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Ecology of Hatchling Alligator Snapping Turtles (*Macrochelys temminckii*)

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ECOLOGY OF HATCHLING ALLIGATOR SNAPPING TURTLES
(MACROCHELYS TEMMINCKII)

A Master's Thesis

Presented to

The Graduate College of
Missouri State University

In Partial Fulfillment

Of the Requirements for the Degree
Master of Science, Biology

By

Sarah Spangler

December 2017

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ECOLOGY OF HATCHLING ALLIGATOR SNAPPING TURTLES
(*MACROCHELYS TEMMINCKII*)

Biology

Missouri State University, December 2017

Master of Science

Sarah Spangler

ABSTRACT

Little is known about the first year of life for many of the world's freshwater turtles. This is due in part to their cryptic nature and the difficulty of locating hatchlings in the wild. The lack of information about this demographically important age group has led researchers to draw conclusions from indirect inferences about survival rates and ecological roles of hatchlings that may or may not be accurate. To begin filling in some of these gaps, I focused on the first year in an alligator snapping turtle's life. I studied: (1) circadian and circannual patterns of activity, (2) growth rates and how they are related to activity rates, (3) habitat preferences, (4) fall movement patterns, and (5) predation patterns. My study site was within the species' natural range in southeastern Oklahoma. Unlike adults, hatchlings followed a predominantly diurnal activity pattern for much of the year, with peak activity occurring during the mid-hours of the day. The diurnal habit of hatchlings may be a strategy to temporally partition themselves from nocturnal predators. There were no significant relationships between growth rates and activity rates during any period, potentially due to small sample size. Hatchlings were located in areas of increased cover and shallower water depths, when compared to random locations. Their movement patterns were characterized by an initial movement away from the site of release to a location with suitable habitat characteristics, and they tended to stay at these locations for extended periods. I documented depredation by fish, but not by terrestrial predators such as raccoons.

KEYWORDS: *Macrochelys temminckii*, hatchling, movement, habitat, depredation

This abstract is approved as to form and content

Day B. Ligon, PhD
Chairperson, Advisory Committee
Missouri State University

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Approved:

Day B. Ligon, PhD

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In the interest of academic freedom and the principle of free speech, approval of this thesis indicates the format is acceptable and meets the academic criteria for the discipline as determined by the faculty that constitute the thesis committee. The content and views expressed in this thesis are those of the student-scholar and are not endorsed by Missouri State University, its Graduate College, or its employees.

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I dedicate this thesis to my wife, Leighanna Rickman.

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OVERVIEW

Due to limited information regarding the first years in the life of a turtle, they are often termed the “lost years” or “missing links” in a species’ life history (Carr, 1987; Morafka, 1994). While the stability of a population is dependent upon survival at all age classes (Congdon et al., 1993; Congdon et al., 1994; Heppell et al., 1996), insufficient information on the most vulnerable years can lead to inferences that end in poor management decisions (Pullin and Knight, 2003). For hatchling freshwater turtles, the deficit in knowledge largely stems from difficulty in locating and monitoring small turtles in their natural habitats (Wilbur, 1975; Congdon et al., 1994).

Activity patterns of freshwater hatchling turtles have not been well described in the literature. Most studies of hatchling turtles’ activity patterns tend to be associated with nest emergence behavior and experiments focused on survival during the overland trek from a nest to an aquatic habitat (Burger, 1976; Janzen, 1993; Janzen et al., 2000a,b; Tuttle and Carroll, 2005; Tucker et al., 2008). Therefore, I set out to study several aspects of the ecology of hatchling alligator snapping turtles (*Macrochelys temminckii*) to fill in missing gaps in the literature.

Chapter 1 focuses on circadian and circannual activity patterns of hatchling *M. temminckii* in a semi-natural environment. These patterns were assessed using the signal change method (Tucker et al., 2014) that allowed differentiation between bouts of activity and inactivity, but does not lend itself to ascribing higher resolution characterization of behaviors that contribute to overall activity. Effect of temperature on activity was also addressed to better characterize seasonal changes. Furthermore, Chapter 1 investigates

the relationship between levels of activity for specific hatchlings with growth rates, with the assumption that high activity rates likely stem from more active foraging.

Chapter 2 focuses on movement patterns of hatchling *M. temminckii* in a natural system after release. In this chapter, habitat characteristics were quantified and associations are made between what is considered preferable habitat. Chapter 2 describes instances of depredation and makes inferences about the lack of depredation by raccoons (*Procyon lotor*), a known common predator of hatchling turtles.

This study has been approved through the Missouri State University Institutional Animal Care and Use Committee (Approved: 9/29/15; IACUC ID 16-005.0).

ACTIVITY PATTERNS AND GROWTH RATES OF HATCHLING ALLIGATOR SNAPPING TURTLES (*MACROCHELYS TEMMINCKII*)

Abstract

Descriptions of circadian and circannual activity patterns for a species provide insight into ecologically important behaviors. However, daily activity of a species can be difficult to assess and therefore a generalization about annual activity often serves the purpose of describing both circadian and circannual activity. While circannual patterns allow inferences on reproductive cycles, they do not provide information for sexually immature age classes. Freshwater hatchling turtles are an understudied age class due in part to the difficulty in monitoring small, cryptic, aquatic species. However, understanding their circadian and circannual activity patterns may lead to greater success in head-start programs, which are being utilized more frequently as populations decline. Alligator snapping turtle (*Macrochelys temminckii*) are one such species that is part of a captive breeding and head-starting program. In this study the daily and seasonal activity pattern of hatchling *M. temminckii* were categorized by using an automated receiver that allowed continuous monitoring of activity. A temperature profile of the environment was recorded by data loggers to assess the role temperature plays in the activity of a freshwater ectotherm throughout the year; while growth measurements were collected to test for relationships with activity. Activity patterns were significantly diurnal during months of increased water temperature, however they remained diurnal even during the coldest months of the year when activity was minimal. There was no significant relationship between growth rates and activity rates during any period.

Introduction

As with most animals, turtles typically exhibit predictable circadian and circannual activity patterns. Such patterns vary among taxa, but are often influenced by environmental variables such as temperature, humidity, day length, rainfall (and availability of standing water), and the activity patterns of concomitant predators and prey (Lovich, 1988; Lindeman, 1996; Nieuwolt, 1996; Cooley et al., 2003; Ernst and Lovich, 2009). The seasonal activity patterns of many turtle species are well described, likely because these annual patterns correspond with other traits of biological importance such as foraging, mating, and nesting seasons (Pluto and Bellis, 1988; Brown and Brooks 1993; Thomas et al., 1999). Daily activity patterns, on the other hand, are often less carefully described, and species' patterns are sometimes painted with a broad brush and with little explicit supporting evidence (Ernst and Lovich, 2009). With few exceptions, species are typically assigned to one of three categories—diurnal, crepuscular, or nocturnal—with little recognition of how activity patterns may vary temporally or among different demographic groups.

Circadian activity patterns of a species can vary demographically, and, in fact, differences in the behavior of females and males are often specifically compared to gain insights into mating strategies and reproductive patterns (Brown and Brooks, 1993; Thomas et al., 1999; Grayson and Dorcas, 2004). Age-specific variation in activity is less frequently addressed (Standing et al., 1997; Tuttle and Carroll, 2005). In general, hatchling turtles are more cryptic and difficult to monitor than their adult and sub-adult counterparts, and therefore activity patterns in this group are rarely studied. However, there are exceptions, and several studies of terrestrial turtles and tortoises have focused

on behavior of hatchlings and young juveniles during the first year post-hatching (Berry and Turner, 1986; Keller et al., 1997; Epperson and Heise, 2003; Pike, 2006; Sievers, 2015). Fewer studies have reported activity patterns of hatchling freshwater turtles, a deficit that likely stems from the logistical challenges involved in monitoring small aquatic animals. However, among species for which data are available, ontogenetic shifts in activity are frequently evident (Ernst et al., 1989a; Tucker et al., 1995; Thomas, 2002). Such differences are not surprising—hatchling turtles differ in many important ways from adult conspecifics. For example, adult turtles may exhibit activity when engaged in foraging, thermoregulation, predator avoidance, and behaviors associated with reproduction such as mate searching and nesting (Gibbons, 1990). In contrast, foraging, thermoregulation, and predator avoidance are relevant for hatchlings, but activities related to reproduction are not. Furthermore, the specific nutritional resources and predators with which hatchlings are concerned often differ from those of adults (Clark and Gibbons, 1969; Janzen et al., 2000a), thereby necessitating different activity patterns.

In this study, I quantified daily and seasonal activity patterns of hatchling alligator snapping turtles (*Macrochelys temminckii*). I predicted that overall activity levels would vary seasonally, and that they would vary predictably with water temperature. Additionally, I hypothesized that because *M. temminckii* seldom bask (Carr et al., 2011) most activity during this life stage would be dedicated to foraging, and therefore that individuals that exhibited more activity would also exhibit faster growth rates.

Materials and Methods

Location. I conducted my investigations from 2015–2016 in an outdoor pond (dimensions: 25 × 12 m) at Tishomingo National Fish Hatchery (Appendix A). A chain-link fence with aluminum flashing positioned around the bottom and two electrified wires—one on top and one along the bottom—surrounded the pond to exclude mammalian predators. However, there was still potential for predation by avian, reptilian, and amphibian predators. The pond had a relatively uniform bottom with steeply sloped sides, and averaged ~1 m deep. Logs were positioned along the shoreline to provide possible cover for the hatchlings. Vegetation in the pond primarily consisted of coontail (*Ceratophyllum demersum*), pondweed (*Potamogetonaceae* sp.), and cattails (*Typha latifolia*), and the pond was stocked with western mosquitofish (*Gambusia affinis*) and fathead minnows (*Pimephales promelas*) as potential prey items for hatchling *M. temminckii*. The pond was also a habitat for myriad macroinvertebrates, including damselfly, dragonfly, and mayfly nymphs as well as crayfish (superfamily: Astacoidea), several frog species (American bullfrog, *Lithobates catesbeiana*; southern leopard frog, *Lithobates sphenoccephala*; Blanchard's cricket frog, *Acris blanchardi*) and their larvae. Snakes, including diamondback water snakes (*Nerodia rhombifer*), cottonmouths (*Agkistrodon piscivorous*), and ribbon snakes (*Thamnophis proximus*), were common in the surrounding habitat but rarely seen in the study pond, possibly due to exclusion by the metal flashing. The pond received inflow from a nearby creek, from which fry and small fish could populate the pond incidentally.

Activity patterns and thermal profiles. Fifteen turtles equipped with radio transmitters (L.L. Electronics, Mahomet, IL or Holohil Corp., Ontario, Canada) were

released into the fenced outdoor pond on 25 September 2015 to quantify the daily and seasonal activity patterns of hatchling *M. temminckii*. The transmitters weighed 1.9 g each and were approximately 11 mm long with a 100-mm long whip antenna.

Transmitters were attached with waterproof epoxy (Marine Epoxy; Loctite, Westlake, OH, USA) to the hatchlings' carapace between the midline vertebral ridge and the right or left lateral ridges (Appendix B). Hatchlings were reweighed after transmitter attachment, with the proportion of transmitters mass to hatchling mass initially being between 10–11% of hatchlings' mass. By the last measurement event, transmitters averaged 8% of hatchlings' mass. An antenna set atop a 9-m tall tower was connected to an automatic receiving unit (ARU) (Sparrow Systems, Fisher, Illinois, USA) stationed just east of the pond. The ARU was used to collect activity data using the signal change method (Tucker et al., 2014). Signal strength in decibel-milliwatts (dBm) for each transmitter was recorded each minute for the duration of the study.

The nominal battery life of the transmitters was 60–90 days. However, to minimize the risk of premature battery failure, the hatchlings were hand-captured approximately every 56 days. This schedule resulted in a total of six rounds of transmitter replacement for each animal, in order to capture most of a year's worth of activity data. Upon recapture, each turtle was weighed and measured prior to removing the transmitter. The transmitters were removed from the animals using a rotary tool to separate the epoxy from the carapace of the turtle. A new or re-furbished transmitter was attached in the same manner as described above. The hatchlings were weighed and measured again before being released back to the location in which they were found, and releases occurred within 24 h of capture. Despite the conservative replacement schedule, some

transmitters failed before they were retrieved. Therefore, the number of hatchlings being monitored decreased over the duration of the study. At the conclusion of the study, in August 2016, four hatchlings were recaptured.

Three temperature-recording data loggers (Thermocron iButton, model DS1922L, Maxim Integrated Products, Inc., Sunnyvale, CA) were secured in waterproof containers, attached equidistantly from one another to a length of plastic pipe, and then secured at the deepest portion of the pond to record surface, middle, and deep water column temperatures. I also deployed a single temperature-recording logger attached to a cinderblock and placed it in shallow water on the south side of the pond. This location was near cattails, and previous observations indicated that hatchlings often inhabited this portion of the pond. The data loggers were programmed to record temperatures at a resolution of 0.5 °C at 68-min intervals to capture 365 days of data.

Analyses. Diel activity patterns were analyzed using repeated measures analysis of variance (ANOVA) and, when appropriate, Tukey's post-hoc t-tests. Average minutes active were pooled by hour of day for each individual to generate values that reflected average hourly activity rates. Seasonality in average time spent active was examined by dividing the study into six intervals of 54–55 day duration (Interval 1 = 27 September–19 November; Interval 2 = 20 November–12 January; Interval 3 = 13 January–6 March; Interval 4 = 7 March–29 April; Interval 5 = 30 April–23 June; Interval 6 = 24 June–17 August).

Repeated measures ANOVA and Tukey's pair-wise t-tests were also used to analyze activity patterns across temperatures. As above, data were separated into six time intervals, and average activity data were pooled by 1° increments for each individual,

resulting in values that reflect average activity rates per 1 °C temperature increments.

Data lost to failed transmitters (and possibly to depredation) limited the extent of growth data available, as the number of turtles that were released at the beginning of the study were not all available for measurement at the end. Therefore, my assessment of growth rates is restricted to the period 19 October–17 March. This period was divided into three periods corresponding with: warm but falling water temperatures (daily mean temperatures ranged from 17.65–25.40 °C), cool winter-time temperatures (6.09–20.09 °C), and cool late winter temperatures (7.28–18.49 °C). These periods spanned 19 October–23 January (period 1), 24 January–17 March (period 2), and 18 March–8 April (period 3); the duration of each period differs because they were defined by when turtles were recaptured for measurements and to replace radio transmitters. To test whether average activity rates influenced growth rates, I conducted linear regressions of growth rates on average activity rates during each of the three periods. Growth rates were calculated as change in mass per gram of initial mass per day to correct for variation in hatchlings' size at the onset of the study and for slight differences in the time between measurements for individual turtles. Minitab 17 (Minitab, Inc., State College, PA, USA) was used to perform all statistical tests. The significance threshold was set at $\alpha=0.05$ for all tests.

Results

There was a significant effect of time of day on the average time spent active across all hatchlings for the entirety of the study tested (27 September, 2015 – 17 August, 2016) ($F_{23, 57874} = 144.65$, $P < 0.001$) (Figure 1), and this effect remained significant

when the study's duration was divided into six discrete time intervals (Figure 2). Post-hoc pairwise comparisons indicated that hatchlings consistently exhibited diurnal activity patterns; activity rates between the hours of 08:00 to 15:00 showed no significant differences, but were higher than all other hours of the days when analyzed over the entire study duration. Similarly, intervals 1–6 all indicated that the mid-portion of the day always had higher activity than during other hours. However, during intervals 2 and 3 (20 November–6 March), which correspond with low water temperatures (Figure 3), the differences between means was less pronounced and for interval 2 only the hours of 03:00, 05:00, and 06:00 were significantly lower than the middle hours of the day. Intervals 5 and 6 both showed a trend in significantly increased activity during the mid-hours of the day when compared with the evening hours.

Average water temperature for intervals 1–6 ranged from 11.88 °C, during interval 2, to 31.15 °C, during interval 6 (Figure 3). There was a significant effect of temperature on average percent of time spent active for the entire duration of the study ($F_{29,291} = 4.01$, $P < 0.001$) (Figure 4). There were significant effects of temperature on average percent of time spent active for intervals 1,3,4,5, and 6 as well ($P < 0.05$), but not interval 2 ($P = 0.92$) (Figure 5). Post-hoc pairwise comparisons for the effect of temperature on the percentage of time spent active at each temperature increment for the entire study were largely non-significant, most likely due to a small number of hours at which extreme temperatures occurred. However, during specific date ranges, the high and low temperatures were significantly different. During interval 1, temperatures 25–27 °C all had significantly higher average percent of time spent active by hatchlings when compared to temperatures 14–17 °C. Yet, during interval 2 there were no significant

differences between any of the average percent of time spent active for any of the temperatures experienced. During interval 3, average percent of time spent active at the temperatures of 12, 13, and 14 °C were significantly different from 5 °C, but these were the only significant differences in temperature-specific activity rates. The trend was similar for interval 4, as well. Activity during intervals 5 and 6 cleanly split into two groups, daytime and nighttime, within each of which activity rates were consistent.

There was no significant relationship between growth rates and activity rates, potentially due to small sample size (Period 1, $t_4 = 1.94$, $P = 0.12$, $R^2 = 0.49$; Period 2, $t_4 = -0.21$, $P = 0.84$, $R^2 = 0.01$; Period 3, $t_4 = 1.67$, $P = 0.17$, $R^2 = 0.41$) (Figure 6).

Discussion

Macrochelys temminckii have been described as predominantly nocturnal, although this conclusion apparently has only limited support in the literature (Allen and Neill, 1950; Ewert et al., 2006). However, there are several published observations of daytime and evening activity, and authors have characterized these instances as deviations from the typical activity patterns for the species (Ewert, 1976; Harrel et al., 1996; Ewert et al., 2006). In contrast, the activity patterns that I documented for hatchling *M. temminckii* were clearly diurnal during times of the year when they were active. This pattern disappeared during the coldest intervals, but only because the turtles became inactive—not due to a shift to an alternative daily activity schedule.

It is important to recognize that measuring activity using the signal change method provides a measure of changes in distance and orientation of a radio transmitter affixed to an animal relative to a stationary receiving antenna, but does not ascribe

behaviors to detected movements (Tucker et al., 2014). Therefore, during bouts of recorded activity, animals might be engaging in behaviors of great ecological consequence, such as foraging or mating, or they may be engaged in something more mundane such as burying in mud. Similarly, bouts of inactivity cannot necessarily be inferred to indicate periods of sleep or torpor; it is equally possible that intervals of low activity correspond with bouts of sit-and-wait foraging. Despite these limitations on interpreting signal change data, the consistently high daytime activity rates that I observed can only reasonably be inferred to indicate that hatchling *M. temminckii* are ecologically diurnal.

There are three possible explanations for the apparent contradiction in the activity patterns of *M. temminckii* described in this study (wholly diurnal) to that previously reported in the literature. First, the conclusion that *M. temminckii* are predominantly nocturnal is supported by very limited data (Ewert et al., 2006); therefore, it is conceivable that previous researchers have simply drawn inaccurate conclusions. Second, much of the evidence for nocturnal activity came from populations in Florida and Georgia (Allen and Neill, 1950; Johnson, 1989; Moler, 1996; Jensen and Birkhead, 2003), and in fact some is likely derived from a different species, the recently described *Macrochelys suwanniensis* (Allen and Neill, 1950; Thomas et al., 2014). I conducted my study in a more northern location in Oklahoma, and it is possible that geographical and/or phylogenetic variation explains the apparently conflicting conclusions. Finally, it is possible that *M. temminckii* generally is nocturnal, but that the activity patterns of seldom-observed hatchlings follow a distinctly different pattern than do those of older age classes.

If hatchling *M. temminckii* do in fact follow an activity pattern that differs from that of older conspecifics, it seems plausible that it could be a means of reducing predation risk. Although hatchling *M. temminckii* are larger than hatchlings of other North American freshwater turtle species, they are nonetheless at great risk until they attain a larger size (Dreslik et al., 2017, chapter 1). The relative absence of nocturnal activity may effectively reduce exposure to predators. As previously noted, hatchling turtles are at risk from a wide variety of nocturnal and diurnal predators; however, evidence suggests that raccoons (*Procyon lotor*) may have the greatest impact on young turtles nearly everywhere they co-occur (Seigel, 1980; Stancyk et al., 1980; Christiansen and Gallaway, 1984; Congdon et al., 1987; Garmestani and Percival, 2005; Ernst and Lovich, 2009), and this relationship has been documented for alligator snapping turtles specifically (Redmond, 1979; Holcomb and Carr, 2013; Dreslik et al., 2017). Other predators, such as river otters (*Lontra canadensis*) (Ligon and Reasor, 2007), great blue herons (*Ardea herodias*) (Ligon, pers. obs.) and even adult *M. temminckii* (Sloan et al., 1996; Ligon, pers. obs.) are known to prey upon hatchlings, but I predict that their impact would be less influential in shaping activity patterns than that of raccoons, for two reasons. First, as mentioned, the overall predation rate by raccoons is likely higher than by any other species. Therefore, this single predatory species likely represents a strong force in natural selection. Second, of the several documented predators, only raccoons adhere to a reasonably strict nocturnal foraging pattern (Sharp and Sharp, 1956; Greenwood, 1982; Kaufmann, 1982). *Ardea herodias*, *L. canadensis*, and adult *M. temminckii* all reportedly forage both day and night (Black and Collopy, 1982; Ewert et

al., 2006; Martin et al., 2010). Therefore, adjusting the timing of activity might do little to alter their exposure to these predators.

I cannot dissociate potential changes in activity rates due to water temperature from other seasonal variables such as day length. However, it seems likely that much of the reduction in activity during the coldest intervals was in fact due in large part to low temperature itself. Interestingly, some level of activity was observed at all temperatures experienced throughout the study. Activity that occurred during the coldest intervals—and at the lowest temperatures occurring within those intervals—provide evidence that hatchling *M. temminckii* do not achieve the deep states of torpor during the winter that some other aquatic turtle species do (Ernst, 1972; Obbard and Brooks, 1981; Ernst et al., 1989b; Meeks and Ultsch, 1990; Ernst et al., 2014). However, this might vary with latitude. Winter activity of *M. temminckii* has not previously been described; it is possible that the infrequent low-temperature movements that I documented were to the surface to breathe, or may have been triggered by a perceived predatory threat. The absence of growth during the coldest interval suggests that turtles likely were not engaging in foraging behavior.

The high activity rates that occurred at extreme temperatures might indicate that hatchling *M. temminckii* seek seasonally-adjusted moderate water temperatures; the high rates of activity at comparatively cold and warm temperatures could be attempts to find alternative thermal microclimates. Interestingly, evidence of moderating thermoregulatory behavior in other *M. temminckii* demographic groups is mixed. In a study conducted in northern Louisiana, movements (which are different than but likely correlated with activity as measured using the signal change method) of juvenile *M.*

temminckii were positively correlated with water temperature (Harrel et al., 1996).

However, even when water temperature reached its maximum in July (29.1 °C), turtles did not retreat from near-shore refugia to deeper, cooler water. In contrast, in a telemetry study conducted in eastern Oklahoma, adult *M. temminckii* moved downstream to deeper water during hot summer months (Riedle et al., 2006). Thermoregulatory behavior was observed in a study in eastern Texas, as well; adult *M. temminckii* apparently thermoregulated by selecting microhabitats that were warmer and more stable than at randomly selected locations (Fitzgerald and Nelson, 2011).

Predictably, there was no relationship between activity and growth rates during the coldest winter interval because both rates were extremely low and exhibited little variation among individuals. This is consistent with observations that adult *M. temminckii* do not feed when water temperatures are below 18 °C (Allen and Neill, 1950). During the first and third periods over which growth was measured, 41–49% of the variation in growth was attributable to variation in activity rates. Although there was no significant relationship between growth and activity rates, possibly due to my small sample size, the positive trend between growth and activity during the warmer fall and spring intervals were likely due to higher average water temperatures stimulating higher and more variable activity rates and foraging. High growth rates are a common evolutionary strategy to increase survival, and many studies of hatchling freshwater turtles have confirmed that “bigger is better” in a variety of important ways (Miller et al., 1987; Janzen, 1993; Miller, 1993; Janzen et al., 2000a,b). Larger size correlates with increased locomotor performance (Miller et al., 1987; Janzen, 1993; Miller, 1993) and larger hatchlings also exhibit increased foraging success during feeding trials (Froese and

Burghardt, 1974). Furthermore, larger hatchling turtles tend to be faster, which might lead to achieving greater survival rates through enhanced predator escape or prey acquisition (Froese and Burghardt, 1974; Miller et al., 1987; Janzen, 1993; Miller, 1993).

In conclusion, hatchling *M. temminckii* are diurnal throughout the year, and there is the potential that individuals that are more active tend to exhibit faster growth rates. Both traits may contribute to a higher probability of survival through a combination of predator (raccoon) avoidance and limiting the time of exposure to gape-limited predators. Annual activity patterns were similar to those reported for other age classes, with high activity rates occurring during warm periods and low (but not negligible) activity rates during cold periods. In light of the fact that *M. temminckii* conservation relies on head-start efforts, it is possible that early exposure to naturally occurring seasonal cycles may enhance future post-release behavior and survival. Therefore, it may be beneficial in such programs to rear hatchlings outdoors with exposure to natural cycles.

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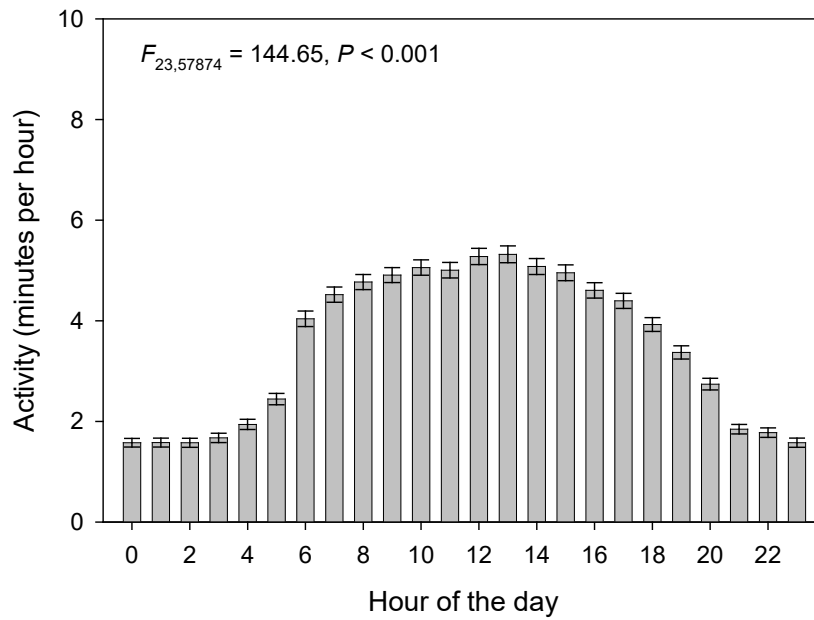


Figure 1. Average daily activity patterns of hatchling alligator snapping turtles measured from 27 September, 2015 through 17 August, 2016. Data were obtained from 15 hatchlings that were monitored for variable intervals during the study period. Error bars indicate ± 1 standard error.

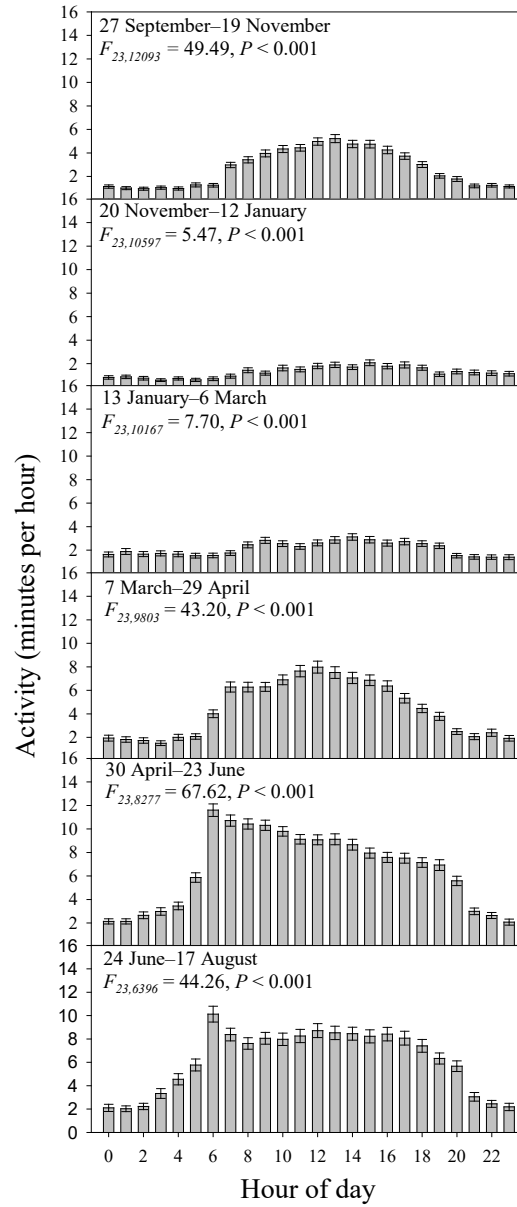


Figure 2. Activity patterns exhibited by alligator snapping turtles during their first year after hatching. The study period was divided into six discrete time periods to examine variation in activity patterns. Fifteen individual hatchlings were included in the study, but sample size varied throughout the year, ranging from 5–10, due to periodic transmitter failures. Error bars indicate ± 1 standard error.

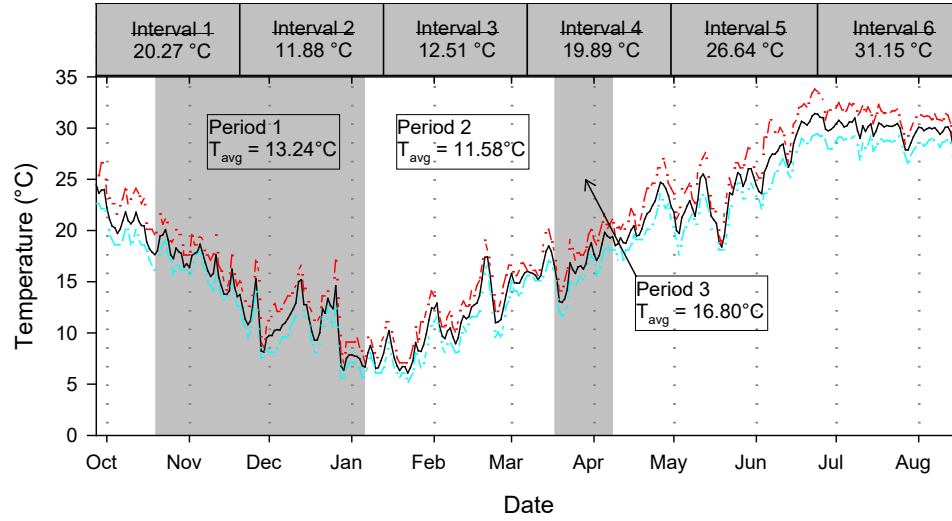


Figure 3. Temperature profile for the duration of the study as collected by a near-shore data logger that was at a depth frequented by hatchling turtles. Minimum temperature is shown in blue, average temperature is shown in black, and maximum temperature is shown in red for each day. Timing and average water temperatures for Periods 1–3 and Intervals 1–6 are indicated.

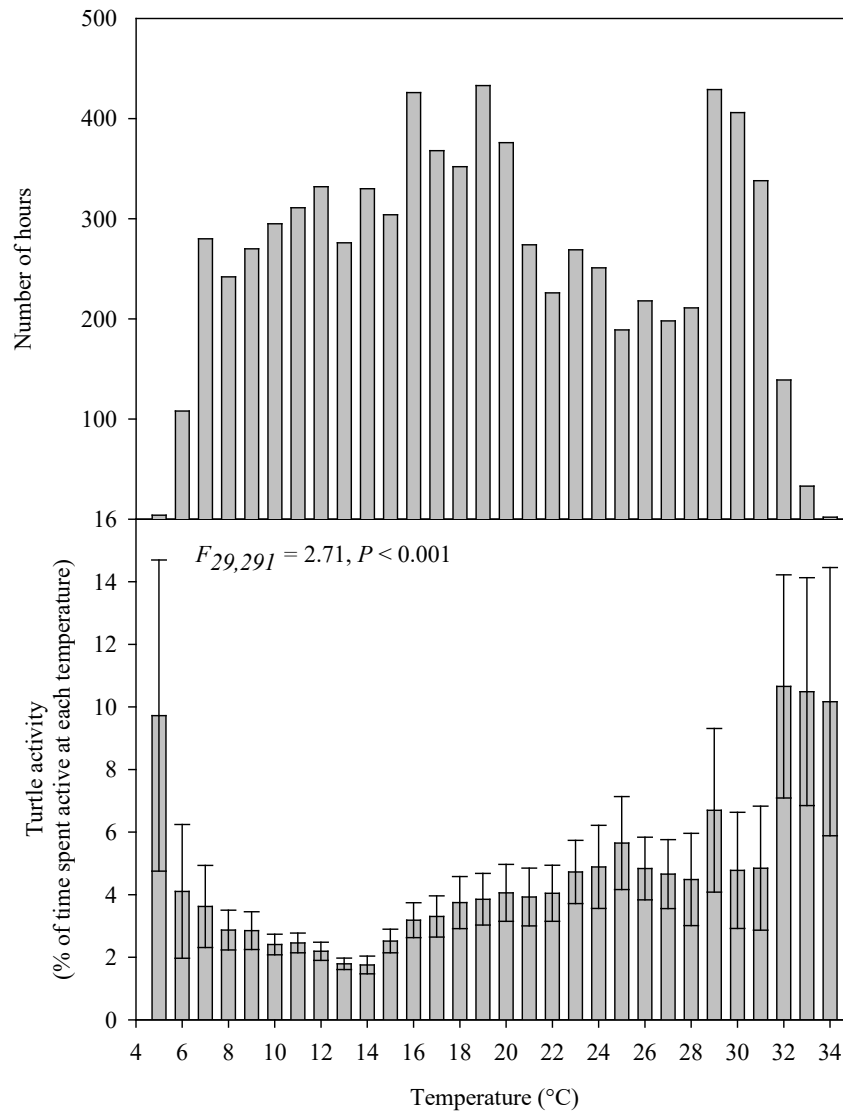


Figure 4. The upper graph indicates the number of hours for which each water temperature increment occurred over the duration of the study. The lower graph indicates the mean proportion of time at each temperature increment that hatchling alligator snapping turtles were active. Data were obtained from 15 turtles, for which activity was monitored from 27 September, 2015 to 17 August, 2016. Error bars indicate ± 1 standard error.

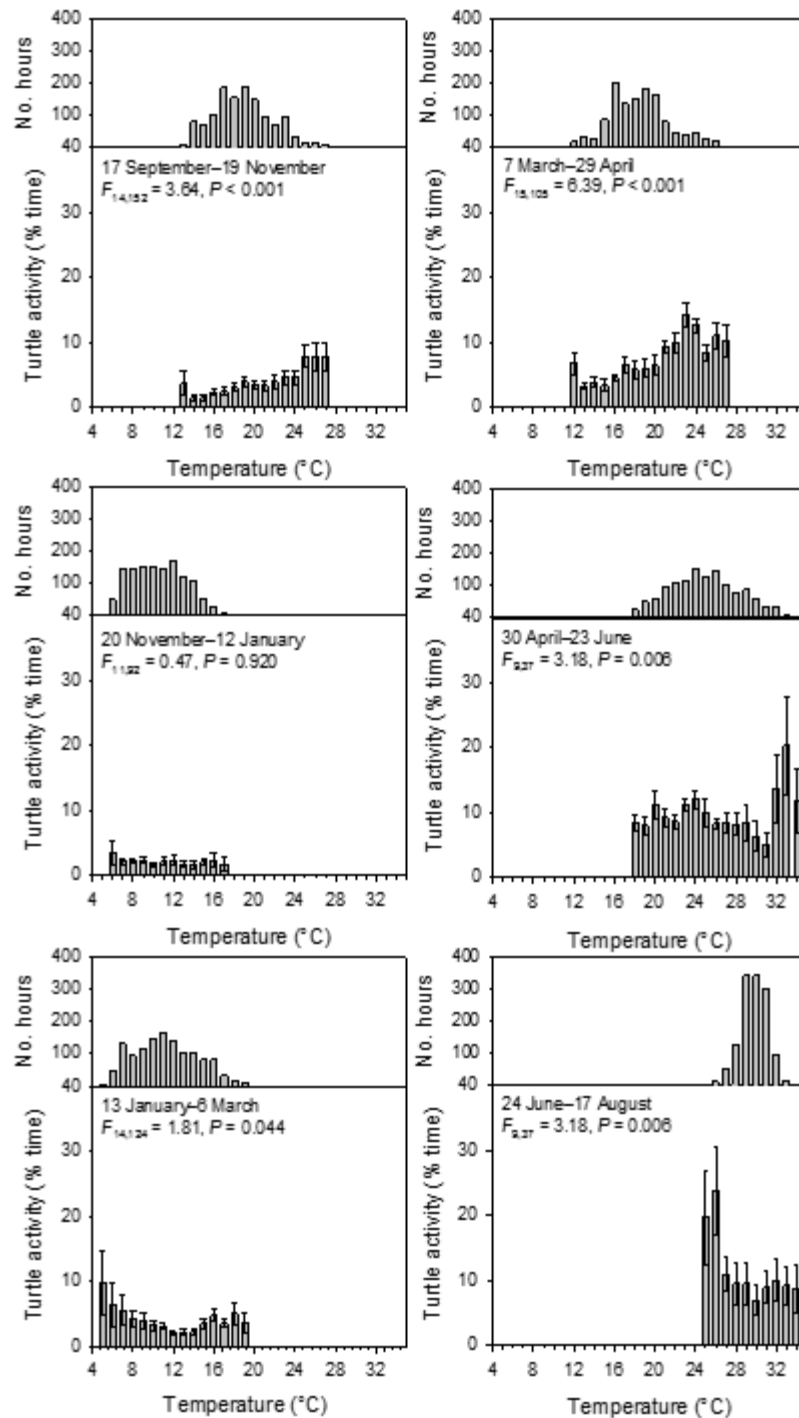


Figure 5. The top portion of each pair of graphs indicates the number of hours for which each water temperature increment occurred over the duration of a time interval. The bottom portion of each pair of graphs indicates the mean proportion of time at each temperature increment that hatchling alligator snapping turtles were active. Data were obtained from 15 turtles for which activity was monitored for different durations between 27 September, 2015 and 17 August, 2016. Error bars indicate ± 1 standard error.

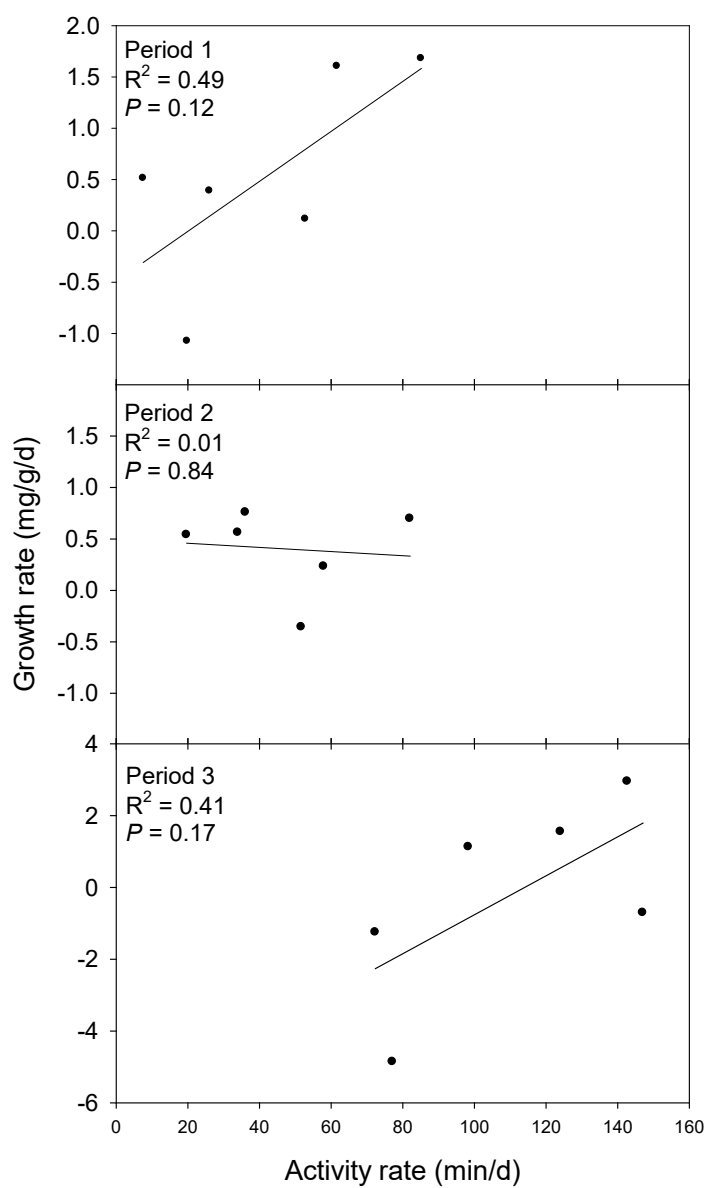


Figure 6. Regression analyses of average activity rates of hatchling alligator snapping turtles against growth rates for three different time periods: 19 October–23 January (period 1), 24 January–17 March (period 2), and 18 March–8 April (period 3).

**MOVEMENT PATTERNS AND HABITAT ASSOCIATIONS OF HATCHLING
ALLIGATOR SNAPPING TURTLES
(*MACROCHELYS TEMMINCKII*)**

Abstract

Hatchling turtles have a reputation for being cryptic and secretive; as a result, there are few species for which habitat associations and movement patterns of hatchlings and small juveniles are well understood. Such data are important because hatchlings may experience high mortality rates, making them a sensitive life stage whose success has important impacts on overall population stability. Additionally, among species in which hatchlings and adults occupy distinctly different niches, conservation of resources for both is necessary for effective management. The aim of my study was to characterize the movement patterns, habitat use, and sources of mortality of hatchling alligator snapping turtles (*Macrochelys temminckii*) in a southeastern Oklahoma stream. Movement patterns were typically characterized by an initial move away from the site of release, followed by prolonged occupancy of an area with increased cover and shallow water depth, when compared to random locations. Of the 12 turtles released, three were preyed upon by fish and seven were confirmed to be alive in mid-November, eight weeks after the study was launched. A single hatchling turtle was washed downstream during high flow events, and the fate of another turtle could not be confirmed at that time, either because they were transported away from the study area by a predator or because their transmitters failed prematurely. Surprisingly, I found no evidence of depredation by raccoons (*Procyon lotor*), a common predator of hatchling turtles.

Introduction

As is the case for most taxa, turtles experience varying mortality rates at different life stages, with eggs and hatchlings typically being most vulnerable and mortality rates decreasing with growth. Adults of many species enjoy >95% annual survival (Iverson, 1991; Congdon et al., 1993; Congdon et al., 1994; Shine and Iverson, 1995), but the stability of a population is contingent on adequate survival at all life stages (Congdon et al., 1994; Heppell et al., 1996; Dreslik et al., 2017). Early life stages of many turtles are difficult to monitor in the wild and calculating survival rates is difficult. For example, the nests of at least one species (*Chelodina rugosa*) are laid underwater, making embryo survival impractical to monitor (Kennett et al., 1993). Similarly, hatchlings of many turtle species are small and secretive, and therefore are rarely caught. For this reason, hatchling survival rates are often inferred from other life history parameters (Wilbur, 1975; Congdon et al., 1994; Pike et al., 2008). Sea turtles offer an extreme and oft-cited example of the problems of secrecy and low-detectability in assessing hatchling life history. The ambiguity surrounding the first several years of a sea turtle's life was so extreme that this time frame has been termed "the lost years" (Carr, 1987). Technological advancements have improved researchers' ability to study some variables during this early life stage, such as diet, incubation temperature effects on fitness, and movement patterns (Booth et al., 2004; Reich et al., 2007; Mansfield et al., 2014; Wood et al., 2014; Anderson et al., 2015), but natural history studies of hatchling turtles remain substantially more challenging than investigations of other life stages. As more turtle species experience population declines and conservation measures become ever more critical, understanding the ecology and life history parameters of early, enigmatic, life stages is a

pressing issue. Critical but often missing pieces of information include early dietary and habitat preferences, activity patterns, and growth and survival rates (Ernst and Lovich, 2009).

Conservation actions often cannot be delayed until the entire life history of a species is known; therefore, conservation action plans are often developed and executed based on relatively limited knowledge of only a portion of a species' life history (Congdon et al., 1993; Semlitsch, 1998; Semlitsch, 2002). These potentially incomplete management plans are not due to a lack of effort on the part of the decision makers, but rather due to a lack of scientific evidence informing appropriate practices (Pullin and Knight, 2003). Often, information is especially lacking for the life stages of species during which individuals are most cryptic or secretive, typically during the first several years. Early age classes of most aquatic turtles are small and well camouflaged. These traits impede reliable and consistent monitoring and recapture of individuals at regular intervals, which in turn increases the difficulty of detecting hatchlings in natural environments to determine habitat preferences. It is also extremely challenging to monitor movement and dispersal patterns, and to quantify predation and mortality rates (Morafka et al., 2000; Pike et al., 2008). Due to these challenges, most studies of hatchling turtle ecology have focused on emergence and movement away from nesting sites, predation rates during dispersal from the nest to water, and sex determination during incubation (Vogt and Bull, 1984; Semlitsch and Gibbons, 1989; Ewert and Nelson, 1991; Kolbe and Janzen, 2002; DeGraaf and Nein, 2010; Miller and Ligon, 2014).

The alligator snapping turtle (*Macrochelys temminckii*) is an aquatic turtle species

that, due to declining numbers, is a species of conservation concern and reintroduction efforts. It is also a species for which there are many gaps in what is known of hatchling and juvenile life history and ecology. The ramifications of these gaps in our understanding of the species' life history were highlighted by policy makers when it was denied protection under the Endangered Species Act (1973) in part because of insufficient information regarding its life history (Riedle et al., 2008). With the declines alligator snapping turtle populations have incurred across their range over the past several decades, it has become imperative to improve our understanding of the life history of this species so that future species status assessments are accurate (Reed et al., 2002).

Alligator snapping turtles are long-lived and iteroparous, and populations are sensitive to the removal of just a few adults (Congdon et al., 1993; Congdon et al., 1994; Reed et al., 2002). Population viability assessment models demonstrate that reduction in female adults by as little as 2% annually can cause rapid declines (Reed et al., 2002). Alligator snapping turtles reach reproductive maturity at 11–21 years of age (Dobie, 1971; Tucker and Sloan, 1997). As such, there is more than a decade during which these animals are sexually immature. While there have been many studies of adult alligator snapping turtles, and a small subset that include sub-adults, the first few years remain little-studied. While the protection of reproductively mature adults is critical to the future success of the species, it is also critical to ensure that the needs of the most vulnerable early life stages are also addressed.

Home range and movement patterns of alligator snapping turtle hatchlings were studied in northern Louisiana (Bass, 2007). Daily movement of hatchlings were greatest in the spring, and temperature and precipitation correlated with an increase in distance

moved (Bass, 2007). Average home range size was larger in the fall than the spring or summer, and hatchlings showed a selection for certain habitat characteristics, such as shallow water, submerged woody structures, emergent woody plants, and floating aquatic vegetation (Bass, 2007). This study is one of the few field studies that has been conducted on hatchling alligator snapping turtles, and it provides useful insights into the ecology and life history of this age class. However, alligator snapping turtles inhabit a range that spans almost 6.5° latitude; studies across the species' range may be necessary to accurately characterize within-species variation.

The aim of my study was to assess movement patterns, habitat selection, and survival of hatchling alligator snapping turtles in a natural setting from emergence from the egg until the middle of winter (September–January), when activity presumably decreases significantly. This time period is crucial, as hatchlings are likely highly susceptible to predation due to lack of experience in their habitat, as well as their diminutive size. This is also a time during which hatchlings are likely learning the locations of resources (e.g., food, refugia), and thus must choose suitable habitat characteristics for survival.

Materials and Methods

My study site was located in Pennington Creek, a spring-fed tributary of the Washita River in southeastern Oklahoma. The portion of the creek that I used was a segment (~345 linear m) near the upper portion of the drainage. It was characterized by a slow flowing pool (~780 m²) bordered both upstream and downstream by a series of cascades (Figure 1). Structures throughout the pool included submerged and partially

submerged logs, overhanging trees, piles of organic debris, boulders, beaver lodges, and deeply undercut banks. The substrate in the creek was spatially heterogeneous and included areas dominated by silt, mud, sand, gravel, boulders, bedrock, and densely compacted clay. The depth along the midline of the pool ranged from 0.25–2.60 m deep, although much shallower conditions occurred along some edges and embankments within the creek. Vegetation in the creek was primarily yellow pond lily (*Nuphar lutea*). There was not an abundance of emergent vegetation, but lizard's tail (*Saururus cernuus*) and green algae (*Spirogyra* spp.) occurred in varying amounts throughout the seasons. The surrounding landscape vegetation is regionally characterized as cross-timbers and was predominately defined by oaks, elms, and cedars, along with a variety of understory species, including buckbrush (*Symphoricarpos orbiculatus*) and invasive multiflora rose (*Rosa multiflora*).

Twelve hatchling alligator snapping turtles were selected for release and subsequent monitoring in Pennington Creek. Hatchlings were selected from five clutches produced in 2015 by a captive population of adult alligator snapping turtles at Tishomingo National Fish Hatchery. Prior to release, each hatchling's straight carapace length, plastron length, and mass were measured before attaching a transmitter (Table 1). Each transmitter weighed 1.9 g and was 11 mm long with a 10 cm long whip antenna (two manufacturers were used: L.L. Electronics, Mahomet, IL and Holohil Corporation, Ontario, Canada). Transmitters were attached to the carapace in between the midline vertebral ridge and the right or left lateral ridges with waterproof epoxy (Marine Epoxy; Loctite, Westlake, OH, USA). Each hatchling was released at a different location on the banks of the pool. Hatchlings were relocated daily after release (with exceptions)

following their release on either 13 September 2015 ($n = 10$) or 5 October 2015 ($n = 2$), using a radio receiver (model R-1000, Communication Specialists, Inc., Orange, CA) and directional antenna (model RA-23, Telonics, Mesa, AZ). These daily re-locations were conducted until the end of October, when activity began to decrease as water temperatures declined. The hatchlings were then tracked monthly until either their transmitter failed or they moved out of the study site and could not be relocated. All radio tracking concluded in February 2016.

Upon locating each hatchling, I recorded the location, distance from the last location, water temperature at the top and bottom of the water column, canopy cover, and water depth. I initially recorded distance to the nearest bank and substrate composition, but consistently interpreting these variables proved impossible because hatchlings were frequently in undercuts beneath banks and substrates of hard clay was indiscernible from bedrock or cobble when water became turbid. Therefore, these variables were not included in analyses. Habitat measurements obtained at hatchlings' locations were paired with comparable measurements at random locations. Random locations were determined by checking the fraction of a second recorded by a digital stopwatch, with 1) even number indicating upstream and odd number indicating downstream, 2) a second observation determining the number of meters away from a hatchling's location, and 3) a third observation determining the proportional distance across the stream from right-hand bank.

Hatchlings were periodically located and re-captured for transmitter replacement and to collect morphometric data. Epoxy was allowed to cure overnight before releasing animals at the location of recapture.

Water depth, over story canopy cover, and temperature that were measured at turtles' locations and paired random points were compared using paired t-tests. Minitab 17 was used for all statistical analyses, with a significance threshold of $\alpha = 0.05$ for all tests.

Results

Habitat Use. Hatchling alligator snapping turtles collectively were located a total of 327 times from September 2015 to February 2016. The number of times each hatchling was located varied due to differences in release date, transmitter failures, failure to relocate, and depredation. Hatchlings exhibited selection for shallower water depths than was randomly available (at hatchlings' locations, mean = 23 cm, range = 1–245 cm; at random locations, mean = 177 cm, range = 2–2600 cm, $t = -7.25$, $df = 326$, $P < 0.001$). On average, hatchlings were located in areas with more canopy cover than at random locations (mean canopy cover at hatchlings' locations = 45%; mean canopy cover at random locations = 24%, $t = 10.09$, $df = 326$, $P < 0.001$). There was no significant difference in water temperature selected by hatchlings and water temperature at random locations (mean temperature hatchlings' locations = 19 °C, mean temperature at random locations = 19 °C, $t = -1.89$, $df = 322$, $P = 0.06$).

Movement. Hatchlings ($n = 12$) were each tracked on 7–41 occasions, with the number affected in 5 cases by transmitters failing before they were scheduled to be replaced, depredation, or movement out of study area associated with high water flow events. Overall, hatchlings exhibited no change in location between relocation events 51% of the time, and individuals remained at the previous day's location 13–75% of the

time. When movements did occur between relocation efforts, most movements were <1 m; movements >5 m were rare (Figure 2). Hatchlings that did change locations between tracking events, moved 2.76–19 m (median) (Table 2). The following are descriptions of movement patterns of each hatchling during the time in which it was tracked.

Hatchling Movements (Figure 3, Table 2). *Hatchling 1:* Hatchling 1 was located 41 times in a 151-day period, with a consecutive 29-day period of consecutive locations. Over the 41-day period this hatchling was tracked, it moved a total of 139 m. Although this hatchling typically did not move between tracking events, when it did move its median movement was 3.60 m. Hatchling 1 was inactive for 71% of the days in which it was tracked. However, it was also the turtle with the greatest movement overall, at 139 m in 41 days. Its largest single-day movement was 79 m from the last known location. At the time of release on 13 September, it was observed crawling into an undercut in the bank. Over the course of the first 4 days its movement was minimal, at 2.14 m. Nine days after release, it left the undercut and moved 79 m upstream, navigating over two low waterfalls, and crossed from the left bank to the right bank of the stream. Thereafter, it remained in a deep undercut with substrate of bedrock and cobble for 22 consecutive days, until it was captured to on 24 October to replace its transmitter and collect morphometric data. It was released at the location of capture within 24 hours. The transmitter signal remained in the same location throughout monthly radio tracking events in November, December, and January. However, the transmitter was recovered on 23 January, 2016 and was no longer attached to the turtle. It is very likely that the transmitter became detached from the turtle during recovery efforts.

Hatchling 2: Hatchling 2 was released on 13 September into shallow water on the right-hand side of the creek. It was located on just eight separate days, with a seven-day period of consecutive daily locations. Over the eight days this hatchling was tracked, it moved a total of 26 m, with a median movement of 3.35 m. Its largest movement was 9 m from its location on the previous day. It moved upstream to an undercut bank with fibrous roots hanging down. After 10 days, I confirmed its location in a muddy bank by touch, at which point I could also visually just make out the posterior edge of its carapace sticking out from under the bank (Figure 3C). On day 11, the pinging from the transmitter was accompanied by a ticking noise, and I was unable to locate the hatchling. I did not attempt to relocate the turtle for six days, and when I returned the transmitter rapidly moved large distances within the pool. As a result, I was unable to pinpoint a location. The same experience occurred for three days, and then the transmitter remained at a depth of >1 m for the rest of the life of the transmitter. My conclusion is that the hatchling was preyed upon by a fish, which swam with the transmitter in its gut for several days, and then eventually defecated the transmitter onto the creek bottom.

Hatchling 3: Hatchling 3 was released on 13 September in an area directly below the upper falls where there was a large shallow area that extended at a consistent depth and then quickly dropped off. Within this shallow area was a tree that had fallen over and the root had formed a tunnel where it met the bank. There were debris piles all around the fallen tree and in the tunnel that was formed by the tree, and this was where the hatchling was released. There was a copious amount of sticks and leafy debris that the hatchling moved around in throughout the first 34 days of tracking. The hatchling was located on 35 separate days, with an initial seven-day period of consecutive daily

locations. Over the 35 days it was tracked, this hatchling moved a total of 26 m. Although it did not change locations over 50% of the days it was tracked, when it did move its median movement was 0.78 m. Its largest movement was 8 m from its last known location, which was two days prior. On 19 October, it was captured for transmitter replacement and to collect morphometric data, then re-released at the location of capture within 24 hours. On 13 November, the hatchling had moved above the set of low falls at the upstream end of the pool, and was in an undercut that had fibrous roots hanging down (Figure 3D). During the December and January tracking events, I was unable to locate the hatchling, possibly due to transmitter failure or the hatchling moving beyond the portion of stream to which I had access.

Hatchling 4: Hatchling 4 was released on 13 September into a debris pile along left-hand side of the river. It was located on 40 separate days, with a 32-day period of consecutive daily locations. Over the 40 days it was tracked, Hatchling 4 moved a total of 101 m with a median movement of 0.33 m. Its largest movement was 27 m from its last known location; however, the signal was very weak and difficult to locate. This was the last time in which the transmitter was working or within the study site; it is unclear whether this was due to depredation by a terrestrial predator or a malfunctioning transmitter. The hatchling moved along the shore and then on the ninth day after release it moved to a half-submerged log oriented horizontally in the water with one end against the bank (Figure 3E). The hatchling moved around beneath the log for the next 23 days, during which I repeatedly visually confirmed its location. After a recapture and release event on 18 October for transmitter replacement and collection of morphometric data, the hatchling moved away from the log for two days, and then back to the log. On 13

November, the hatchling moved 14 m upstream. A month elapsed without efforts to locate it, and when my tracking efforts re-started, the hatchling could not be relocated.

Hatchling 5: Hatchling 5 was released on 13 September on the left-hand side of the creek into a small debris pile. It was located on 13 separate days, with a seven-day period of consecutive daily locations. Over the 13 days it was tracked, the hatchling moved a total of 53 m with a median movement of 0.59 m. Its largest movement was 27 m from its last known location, which occurred four days prior. There was visual confirmation five days after release, but on the tenth day of tracking the signal moved erratically. The transmitter remained at the same location in >1 m of water for the remainder of the life of the transmitter. My conclusion is that, like Hatchling 2, Hatchling 5 was preyed upon by a fish, which swam with the transmitter in its gut for several days, and then eventually defecated the transmitter onto the bottom of the creek. Attempts to retrieve the transmitter were unsuccessful.

Hatchling 6: Hatchling 6 was released on 13 September on the right-hand side of the creek. It was located on 40 separate days, with a 19-day period of consecutive daily locations. Over the 40 days it was tracked, the hatchling moved a total of 47 m. The hatchling had not moved from its previous location on 75% of the days that it was tracked, but when it did move its median movement was 2.67 m. Its largest movement was 19 m from its last known location, which was recorded seven days prior. Upon its initial release, it moved downstream along the bank until it reached an undercut with green briar and multi-flora rose hanging down in front of it. It remained very close to this location for the remainder of the days it was tracked. I made tactile confirmation of its location on multiple days during this time period, including on 18 October when I

recaptured it for transmitter replacement and collection of morphometric data, before releasing it within 24 hours. It moved up- and downstream, but each movement was typically <1 m. After 23 January, I could not relocate the hatchling.

Hatchling 7: Hatchling 7 was released on 13 September in an undercut on the left-hand side of the river. The undercut was shallow, but the bank quickly dropped off. I located Hatchling 7 on seven separate days, with a five-day period of consecutive daily locations. Over the seven days it was tracked, the hatchling moved a total of 108 m. Although the hatchling was only locatable for a short period of time, it did not change its location over 50% of the time. However, when it did move, its median movement was 14 m. Its largest movement was 89 m from its last known location, which was taken six days prior on the day it was released. Shortly after its release, the signal became erratic, giving a strong reading that would quickly fade, as if going very deep. My conclusion is that this hatchling, too, was preyed upon by a fish, which swam with the transmitter in its gut for several days, and then eventually defecated the transmitter onto the bottom of the creek.

Hatchling 8: Hatchling 8 was released on 13 September on the right-hand side of the creek, just above the lower falls at the downstream end of the pool. It was released into a shallow area with woody debris piled up on the substrate. It was located on 32 separate days, with a 20-day period of consecutive daily locations. Over the 32 days it was tracked, the hatchling moved a total of 125 m. Although the hatchling did not change locations over 50% of the time it was tracked, when it did move its median movement was 1.70 m. Its largest movement was 56 m from its last known location, which was taken nine days prior. For the first five days after its release, the hatchling moved downstream but stayed very close to its release location. The sixth day after release, it

moved 10 m downstream, towards one of the downstream waterfalls. I did not attempt to track this turtle for six days, and upon my return I could not relocate it. However, 20 days after its release, I detected its signal again and visually confirmed the hatchling's location 56 m from its original release location. It moved below one of the upstream waterfalls to a very shallow area in which the substrate was bedrock. At the time there was a single leaf covering the hatchling. It continued to move downstream and I again visually confirmed its location under a small quantity of floating algae. The hatchling moved 19, 18, and then 10 m on three consecutive days. It ended its movements under a small boulder that was in a small eddy on the right-hand side of the creek, located just above one of the downstream waterfalls (Figure 3B). It stayed at this location and was visually confirmed to remain there for 17 days, with a recapture event on 18 October for transmitter replacement and collection of morphometric data before re-releasing at the location of capture within 24 hours. It changed locations but consistently remained under the boulder before and after each release. Three days after its second release, the creek received >12 cm of rain over the course of two days (Figure 2), and the hatchling was no longer located under the rock. The best signal from its transmitter was within the set of cascades directly below the boulder, but the current was too dangerous to enter the stream during the high flow period. Two days after the rain event, the hatchling was >300 m downstream from its last known location. It remained on the right-hand side of the creek where it was observed multiple times, with its head oriented toward a muddy bank or in a shallow undercut. After a 2-week gap in tracking, I was unable to relocate this turtle.

Hatchling 9: Hatchling 9 was released on 13 September on the left-hand side of the creek, almost directly above the set of lower falls. There was a crescent-shaped

shallow area with woody debris and large branches on the substrate. There was also an undercut area with fibrous roots hanging down in the bank. It was located on 39 separate days, with a 31-day period of consecutive daily locations. Over the 39 days it was tracked, the hatchling moved a total of 67 m with a median movement of 0.50 m. Its largest movement was 16 m from its last location on the previous day. The hatchling stayed near the undercut where a large elm tree was coming out of the bank for the first nine days after release. After six days without tracking, the hatchling was located 8 m downstream in a pile of fallen trees in the creek. The hatchling continued moving downstream and moved below the lower set of falls. I visually confirmed the location of the hatchling below the falls in a shallow pool lying on the sandy substrate in tree roots. The hatchling then moved to mid-channel and occupied the roots of a downed tree in the creek on 7 October. It was captured within the root wad on 19 October for transmitter replacement and collection of morphometric data, before being released within 24 hours. It moved throughout the root wad and was observed numerous times for the remainder of the 11-day period for which it was tracked. It remained in the root wad during a tracking event in November, but I was not able to relocate it in December, potentially due to transmitter failure.

Hatchling 10: Hatchling 10 was released on 13 September along the bank of the far-right arm of the creek, on the left-hand side of the arm, into a shallow area along the side. It was located on 38 separate days, with a 22-day series of consecutive daily locations. Over the 38 days it was tracked, the hatchling moved a total of 46 m with a median movement of 0.39 m. Its largest movement was 10 m from its last known location, which was the day prior. Upon release, the hatchling moved downstream along

the bank and in the undercuts, where I was able to make tactile confirmation of its location. The hatchling was in a location in which it was not completely submerged in water, although it was hidden by the undercut. It subsequently moved to a small “grass island” that was formed at the tip of a peninsula that was separated from the shoreline by water. The hatchling moved around the grass roots on the “island” and was seen clinging to the roots many times, with its head oriented upward (Figure 3A). The hatchling was also found in small undercuts on the “grass island” and around the base of the yellow pond lily that surrounded the “grass island”. Fifteen days after its release, it was captured for transmitter replacement due to a malfunctioning transmitter. For 13 days after re-release, the hatchling moved around the “island”, until I recaptured it for another transmitter replacement and to collect morphometric data, before releasing it at the location of capture within 24 hours. The hatchling then started moving up the right-hand side bank of the middle arm of the creek, into a large pile of woody debris. The hatchling continued to move upstream and I made visual confirmation of its presence when it sat completely exposed under 14 cm of water. It moved to a location that was very shallow (2 cm), with the shallow area extending out from the bank for approximately 1 m. The hatchling moved 2.5 m downstream from this location, and moved into an undercut. On the last day of successful tracking, the hatchling was seen barely tucked into the undercut, but completely covered in mud with its head oriented towards the bank.

Hatchling 21: Hatchling 21 was released on 5 October at the “grass island” that hatchling 10 stayed at for an extended period of time (Figure 3A). It was released on the right-hand side of the “grass island”, opposite the side that hatchling 10 was typically located. It was located on 25 separate days, with a 25-day series of consecutive daily

locations. Over the 25 days it was tracked, the hatchling moved a total of 14 m with a median movement of 0.30 m. Its largest movement was 2.76 m from its last known location, which was on the previous day. Hatchling 21 stayed at the “grass island” for the entirety of the days it was successfully tracked, even after a recapture even on 18 October for transmitter replacement and collection of morphometric data, before re-releasing within 24 hours. During the time it was tracked, I observed it many times either clinging to grass roots, tucked into muddy undercuts, or buried in mud.

Hatchling 22: Hatchling 22 was released on 5 October in a shallow undercut with fibrous roots hanging down in front of it, located on the right-hand side of the river. It was located on nine separate days, with a nine-day series of consecutive daily locations. Over the nine days it was tracked it moved a total of 13 m with a median movement of 0.50 m. Its largest movement was 5 m from its last known location on the previous day. The hatchling stayed in the undercut and moved upstream and downstream, but within 5 m of where it was released for the short period of time it was tracked, before the transmitter’s signal disappeared.

Discussion

The results of my study indicate that hatchling alligator snapping turtles prefer habitats with shallow water and increased canopy cover. This is consistent with habitat preferences that have been reported for other age classes of this species. Juvenile and subadult alligator snapping turtles in Louisiana and Oklahoma reportedly also exhibit a preference for increased canopy cover, association with structure, and shallow water (Harrel et al., 1996; Moore et al., 2014). Adults in Oklahoma also exhibited a preference

for increased cover, and were typically located in shallower water, although a shift occurred during late summer when they moved to deeper water, possibly to avoid the high water temperatures that occur above the thermocline (Riedle et al., 2006).

Although hatchling alligator snapping turtles in my study ultimately experienced a variety of fates, there were some consistencies in their behavior. The turtles that I released into Pennington Creek almost ubiquitously followed the same initial pattern of movement, in which they moved away from the site of release to a location with increased cover and shallow water, and then remained in that area for an extended period of time. The type of cover that turtles elected to associate with varied widely; therefore, I had to rely on strictly qualitative descriptions. Nonetheless, the high frequency with which individual turtles were found associated with structure or cover of some sort highlights its importance, regardless of form. Of the 319 times that I relocated individual turtles, there were just 23 instances in which a hatchling was located fully or mostly exposed in shallow water. However, in these instances turtles never remained exposed long-term, preferring instead to move to other locations. Of the 12 hatchlings tracked on Pennington Creek, eight moved to a location of increased cover and stayed in that location for 17 or more days, often even after a re-capture and re-release for measurements and transmitter replacement. These hatchlings were found in undercuts or beneath structures that included a log, a boulder, and a root wad.

During my study, sample size decreased due to a number of factors, including one hatchling that was lost to transmitter failure before re-capture for replacement. However, eight out of the 12 hatchlings were successfully radio-tracked from the end of September to the end of October, and of those six were recaptured again in November. After

November, the number of successful locations decreased until February, when I was able to locate just one hatchling. The decrease in the number of trackable animals corresponded with reduced frequency of radio tracking efforts, and could have resulted from transmitter failures, depredation, or moving out of the portion of the creek to which I had access.

One hatchling washed downstream during a high-flow event. Interestingly, none of the other hatchlings were swept from their locations during the high flow, and the different fates likely trace to the location of individual turtles when flow increased. Whereas most hatchlings were located under cover along edges of the creek where turbulent flow patterns reduce the stream velocity, the turtle that washed downstream occupied space mid-stream under a boulder. To my knowledge, this is the first study to report hatchling turtles' fate during flooding; however, studies of adults suggest that turtles have some capacity to resist being washed downstream, and are capable of at least short-range homing on occasions when they are displaced by flood events (Ligon, 2001; Jones and Sievert, 2009; Jergenson et al., 2014).

Depredation by raccoons (*Procyon lotor*) of turtle eggs, hatchlings, and even adults of many species is a common theme in many studies of turtle ecology (Siegel, 1980; Christiansen and Gallaway, 1984; Kolbe and Janzen, 2002; Engeman et al., 2005; Buzuleciu et al., 2016). Furthermore, a recent study that was conducted at three geographically disparate sites found that raccoons were consistently the primary predator of juvenile alligator snapping turtles, and it was concluded that young turtles' tendency to remain in shallow water near the shoreline likely increased their detection and predation by raccoons (Dreslik et al., 2017). Raccoons occurred at my study site, and so it was

surprising that I found no evidence of raccoon predation of hatchling alligator snapping turtles. However, although hatchling alligator snapping turtles in my study were usually located in shallow water near shore, it was almost always difficult to access them via the shoreline because the banks were steep, heavily vegetated, and often had deep undercuts that would have been inaccessible to raccoons. Furthermore, the creek bottom dropped off steeply throughout much of my study site; these characteristics would have made patrolling the shoreline difficult for raccoons. This could have important implications for reintroduction efforts for this and other turtle species; selecting release sites that have shorelines that are difficult for raccoons to patrol could improve survival rates of hatchlings and juveniles.

Despite the lack of predation by raccoons, of the hatchlings released into Pennington Creek, at least 25% were preyed upon by fish. The documented cases all occurred within 14 days after release, and their exposure to large fish might have been high during this initial period when hatchlings were moving to locate preferred habitat. Interestingly, experimental studies of fish predation of hatchling turtles have suggested that predation risk is low (Semlitsch and Gibbons, 1989). In one study, aposematically-colored hatchling pond sliders (*Trachemys scripta*) and painted turtles (*Chrysemys picta*) were found to be readily consumed by largemouth bass (*Micropterus salmoides*) when the turtles were anesthetized, but were egested or ignored when the turtles were awake and active. Furthermore, cryptically colored hatchling eastern snapping turtles (*Chelydra serpentina*) were both difficult for fish to swallow and frequently egested (Briston, 1998). These results suggest that largemouth bass do not commonly prey upon turtles. Given that alligator snapping turtle hatchlings are larger than the hatchlings of any other

sympatric turtle species, it appears unlikely that largemouth bass were responsible for the predation events that I observed. Predation patterns of other fish species on hatchling freshwater turtles have not been conducted. However, several other large-bodied carnivorous fish species were present in my study system, including smallmouth bass (*Micropterus dolomieu*), spotted bass (*Micropterus punctulatus*), channel catfish (*Ictalurus punctatus*), and flathead catfish (*Pylodictis olivaris*) (pers. obs.), and may have been responsible for the predation events that occurred.

Although my study represents a limited investigation of just the first several months of life following emergence from the nest, understanding the ecology of turtles during this period is critical because it likely represents the time during which turtles are most at risk. Furthermore, the observation that stream bank morphology might have important implications for predation risk could prove important in reintroduction efforts for this and other aquatic turtle species. Expanding this study into the first full activity season for hatchling alligator snapping turtles would provide important additional insights into annual mortality and growth rates, as well as possible seasonal variation in habitat preferences and activity patterns. Finally, additional studies of fish predation patterns on hatchling turtles are necessary to fully assess the overall impact that fish might have on young turtles.

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Table 1. Straight carapace length, plastron length, and mass of hatchlings collected prior to release, on 12 September, 2015.

Turtle Identification	Straight Carapace Length (mm)	Plastron Length (mm)	Mass (g)
1	38.82	29.83	18.0
2	38.15	29.16	17.7
3	38.06	28.65	17.5
4	37.99	29.81	18.3
5	38.08	29.86	17.2
6	39.73	29.70	18.2
7	38.12	30.03	17.5
8	39.84	29.84	18.3
9	38.68	29.12	16.9
10	36.73	30.50	17.7
21	37.03	27.91	17.0
22	37.93	29.01	17.0

Table 2. Movements of hatchling alligator snapping turtles from September 2015 to January 2016, in Pennington Creek in southeastern Oklahoma. 1-Median distance moved is restricted to days with non-zero movements, while 2-Median distance moved was calculated from the full data set that included days with zero movement.

Turtle ID	# of Days Tracked	% of Days with No Movement	1-Median Distance Moved(m)	2-Median Distance Moved(m)	Maximum Distance Between Locations(m)	Total Distance Moved(m)
1	41	71	3.60	0.00	18.50	138.99
2	8	13	5.00	3.35	9.00	26.03
3	35	54	0.78	0.00	4.16	26.12
4	40	43	1.30	0.33	12.00	100.77
5	13	46	1.37	0.59	4.07	52.56
6	40	75	2.67	0.00	5.00	46.75
7	7	57	14.00	0.00	5.00	108.00
8	32	56	1.70	0.00	19.00	124.50
9	39	38	1.20	0.50	16.00	66.52
10	38	37	0.70	0.37	10.00	46.16
21	25	36	0.65	0.30	2.76	14.29
22	9	22	0.50	0.50	5.00	12.70

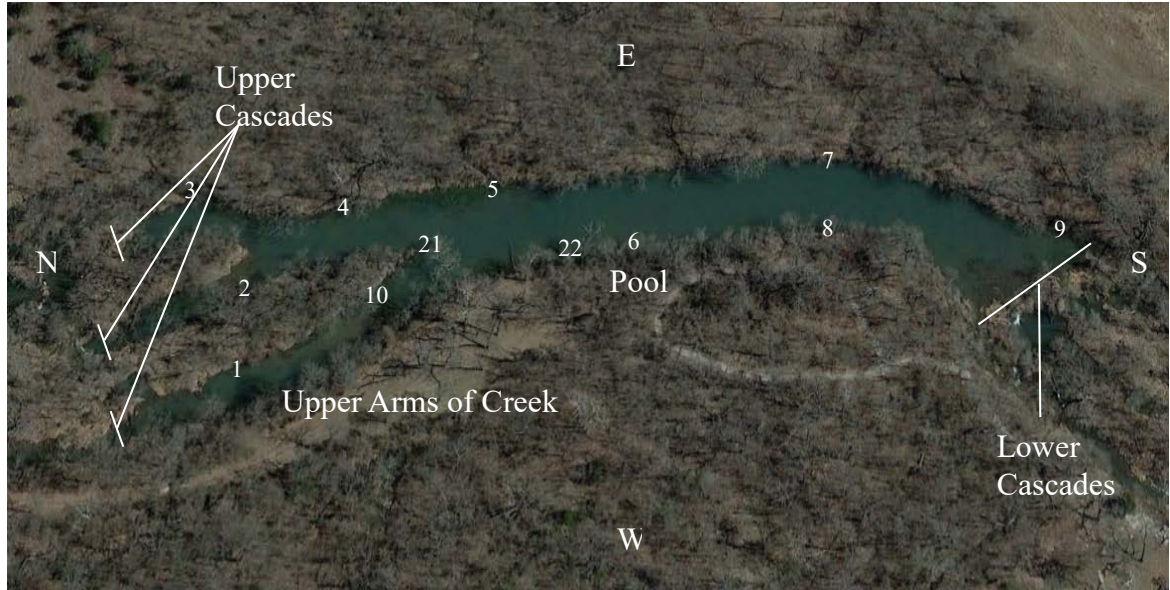


Figure 1. Aerial image of a ~345-m stretch of Pennington Creek in Johnston County, Oklahoma into which hatchling alligator snapping turtles equipped with radio transmitters were released (Google Earth Pro, accessed 15 February, 2016; image date 8 February, 2015). Numbers indicated release locations for hatchlings, with numbers corresponding to hatchlings' identification.

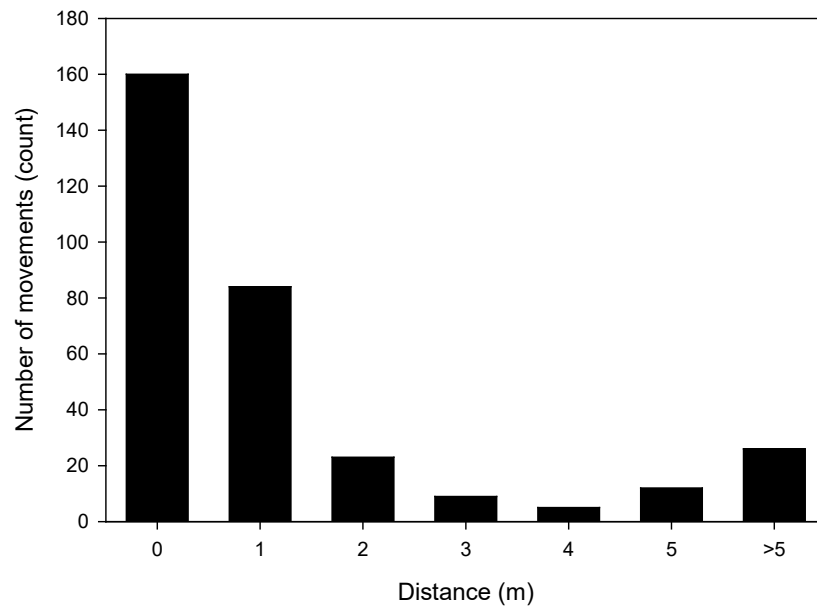


Figure 2. Frequency distribution of distances moved between successive relocations of hatchling alligator snapping turtles during the autumn and winter following hatching.

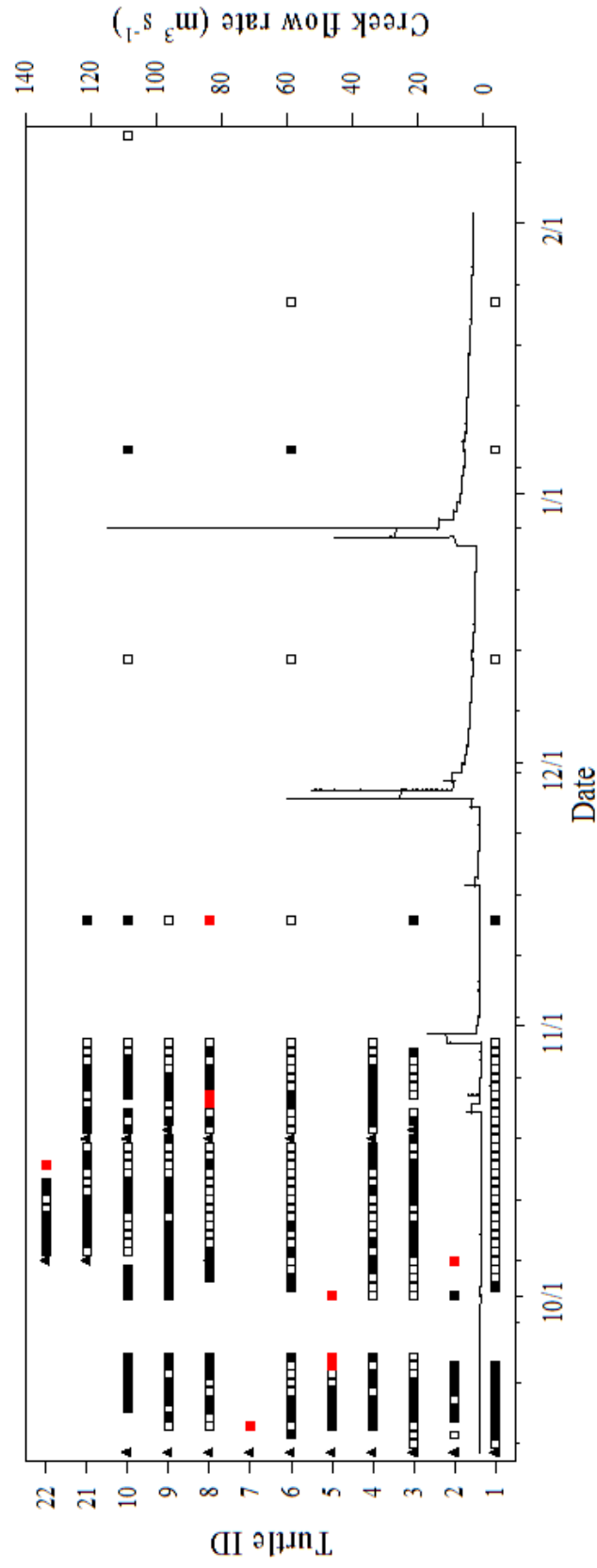


Figure 3. Tracking events for all turtles with water flow from 13 September, 2015 to 11 February, 2016, Pennington Creek, Johnston County, Oklahoma. Triangles = releases, closed squares = movement from previous tracking event, open squares = no movement from previous tracking event, and red squares = noteworthy events (see Results).

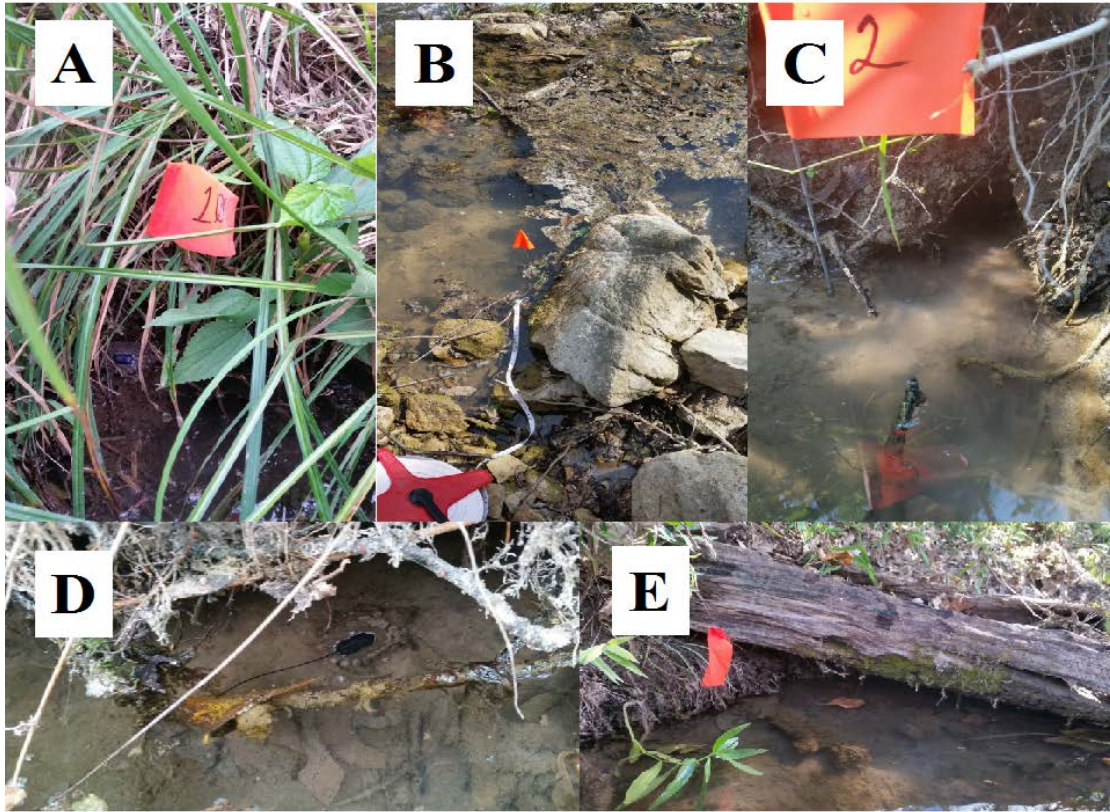


Figure 4. Microhabitats selected by hatchlings from September 2015 to February 2016, in Pennington Creek in Johnston County, Oklahoma. A: Grass overhanging roots, B: a boulder with a cavity under it, C: a cavity in a muddy bank, D: undercut in a bank, and E: a shallow area under a half-submerged log.

SUMMARY

Understanding the ecology of hatchling alligator snapping turtles (*Macrochelys temminckii*) is critical for developing life tables and making conservation decisions. My thesis research highlights hatchling alligator snapping turtles' activity patterns, effects of temperature on movement patterns, habitat associations, and depredation. Therefore, my thesis contributes novel information that may influence management decisions made on the species' behalf.

The circadian rhythms of hatchlings are diurnal. Hatchlings maintain this diurnal pattern even during the coldest months of the year, although overall activity decreases dramatically during the winter months. Unsurprisingly, temperature affects hatchling alligator snapping turtle's activity; however, it was surprising that an increase in activity occurred at extreme high and low temperatures.

As has been described for other age classes of this species, hatchling alligator snapping turtles were associated with shallow water and dense canopy cover, both of which tend to correspond with near-shore refugia. Hatchlings also exhibited a tendency to move away from a release site and then remained in a location with shallow water and increased canopy cover for extended periods. While no depredation by terrestrial predators was documented, 25% of hatchlings in this study were preyed upon by fish of unknown species.

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APPENDICES

Appendix A.

Aerial view of the fenced pond at Tishomingo National Fish Hatchery that was used in my study (Google Earth Pro, accessed 21 August, 2017; image date 8 February, 2015). Yellow polygon demarcates the fence that encloses the pond, and the star symbol indicates the location of the radio tower and automated receiving unit. Hatchling alligator snapping turtles released into this pond were used to study daily and seasonal activity patterns, temperature preferences, diet preferences, and comparative growth rates.



Appendix B.

Transmitters were attached to hatchlings using epoxy, and transmitter placement was to either the right or left of the vertebral ridge, dependent upon fit.

