotic streams) at its range edge can inform on the habitat needs for this candidate species and is important to *M. temminckii* populations range wide. For the duration of a year, we quantified *M. temminckii* movement and habitat use within a small lotic stream in eastern Texas. Our objectives were to determine adult female and juvenile movement patterns including linear home range size, distance between relocations, and movement frequency (i.e., activity), and to investigate differences in microhabitat use between age classes across the year.

MATERIALS & METHODS

We conducted our study from July 2008 to September 2009 along a ~2 km section of Bonaldo Creek, within the Stephen F. Austin Experimental Forest (SFAEF), in southern Nacogdoches County (31.49049° N, -94.78996° W) in eastern Texas (Figure 1). The SFAEF is composed of 728 ha of bottomland hardwood forest, of which 670 ha lies within the Angelina River floodplain, and 310 ha comprises upland pinewoods. Bonaldo Creek is a small, relatively undisturbed tributary of the Angelina River not directly used by any municipality or industry (Russell et al. 2002). Due to the dense canopy of hardwoods, this creek tends to have an abundance of woody debris (i.e., individual logs, log jams, root wads, beaver dams, and downed branches) within the confines of the channel and a thick detritus layer on the stream bottom.

Turtles were captured opportunistically in July and August 2008 using baited commercial hoop nets (1.05 m diameter x 2.1 m in length, with 2.5 cm square mesh) positioned upstream from submerged structures. Upon capture, *M. temminckii* were transported to a lab facil-

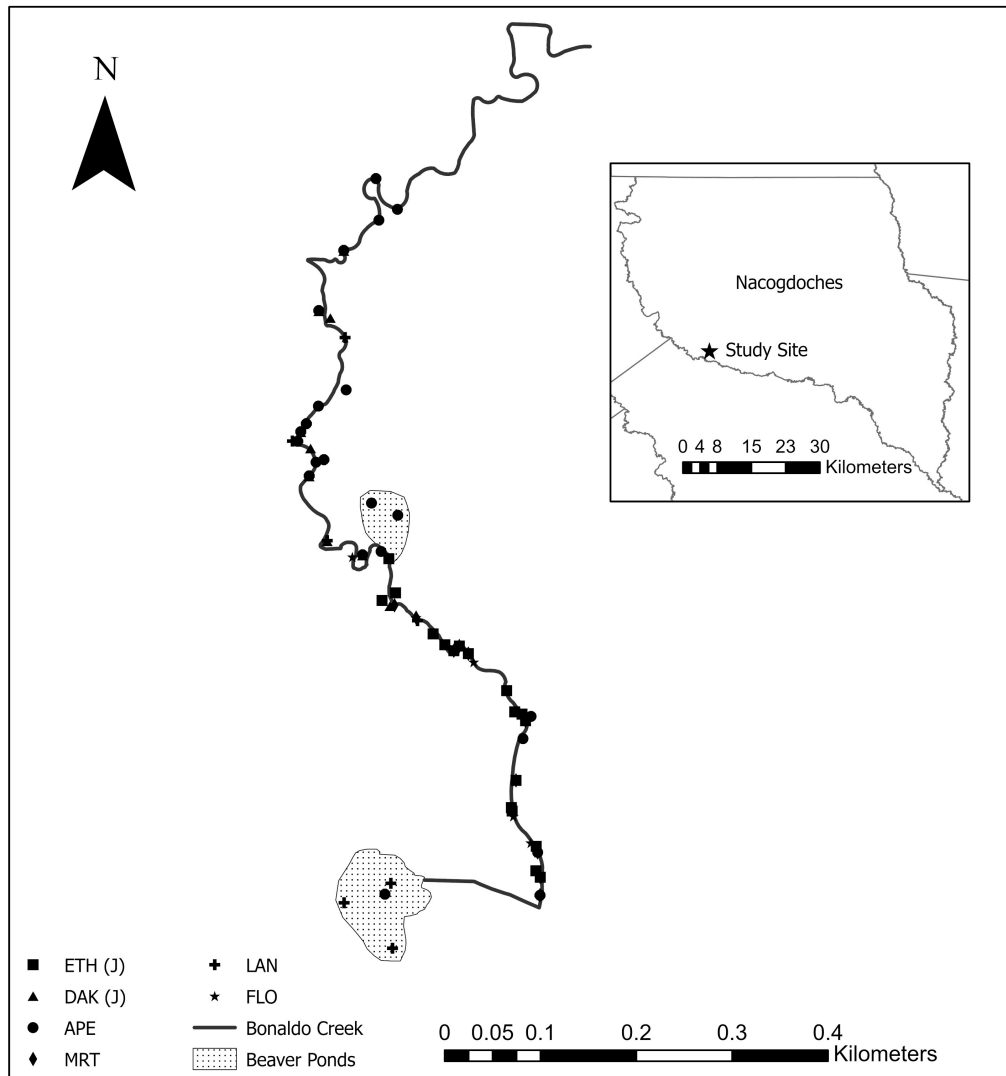


Figure 1. Bonaldo Creek and individual locations of juvenile (i.e., ETH and DAK) and female (i.e., APE, MRT, LAN, and FLO) *M. temminckii* monitored from July 2008 to September 2009 at Bonaldo Creek in the Stephen F. Austin Experimental Forest, Nacogdoches County, TX. The number of relocations for each individual is listed in Table 2. **Inset:** Location of study site in southern Nacogdoches County, TX.

ity for further processing, which included body mass (kg; using spring scales) and curved carapace length (CCL; using a flexible measuring tape), and determination of sex and age class based on tail morphology (Dobie 1971; Table 2). Turtles were marked by filing a unique series of notches in the rear marginal scute following the North American Code

(Cagle 1939). All *M. temminckii* processed in the facility were fitted with VHF transmitters (60 x 11 x 5 mm; ~6.7 g, Wildlife Materials Inc., Murphysboro, Illinois) adhered to the rear carapace using epoxy, then released at the spot of capture the following day.

Turtles were monitored via radiotelemetry two or three times weekly using a 3-element Yagi antenna and a R2100 receiver (Advanced Telemetry Systems, Inc., Isanti, Minnesota). All turtle relocations were recorded using a Garmin™ GPSmap 60CSx unit, and locations were marked with colored ribbons that displayed the time and date of observation with an ID number. A suite of microhabitat variables was collected at each turtle location including water temperature (°C), water depth (cm), stream width (to the nearest 0.5 m), and percent canopy closure (%) measured with an ocular tube (11.5 cm long by 5.0 cm in diameter). We also categorized structure type as one or more of the following: 1) log jam, 2) submerged vegetation, 3) tree roots, 4) floating vegetation, 5) bank undercut, 6) bare bottom, 7) overhanging branches, or 8) flotsam, with associated structural densities reported as either none, sparse, common, or abundant. These structure types are well documented as potential microhabitat features utilized by wild populations of *M. temminckii* and are common features in lotic environments (Hyder et al. 2021; Cozad et al. 2023).

Turtle locations were imported into ArcGIS® version 9.3 (Environmental Systems Research Institute Inc., Redlands, California) to analyze the home range and movement patterns. Within the GPS-mapped area occupied within Bonaldo Creek, linear home ranges were calculated by determining the maximum linear distance for each individual, then pooled based on age class. To assess movement in each age class, we obtained the distance moved (in meters) between consecutive relocations. Movement frequency was calculated by the proportion of individuals that moved between relocations. We analyzed differences in linear home range, distance moved between relocation, and frequency of movement for adult females and juveniles using non-parametric, unpaired Wilcoxon rank-sum tests (Buchanan et al. 2017).

Table 2. Demographics and linear home range size of *M. temminckii* tracked from July 2008 to September 2009 in Bonaldo Creek at the Stephen F. Austin Experimental Forest in Nacogdoches County, Texas. Upon capture, turtles were classified as adults (A) or juveniles (J). Based on the criteria in Dobie (1971), adult turtles were sexed as females (F) or undetermined (U) based on pre-cloacal tail length to body size. Curved carapace length (CCL), Body mass, and maximum linear distance (MLD) were recorded upon initial capture.

Turtle ID	Age Class	Sex	CCL (cm)	Mass (kg)	MLD (m)	Number of Relocations
APE	A	F	48.8	18.8	1396	73
FLO	A	F	41.2	13.4	1128	85
LAN	A	F	43.0	12.0	1353	72
MRT	A	F	50.6	21.8	405	54
ETH	J	U	30.0	4.8	440	90
DAX	J	U	32.5	5.3	997	27

To investigate differences in movement across the duration of sampling, the average distance moved by each age class was calculated across time (i.e., day of the year). During a short period in the winter of 2009 (JD 2454814–JD 2454857), both adult females and juveniles were only sporadically monitored, limiting the ability to accurately fit linear models to interpret movement over time. However, monitoring was consistent enough across time to determine when *M. temminckii* may increase or decrease activity. Therefore, General Additive Models (GAM) were fitted to each age class across the length of the study. We compared model outputs for each group and determined the correlation coefficients for naturalized splines identified by our GAM analyses. We then tested for differences between groups based on these distributions. Models were fitted using the package ‘mgcv’ and ‘gam’ packages in R (R Core Team 2023).

To assess habitat use of *M. temminckii*, we performed Non-metric Multidimensional Scaling (NMDS) to determine if adult females and juveniles overlapped in overall habitat use. We then tested for significant differences between age classes with Permutational Analysis of Variance (PERMANOVA; Anderson 2017). To further explore how microhabitat use may differ between females and juveniles

across time, we binned microhabitat data across Julian Days into quarterly periods in accordance with typical regional seasonal time periods. Then we constructed logistic regression models to determine if certain microhabitat variables were more likely to be used by females or juveniles with season as an interaction (Buchanan et al. 2017). We selected the best model based on Akaike information criterion corrected for small-sample size (AICc), identified which microhabitat variables were significant based on the model output coefficients, and then used a Chi-squared test to interpret the differences between juveniles and females between those selected microhabitat features. All of the microhabitat analyses were performed using the ‘vegan’ and ‘aod’ packages in R (R Core Team 2023).

RESULTS

We obtained 401 relocations on six *M. temminckii* (4 females; 2 juveniles) between July 2008 and September 2009 (Figure 1; Table 2). An additional juvenile was only monitored for a short period of time, in which it only made five recorded movements. Because the transmitter could not be recovered and no movement was observed for this individual during the remainder of the study, we assumed a mortality event or transmitter failure may have occurred and this individual was removed from our analyses.

The median linear home range for all turtles was 1062 m (range = 405–1395 m). Females generally had slightly longer median home ranges (1240 m; range = 1128–1396 m) than juveniles (718 m; range = 440–997 m), although this difference was not significant (*Wilcoxon test*, $W = 6$, $p = 0.53$, effect size $r = 0.38$; Table 2). Distance moved between relocations did not differ between age classes, although females had a greater tendency to make longer distance movements overall (*Wilcoxon test*, $W = 177$, $p = 0.24$, effect size $r = 0.06$; Figure 2). The overall frequency of movement between relocations was similar

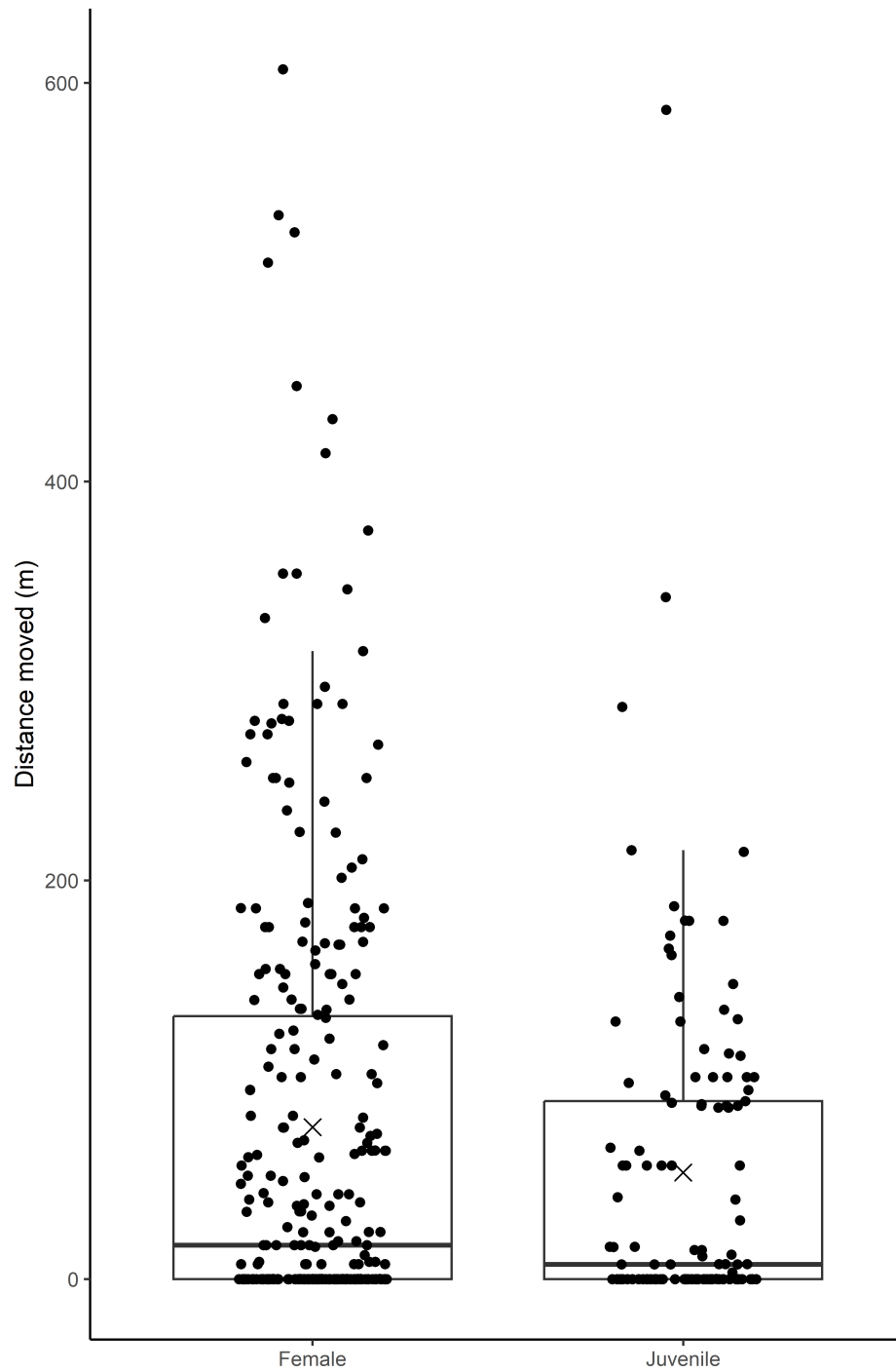


Figure 2. Boxplots of distance moved between telemetry checks of adult female (F) and juvenile (J) *M. temminckii* pooled from July 2008 to September 2009. Black dots represent individual relocations for each age class. The mean distance moved for each age class is noted by X.

between groups, as juveniles moved 53% of the time and females moved 55% of the time (*Wilcoxon test*, $W = 3.5$, $p = 1.0$, effect size $r = 0.51$; Figure 2)

Females and juveniles exhibited similar annual movement patterns (female, $R^2 = 0.14$, $F = 10.70$, $p = 0.033$; juvenile, $R^2 = 0.24$, $F = 3.99$, $p = 0.0005$; Figure 3). Both females and juveniles decreased their movements in the fall and winter months, although this reduction in movement was more pronounced in juveniles (*Wilcoxon test*, $W = 21$, $p = 0.005$; Figure 3).

We observed no significant difference in overall microhabitat use between adult females and juveniles (*PERMANOVA*; $n = 999$, $F = 17.34$, $\text{Pr}(>F) = 0.61$). Instead, juveniles utilized a smaller subset of available microhabitats utilized by females (Figure 4). However, female microhabitat use expanded in the spring and summer months, whereas juveniles utilized similar microhabitats across the year (Figure 4). Assessing microhabitat preference with logistic regression, the best fit AICc model to predict which microhabitat variables predicted age class was: $Y = \text{Age class} \sim \text{water depth} + \text{Submerged structure (density)} + \text{tree roots (presence; density)} + \text{overhanging vegetation (presence)} + \text{undercut (presence)}$.

None of the models including season as an interaction were ranked highly in the AICc. Based on the above model output, Chi-squared tests revealed that females had a broader niche breadth and utilized more types of microhabitats than juveniles. For example, females preferred microhabitats featuring several types of abundant submerged structure ($\chi^2 = 18.2$, $\text{df} = 3$, $p = 0.003$), while overhanging vegetation was the most common microhabitat feature utilized by juveniles ($\chi^2 = 18.2$, $\text{df} = 3$, $p = 0.045$).

DISCUSSION

This study contributes to the knowledge of *M. temminckii* movement and microhabitat use in low-order stream systems, an important and

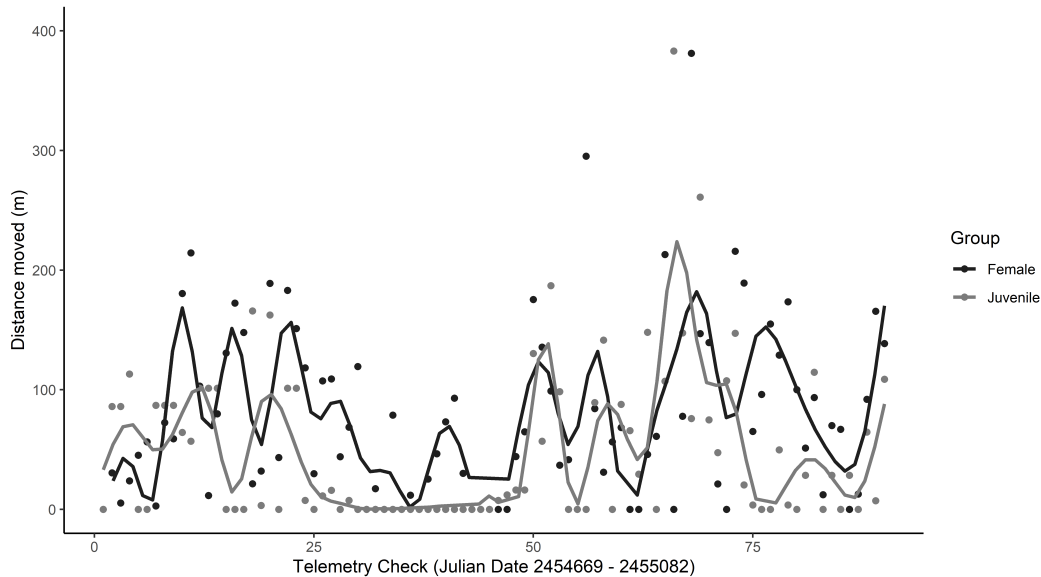


Figure 3. General additive models of average movements (m) of adult female (black dots) and juvenile (grey dots) *M. temminckii* to Julian day (JD) from July 21, 2008 to September 7, 2009 (JD 2454669–JD 2455082) in Bonaldo Creek, Stephen F. Austin Experimental Forest, Nacogdoches County, Texas.

understudied habitat type for this species. As these streams are abundant on the landscape, they can provide abundant accessible microhabitats, facilitate connectivity to other habitats, and may be important for maintaining subpopulations (Riedle et al. 2006; Kessler & Dreslik 2023). In terms of movement and microhabitat selection, we found little evidence to support differences between female and juvenile age classes, although we observed general consistencies to other studies on *M. temminckii* in lotic environments.

Lentic and lotic environments differ in several biotic and abiotic variables that may interact with sex, body size, and life history stage to influence the spatial ecology of aquatic turtles (Ryder & Pesendorfer 1986; Carrière et al. 2009; Silveira et al. 2020). Within the hydrological systems that *M. temminckii* can inhabit, water velocity, productivity, thermal regimes, and habitat structure can vary across space and time (Pearson et al. 2023; Rosenbaum 2023a). The linear home ranges for female turtles in Bonaldo Creek were smaller than what has been reported in lentic systems (Howey & Dinkelacker 2009; Moore et al. 2014). Although this is consistent with other studies in small stream

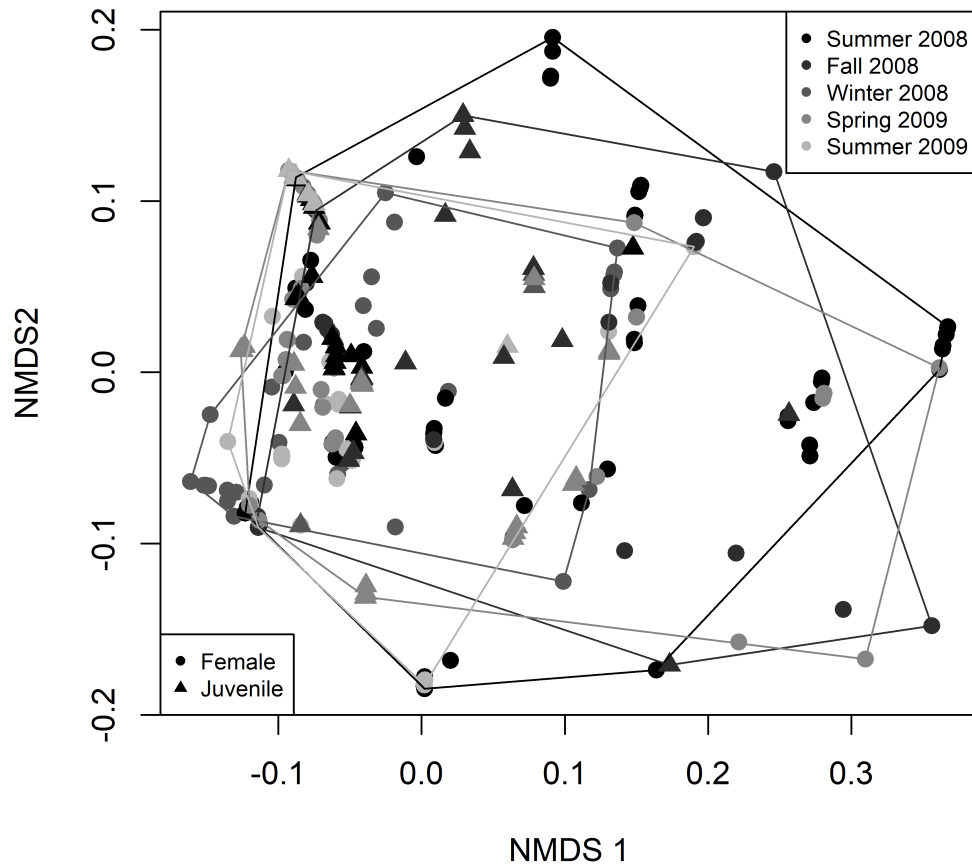


Figure 4. Non-metric multi-dimensional scaling ordination (NMDS) depicting seasonal microhabitat use by *M. temminckii* in Bonaldo Creek, Stephen F. Austin Experimental Forest, Nacogdoches County, Texas. Convex hulls reflect seasonal microhabitat space occupied by adult females (closed circles) and juveniles (closed triangles) in Summer 2008 (July 2008– August 2008; black), Fall 2008 (September 2008–November 2008; dark grey), Winter 2008 (December 2008–February 2009; medium grey), Spring 2009 (March 2009–May 2009; grey), and Summer 2009 (June 2009–September 2009; light grey).

systems in the western extent of *M. temminckii* range (Riedle et al. 2006; Shipman & Riedle 2008; Munscher et al. 2021). Similar to other aquatic turtles, seasonal changes in temperature and habitat connectivity may influence home range size in *M. temminckii* (Carrière

et al. 2009; Fitzgerald & Nelson 2011; Riedle et al. 2016). Small streams (i.e., lotic) or oxbow lakes (i.e., lentic) may become temporally isolated in times of drought and constrict home range size when dispersal ability is limited (Anthonysamy et al. 2014). Alternatively, regular flooding allows access to other environments that may then be exploited (Bodie & Semlitsch 2000; Cozad et al. 2023). The benefit of spatial and temporal variation in habitat connectivity may vary across ontogeny due to variation in resource demands between each age classes. Juveniles may alter their movement behavior to reduce predation risk, while sexually mature females allocate more energy towards gamete development, egg production, and searching for nesting habitats (Tucker & Sloan 1997; Hyder et al. 2021 Spangler et al. 2021; Thompson et al. 2023). Ontogenetic shifts in movement between *M. temminckii* age classes have been reported in previous studies (Bogosian III 2010; Moore et al. 2014; Hyder et al. 2021; Spangler et al. 2021). However, Harrel et al. (1996) found subadult and adult movements were similar in a lotic system in Louisiana. While we did observe that juveniles tended to move less frequently and shorter distances than females in Bonaldo Creek, these patterns were not significant, which is consistent with past studies. Ectotherms, particularly reptiles, have been shown to increase or decrease their home range size, movement distance, or movement frequency based on the spatial organization of habitat (e.g., thermoregulatory refuges; Brown et al. 1994; Fitzgerald & Nelson 2011; Slavenko et al. 2016; Pafilis et al. 2019; Madrak & Lewison 2021). Low-order stream systems under natural conditions possess a high habitat heterogeneity and serve as important reservoirs for maintaining subpopulations of many species in riverine systems (Palmer & Poff 1997; Lyon et al. 2019). Bonaldo Creek is a relatively pristine low-order system in eastern Texas, connected to other low-order creeks and the Angelina River (Kavanagh & Kwiatkowski 2016). Many studies have suggested that *M. temminckii* prefer forested habitats with abundant amounts of in-stream structure (Harrel et al. 1996; Howey & Dinkelacker 2009; Riedle et al. 2006; Rosenbaum et al. 2023b). To this effect, *M. temminckii* may be generalized in their habitat preference, in which habitat at a landscape scale may be a better indicator of occupancy and prevalence than more fine-scale microhabitat selection (Fitzgerald &

Nelson 2011; Cozad et al. 2023; Rosenbaum et al. 2023b). Low-order streams covered by dense overstory canopies may provide an abundance of structural habitats (i.e., submerged structure, root wads, overhanging structure), and in turn, could provide ample resources (i.e., refuge, prey, mating opportunities) to support different age classes of *M. temminckii*. In our study, adult females seasonally exploited a wider array of microhabitats than juveniles, despite not observing differences in seasonal movement between age classes. This further suggest that microhabitat features are widely available for use within this stream, which may be why we observed truncated movement patterns with juveniles and females utilizing similar overall microhabitats.

Understanding movement and habitat use at different spatiotemporal scales is useful to develop predictions on how species will respond to environmental change (Morris 1987; Gibbons & Lovich 2019; Bury 2006). For *M. temminckii*, lotic systems may be important for maintaining populations, but these environments are also greatly affected by both natural and anthropogenic stressors that can alter habitat structure (e.g., floods, droughts, channelization, changes in forest cover, woody debris inputs, etc.; Malmqvist & Rundle 2002; Friberg 2014; Cantonati et al. 2020). Population declines and range contractions have only heightened the need to better understand these key aspects of *M. temminckii* ecology across aquatic environments and spatiotemporal scales.

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