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Activity Patterns Among Head-Started Juvenile Alligator Snapping Turtles (Macrochelys Temminckii)

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ACTIVITY PATTERNS AMONG HEAD-STARTED JUVENILE 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

Parker Ray Golliglee

May 2022

ACTIVITY PATTERNS AMONG HEAD-STARTED JUVENILE ALLIGATOR SNAPPING TURTLES (*MACROCHELYS TEMMINCKII*)

Biology

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ABSTRACT

In contrast to many species of aquatic turtle, Alligator Snapping Turtles (*Macrochelys temminckii*) are putatively nocturnal. Data supporting this assertion are chiefly anecdotal, however, and two recent studies cast doubt on this generalization. Differences in activity patterns may be related to variability in temperature and photoperiod across the species' range and may be influenced by ontogenetic changes, as well. To assess this, I equipped juvenile Alligator Snapping Turtles spanning a range of different ages with activity data loggers. I used 4-year-old turtles were to measure latitudinal differences in activity which were reared in hatchery ponds spanning the species' latitudinal range and located in Kansas, Oklahoma, and Louisiana. I also used 2- and 7-year-olds reared in Oklahoma to investigate ontogenetic changes in activity patterns. Temperature varied predictably with latitude, with warmer water temperatures occurring at lower latitudes. Daily activity patterns defied simple classification, but crepuscular activity was observed more frequently than was predominantly nocturnal or diurnal activity. The effect of latitude on diel patterns was inconsistent, with turtles in Louisiana consistently showing higher levels of activity and occasionally showing differences in daily activity patterns, with peaks of activity occurring where other sites showed lack of activity, from turtles at other sites. Seasonal activity did vary among the three age classes that I tested, with 7-year-old turtles showing higher levels of activity than the other two age classes throughout summer and autumn, and 2-year-old turtles showing higher than expected levels of activity in the winter months. Diel activity did differ some among age classes, but still showed similar periods of high activity around dawn and dusk. My results suggest that the activity patterns of Alligator Snapping Turtles change with latitude and developmental stage and, in combination with previous studies, demonstrate that while nocturnal activity occurs in this species, nocturnality is a poor general descriptor.

KEYWORDS: *Macrochelys temminckii*, activity, ontogeny, latitude, temperature, age

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Approved:

Day Ligon, Ph.D., Thesis Committee Chair

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I dedicate this thesis to my son Danaus Golliglee. I pray that as you grow up, you learn to love all the wonderful beauty the natural world offers and find it just as interesting as I do. I love you bubba, thank you for being such a light in my world.

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INTRODUCTION

Patterns of activity influence many aspects of species' natural history and niche space (Tester & Figala, 1990; Halle, 2000; Theuerkauf, 2009; Wiens et al., 2010; Frey et al., 2017). Timing of activity, whether defined on a diel or seasonal scale, affects exploitation of resources (Collier et al., 1990; Thies et al., 2006), exposure to predators (Nelson & Vance, 1979; Martín et al., 2009), habitat selection (Ferreguetti et al., 2015; Mohd-Azlan et al., 2017), and space use (Fox & Bellwood 2011). Myriad biotic and abiotic factors may influence the activity patterns of individuals, but some, such as geography and life stage, exert predictable and often consistent effects. While there are many forms of activity and many ways we can classify patterns of activity, for the purpose of my research we will consider activity to be defined simply as movement and the pattern which I was interested in was how the amount of activity or movement differed at different times of day and seasonally.

Latitude influences temperature and photoperiod and can also indirectly affect other meteorological factors such as precipitation, wind, and frequency of storms. Populations of species with ranges that span large latitudinal gradients experience different conditions across their geographic range, and therefore may be hypothesized to exhibit predictable latitudinal variation in activity (Dwyer, 1970; Stevens, 1989; Engle & Summers, 1999; Gaston & Chown, 1999; Addo-Bediako et al., 2000; Gaston et al., 2009; Sperry et al., 2010; Cadena et al., 2011). However, even in populations where photoperiod and temperature fluctuations follow predictable seasonal patterns, activity patterns may vary ontogenetically. As individuals of a given species age, changes in physiology and size may influence diet and predation risk, which may result in changes in timing and duration of periods of activity (Pough, 1977; Crump, 1984; Kåster & Schnack, 1994; Lind & Welsh, 1994; Morinière et al., 2003).

Annual temperature profiles correlate predictably with latitude due to variation in insolation and plays a key role in shaping the activity patterns of vertebrates. This is especially true of ectotherms, whose capacity to thermoregulate across a broad ambient temperature range is more limited than it is for endotherms of similar size and body shape (Dawson, 1975; Hailey & Davies, 1986; Grant & Dunham, 1988; Gunderson & Leal, 2015). Thermal preferences contribute substantially to variation in patterns of activity among ectotherms (Adolph & Porter, 1993; Gunderson & Leal, 2015); this may include activity patterns across seasons as well as in response to daily cycles in temperature and light availability (Peterson, 1987; Adolph & Porter, 1993). For example, the foraging behavior of the Common Coral Trout (*Plectropomus leopardus*) have been found to vary seasonally throughout their range in relation to seasonal and latitudinal temperature (Scott et al., 2017).

Photoperiod also changes predictably with latitude, and circadian rhythms are often strongly influenced by photoperiod precisely because of its predictability. Seasonal changes in photoperiod are often linked to consequential activities such as mating, reproduction, foraging, migration, and overwintering (Spieler & Noeske, 1984; Rismiller & Heldmaier, 1988; Canavero & Arim, 2009), and these factors often comprise a sizeable fraction of animals' time budgets.

Changes in physiology and diet often shift over the course of ontogenetic development, and these factors may, in turn, influence when animals choose to be active. (Lind & Welsh, 1994; Morinière et al., 2003; Jensen et al., 2012; Scott et al., 2017). Ontogenetic change in physiology has been shown to be especially important in Common Garter Snakes, where difference in blood oxygen capacity has been shown to allow adults of the species to continue to right themselves when rolled over for up to five times as long a juvenile conspecific (Pough, 1977). Additionally, as predation risks change with ontogeny, the degree to which individuals' activity is dictated by risk management likely decreases. Hatchling Common Snapping Turtles (*Chelydra serpentina*) have been shown to increase survivorship by remaining still in the presence of predators (Janzen, 1995) which adults of the species are less susceptible to (Ernst & Lovich, 2009).

Like many ectothermic vertebrates, turtle activity patterns have been shown to be influenced by temperature and photoperiod (Graham & Hutchison, 1978; Graham & Hutchison, 1979; Lovich, 1988; Tucker et al., 2015). In Common Musk Turtles (*Sternotherus odoratus*), for example, photoperiod and temperature were shown to affect timing of male reproductive behavior. In addition to temperature and photoperiod, turtles also show varying activity at different ages. For example, some species of freshwater turtles have been shown to change overwintering behavior and use of habitat with change in age and size (Pluto & Bellis, 1986) with juveniles of many species including Common Snapping Turtles and Blanding's Turtles (*Emydoidea blandingii*) choosing shallower overwintering sites than older conspecifics (Costanzo et. al., 2008). Additionally swimming ability and antipredator behavior have been found to differ in young turtles relative to older conspecifics (Britson & Gutske, 1993) with species such as the Red-Bellied short-necked turtle showing notable difference in stability and agility between adults and juveniles (Stevens et al., 2018).

The Alligator Snapping Turtle (*Macrochelys temminckii*) is unusual among turtles in its extremely limited use of terrestrial habitats and infrequent basking. Because of these factors, it presumably has limited opportunities to thermoregulate behaviorally (Riedle et al., 2006). Several past studies have described the species as predominantly nocturnal (Lane & Mitchell, 1997; Ewert et al., 2006); however, recent studies suggest that activity patterns of Alligator Snapping Turtles may be more complex than previously recognized, with patterns varying seasonally and ontogenetically and ranging from distinctly diurnal to crepuscular (Spangler, 2017; Van Den Bussche et al., 2018). The seemingly conflicting conclusions among studies may result from the aforementioned factors of latitudinal variation, as the species range spans approximately 7° of latitude (Ernst & Lovich, 2009), or ontogenetic changes in activity patterns. Alligator Snapping Turtles have been reported to exhibit more activity in warmer months than in winter and to change their use of depth seasonally in response to changes in water temperature (Harrel et al., 1996; Riedle et al., 2006). Differences in the behavior of juveniles relative to adults are likely to be influenced by the absence of reproduction and higher predation risk (Ligon & Reasor, 2007; Holcomb & Carr, 2013; Dreslik et al., 2017; Spangler, 2017).

The goals of my research were to document patterns of activity in juvenile *M. temminckii* in relation to both latitude and ontogenetic development. I hypothesized that overall activity rates are higher at lower (warmer) latitudes and that daily activity patterns will become more subdued during colder seasons and at times when day length is shorter. Furthermore, I hypothesized that high midsummer water temperatures suppress activity levels, especially at lower latitudes. During winter, I anticipated higher levels of activity at southern latitudes, and nearly complete cessation of activity at the northernmost part of the species range. Finally, I hypothesized that younger/smaller turtles would exhibit lower levels of activity in comparison to older/larger conspecifics, possibly as a mechanism to reduce detection by predators.

METHODS

Study Species

Alligator Snapping Turtles are the largest species of freshwater turtles in North America (Lane & Mitchell, 1997; Ernst & Lovich, 2009). They are a long-lived species, with some of the oldest in captivity living over 70 years but are believed to be able to live much longer. Alligator Snapping Turtles have been suggested to become sexually mature as early as 11–13 years of age (Dobie, 1971), but it has been found that sexual maturity in this species may be delayed up to until 21 years of age (Tucker & Sloan, 1997). These turtles are known generalist with a perceived preference for fish. Alligator Snapping Turtles engage in sit-and-wait predation where they use a lingual lure to attract prey items (Lane & Mitchell, 1997; Ernst & Lovich, 2009). This species has historic range spanning from the gulf coastal plain up as far north as southern Kansas and up the Mississippi Valley as far as southern Iowa (Ernst & Lovich, 2009).

Study Sites

I monitored Alligator Snapping Turtle activity at three fish hatcheries in the central United States. Hatcheries were selected due to location, willingness to allow the housing of Alligator Snapping Turtles and the familiarity of staff with the care of Alligator Snapping Turtles. My sites were approximately evenly spaced along a latitudinal gradient, and all were within the natural historical range of the species. The locations included Farlington Fish Hatchery in eastern Kansas, Tishomingo National Fish Hatchery in southeastern Oklahoma, and Natchitoches National Fish Hatchery in central Louisiana (Figure 1). These locations are located at intervals of approximately 3° latitude; elevation is variable, but all sites are located <280 m above sea level. At all three locations, turtles had access to emergent vegetation, fish, and aquatic arthropods, and were offered frozen fish to supplement the natural forage. Pond Size differed among the three sites, as did the density of aquatic vegetation (Table 1).

Table 1. Descriptive factors of the three ponds used in the latitude portion of the study.

Pond Location	*Latitude/ Longitude*	*Elevation (m)*	*Pond Bottom Area (m^2)*	*Maximum Depth (m)*	*Vegetation/ Cover*
Farlington Kansas Fish Hatchery	37.649340/ -94.802291	275.0	580	1.1	Thick emergent vegetation throughout
Tishomingo National Fish Hatchery	34.352437/ -96.714869	266.0	260	1.8	Some emergent vegetation at pond edges/ shade mats on the perimeter
Natchitoches National Fish Hatchery	31.740397/ -93.077270	34.0	3,036	1.8	Some emergent vegetation at pond edge

Data Collection and Transmitters

I obtained my turtles from a captive population that was established at Tishomingo National Fish Hatchery. Prior to releasing the turtles into ponds, I measured and weighed each turtle, recorded its previously injected PIT tag code, and epoxied a coded transmitter/data logger (MCFT3 Series; Lotek Wireless Fish & Wildlife Monitoring, New Market, Ontario, Canada) to its carapace between the central and right keels using waterproof epoxy (Loctite Marine Epoxy; Henkel Corp., Westlake, Ohio, USA) (Figure 2).

I used three models of coded transmitters to accommodate a range of body sizes. The smallest of the models (MCFT3-EM-TA) weighed ~15 g and were affixed to 2-year-old turtles ranging 289–676 g. Transmitters intermediate in size (MCFT3-3A-TA; 20 g) were applied to 4-year-old turtles ranging 802–1301 g, and the largest transmitters (MCFT3-L-TA; 30 g) were attached to 7-year-old turtles that ranged 2,495–6,614 g. The transmitters inferred activity from activation of internal triaxial accelerometers. A turtle would be required to move sufficiently in any direction for a transmitter to register activity. Transmitters used and algorithm to assign an activity score based on the combined activation of the accelerometers, for which the units were arbitrary. I also measured the activity score of a cinderblock placed in the pond at Oklahoma to establish a baseline score for no activity. Any value higher than the baseline scores of the cinderblock were considered active. Each transmitter also recorded temperature, and both activity and temperature endpoints were logged at 2-minute intervals.

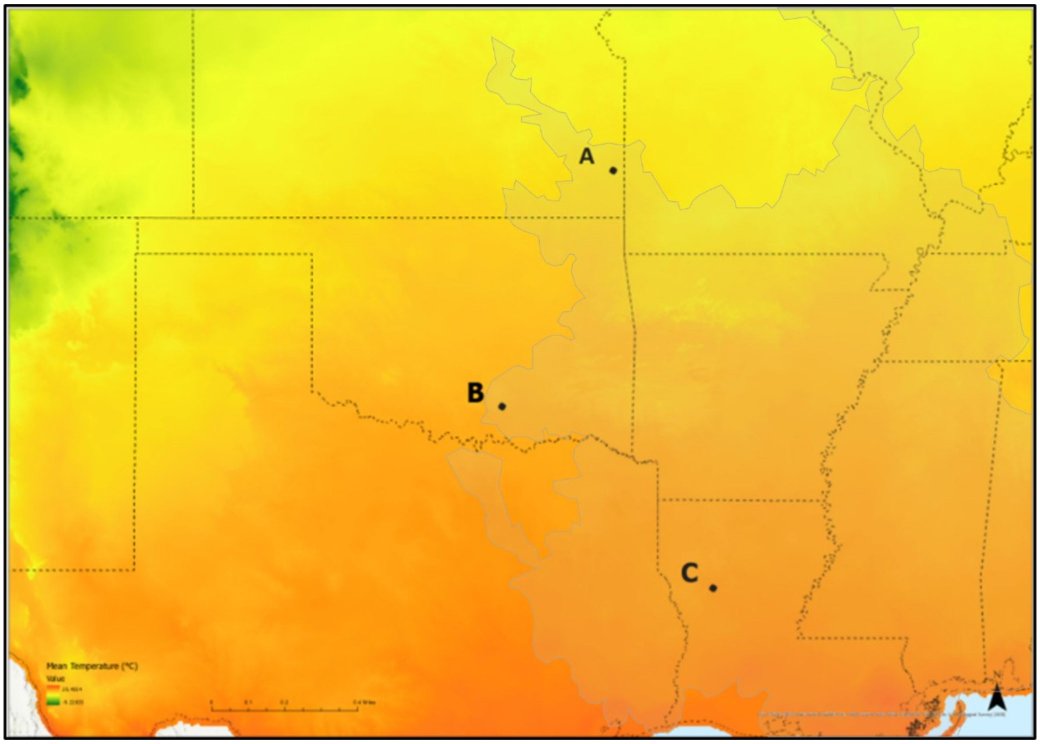

Figure 1. Heat map indicating the mean temperatures at and geographic locations of: (A) Farlington Fish Hatchery (mean annual temperature = 13.7° C), (B) Tishomingo National Fish Hatchery (mean annual temperature = 16.4° C), and (C) Natchitoches National Fish Hatchery (mean annual temp = 18.2° C). Climate data from O'Donnell & Ignizio (2012). The shaded polygon indicates the western geographic distribution of *Macrochelys temminckii*. Adapted from the U.S. Geological Survey, https://nas.er.usgs.gov/viewer/omap.aspx?SpeciesID=1227, accessed on 15 October 2021.

Figure 2. Placement of a transmitter/data logger on a captive-reared 4-year-old Alligator Snapping Turtle (*Macrochelys temminckii*).

Effects of Latitude on Daily and Seasonal Activity Patterns

I applied 20-g data loggers to 27 4-year-old Alligator Snapping Turtles, and then evenly but randomly assigned them the three study sites. All turtles were introduced to their experimental pond between 26 May and 6 June 2019. A single turtle at the northernmost site in Kansas died early in the study and was replaced with another from the same cohort that was similar in size. Following release, the turtles were only disturbed by occasional supplemental feeding of frozen fish and periodic recapture events during which I downloaded data from the loggers. Supplemental feeding was done at the discretion of hatchery staff and was not done regularly. I monitored activity from 7 June 2019 to 7 November 2019. While initially I planned to monitor activity for a full year, I truncated the duration of my study due to multiple transmitter failures that greatly reduced my sample size.

Effects of Age Class on Daily and Seasonal Activity Patterns

In addition to the nine 4-year-old turtles that were part of the latitudinal study, I also equipped an additional 18 turtles (nine 7-year-olds and nine 2-year-olds) in ponds at Tishomingo National Fish Hatchery. I released the 2-year-olds into the same pond that the 4-year-olds occupied; the 7-year-olds occupied a similar but separate pond to eliminate the possibility of intraspecific aggression or predation of the younger/smaller cohorts. I was also forced to truncate the duration of the age study due to transmitter loss and failure resulting in an activity monitoring period from 2 June 2019 to 11 January 2020.

Size

I measured the straight mid-line carapace length (SCL) for each turtle during each recovery. The size of turtles within each study were compared based of either location or age. Due to failure and loss of transmitters as well as the mortality of two turtles in Kansas, not all turtles had equal time to grow, or were not allowed to grow during the same seasons in the case of the turtle which replaced those that died. Because of this, only those turtles in the latitude study that had been in the study for 146–155 days between 23 May and 8 November 2019 at their last measurement were included in size comparisons. This resulted in sample size differing among sites with n = 3, 8 and 9 for populations in Kansas, Louisiana, and Oklahoma, respectively. For turtles involved in the age study, only those that had amassed 146–149 days of growth between 23 May and 19 October 2019 at their last measurement were compared, which resulted in n = 8, 9, and 6 for 2-, 4- and 7-year-olds, respectively. I elected to use carapace length for comparing size among groups, as measurements of length tend to be less variable than measures of mass.

Statistics

I compared initial and final straight-line carapace length (SCL) among sites and age class using a repeated-measures ANOVA. I also compared rates of activity among study sites and age classes using repeated-measures ANOVA tests. I divided the study interval into 2-week periods in order to investigate potential seasonal differences between sites and age classes. To test for differences in monthly and seasonal activity patterns, I also performed repeated measures ANOVAs on data pooled by hour for each two-week period. Due to the large number of tests performed, I conservatively set $\alpha = 0.01$ to minimize instances of type-II statistical error. I also calculated average hourly temperatures for each turtle and compared temperatures among the three study locations. I also used a simple linear regression to test if average daily temperature significantly predicted averaged daily activity.

IACUC Approval

This study was approved by Institutional Animal Care and Use Committee on 4 June 2020 and received Approval #2020-03 (See Appendix).

RESULTS

Size

On average, turtles that were maintained at different latitudes did not differ in body size at the beginning or end of the study ($F_{2,34} = 2.17$, $P = 0.130$), but did grow over the course of 153 days ($F_{1,34} = 8.13$, $P = 0.007$) (Table 2). The increase in average SCL for Kansas, Oklahoma and Louisiana turtles was 12.9 mm,7.7 mm, and 12.5 mm respectively.

Table 2. Initial and final straight mid-line carapace length (SCL) of 4-year-old *Macrochelys temminckii* housed in outdoor ponds at fish hatcheries in Kansas (Farlington Fish Hatchery), Oklahoma (Tishomingo National Fish Hatchery), and Louisiana (Natchitoches National Fish Hatchery). 146–155 days elapsed between the initial and final measurements of each turtle.

Site	**Average SCL (mm)**	
	Mean ± 1 s.d.	Range
	Initial	
Kansas	156.6 ± 15.48	135.4–171.9
Oklahoma	153.1 ± 9.01	143.4–171.5
Louisiana	145.8 ± 7.59	140.4–160.1
	Final	
Kansas	169.5 ± 15.89	148.2–186.4
Oklahoma	160.8 ± 9.72	149.8–184.1
Louisiana	158.4 ± 8.30	144.2–171.1

Carapace length of 2-, 4-, and 7-year-old *M. temminckii* was significantly different between age classes ($F_{2,42} = 233.95$, $P < 0.001$) with 7-year-old turtles being the largest and 2-year-olds being the smallest (Table 3). However, SCL was not significantly different within age classes between the beginning and end of the study ($F_{1,42} = 2.65$, $P = 0.11$)

Table 3. Initial and final straight-line carapace lengths (SCL) of 2-, 4-, and 7-year-old *Macrochelys temminckii* following. The study lasted 146–149 days and all animals were housed in outdoor ponds at Tishomingo National Fish Hatchery in southern Oklahoma.

Age (Years)	**Average SCL (mm)**	
	Mean ± 1 s.d.	Range
	Initial	
Two	117.3 ± 13.58	101.9–139.8
Four	153.1 ± 9.01	143.4–171.5
Seven	252.5 ± 23.5	213.0–282.7
	Final	
Two	122.9 ± 14.21	114.3–143.1
Four	160.8 ± 9.72	149.8–184.1
Seven	263.4 ± 25.6	219.0–295.0

Latitudinal Temperature

Turtles in Louisiana experienced the warmest temperatures (28.5 ± 4.4° C [mean ± s.d.]), while those in Oklahoma experienced intermediate temperatures (25.9 ± 5.6° C) and in Kansas the coldest temperatures (23.2 ± 6.3° C) (Figure 3).

Effects of Latitude on Daily and Seasonal Activity Patterns

I performed a simple linear regression to assess the relationship between average daily temperatures and average daily activity for each site. The relationship was significant at all three sites (KS: $R^2 = 0.309$, $F_{1,151} = 67.673$, $P < 0.001$; OK: $R^2 = 0.187$, $F_{1,152} = 34.891$, $P < 0.001$; LA: $R^2 = 0.339$, $F_{1,152} = 77.898$, $P < 0.001$) (Figure 4).

Across all three sites, rates of activity were highest in early summer and late summer/early autumn (periods A–D and G–I; Figure 5) which were mostly periods of higher temperatures (Fig 3.). These periods of higher activity were separated by a mid-summer decline in activity (periods E and F; Fig 5). By mid-October, activity levels declined to a level that then remained consistent for the winter intervals of the study.

Patterns of daily activity varied among the three sites in 4 of 11 two-week periods (Fig. 5). Turtles located at the southernmost latitude in Louisiana maintained higher activity levels than the two more northern latitudes until the final four weeks of monitoring and exhibited higher levels of activity than the other two sites for 7 of the 11 two-week periods (Fig. 5). Alligator Snapping Turtles that were maintained in ponds in Oklahoma and Kansas exhibited lower rates of activity overall, but with peaks of activity during the early and late summer followed by a decline in late October. In comparison to Alligator Snapping turtles located in Kansas and Louisiana, turtles in Oklahoma exhibited reduced rates of activity in mid-July.

Daily activity patterns defied simple classification at all latitudes. Turtles at the Louisiana study site were more active midday in early summer but shifted to a pattern of mostly pre-dawn morning activity from mid-summer until activity levels declined in October. Turtles at the Kansas and Oklahoma sites also displayed higher levels of activity midday during early summer, while exhibiting activity levels that were similar across a 24-hour cycle for the remainder of the study.

Effects of Age Class on Seasonal and Daily Activity Patterns

Peak activity occurred in early summer and early autumn for all three age classes of turtles that I studied (periods A–C and F–H; Figure 6). Seven-year-olds exhibited higher levels of activity overall than the two younger year classes (Fig. 6), and while activity rates remained high for 2- and 7-year-old turtles throughout summer, 4-year-old turtles exhibited lower activity during mid-summer (Periods D–F; Fig. 6). In addition, 2-year-old turtles recorded higher activity levels than the 4-, and 7-year-old turtles from 17 November to 28 December (Fig. 6). The activity levels of the 2-year-olds during this period was comparable to mid-summer activity levels.

Daily activity patterns differed between the 2-, 4-, and 7-year-old groups in 4 of the 16 two-week periods (Fig. 6). I measured a noticeable decrease in activity for a single two-week period between 6 and 19 October, followed by a two-week period of high activity before activity decreased throughout the remainder of the study period.

Daily activity patterns were inconsistent for 4-, and 7-year-old Alligator Snapping Turtles for the duration of our study. 7-year-old turtles were most active during the day for most of the study, but with peak activity occurring at different times of day throughout. 7-year-old turtles exhibited peak activity before sunrise for four different time periods occurring in mid-summer and early autumn (periods C, E, H, and I; Fig. 6). 4-year-olds exhibited bimodal patterns of peak activity at dawn and dusk for periods in early summer and in late autumn (periods A, B, and K; Fig. 6) but throughout the rest of the study activity levels were similar throughout the day (Fig. 6). Two-year-olds showed the most consistent daily activity patterns with some peaks in the evening and early morning. In contrast, activity was highest in the afternoon and early evening in late October (Period K; Fig. 6)

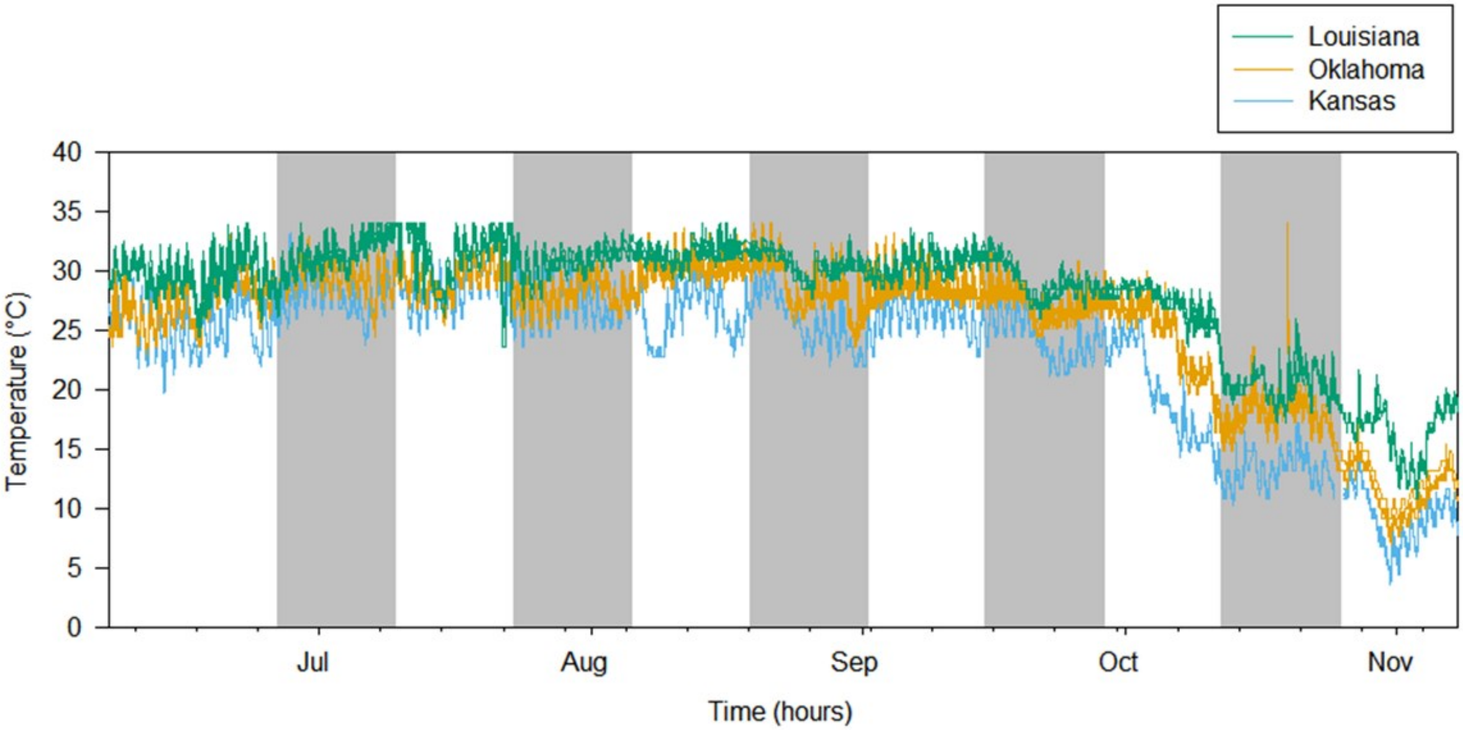

Figure 3. Average hourly temperatures experienced by all Alligator Snapping Turtles (Macrochelys temminckii) included in the study along a latitudinal gradient. Note that each individual is represented by a single line, and that all turtles at a given site are represented by a common color. Alternating shaded columns demarcate the 2-week periods within which activity levels where compared.

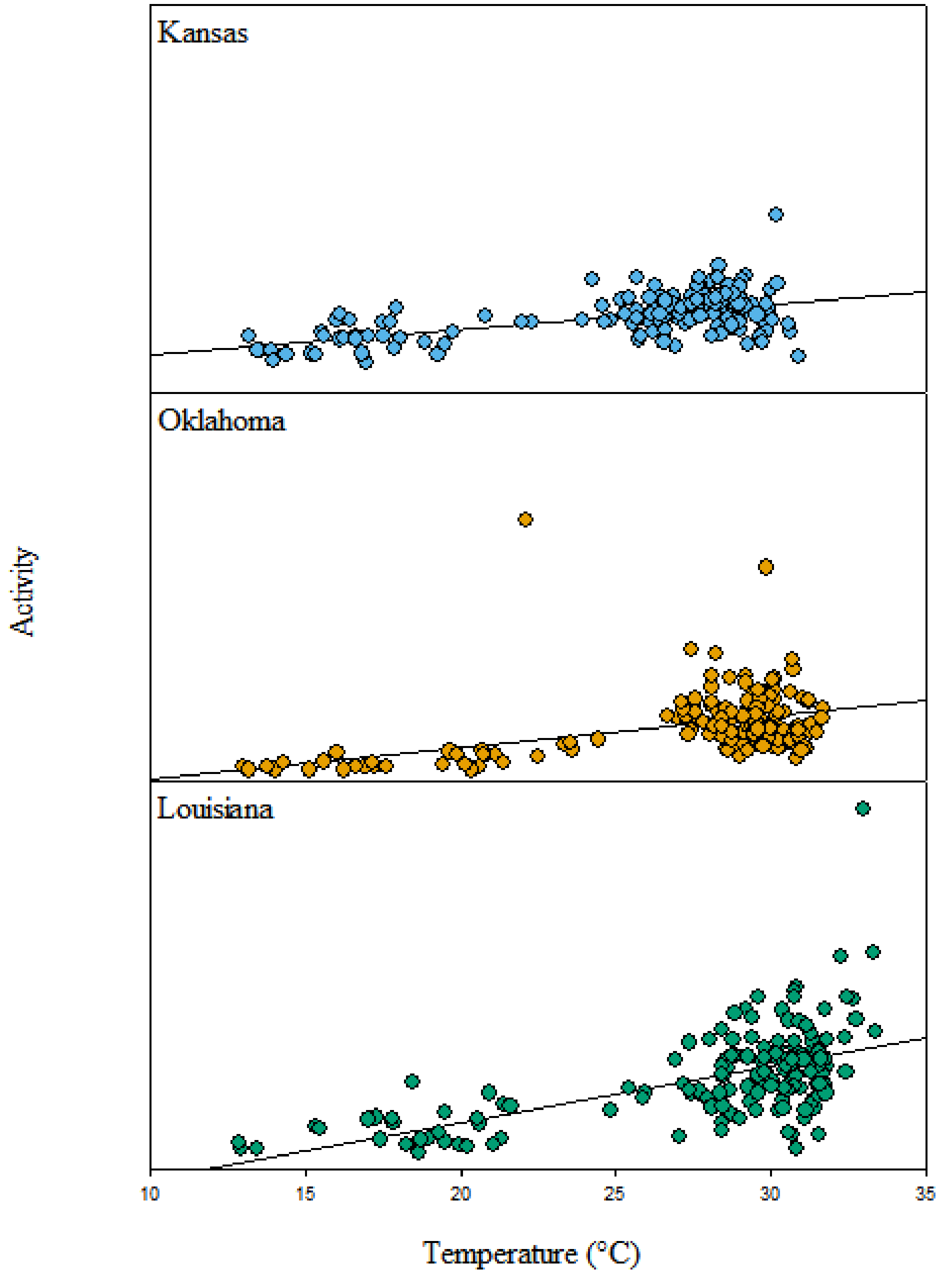

Figure 4. Temperature-Activity Regression plots for all three sites using average daily temperature and average daily activity for each day over the course of the study (n = 152 d for KS and 153 d for OK and LA). Regressions for all three sites were significant (KS: $R^2 = 0.309$, $F_{1,151} = 67.673$, $P < 0.001$; OK: $R^2 = 0.187$, $F_{1,152} = 34.891$, $P < 0.001$; LA: $R^2 = 0.339$, $F_{1,152} = 77.898$, $P < 0.001$). All three sites showed a positive relationship between temperature and activity. Y-axis is unitless due to arbitrary units reported by data loggers.

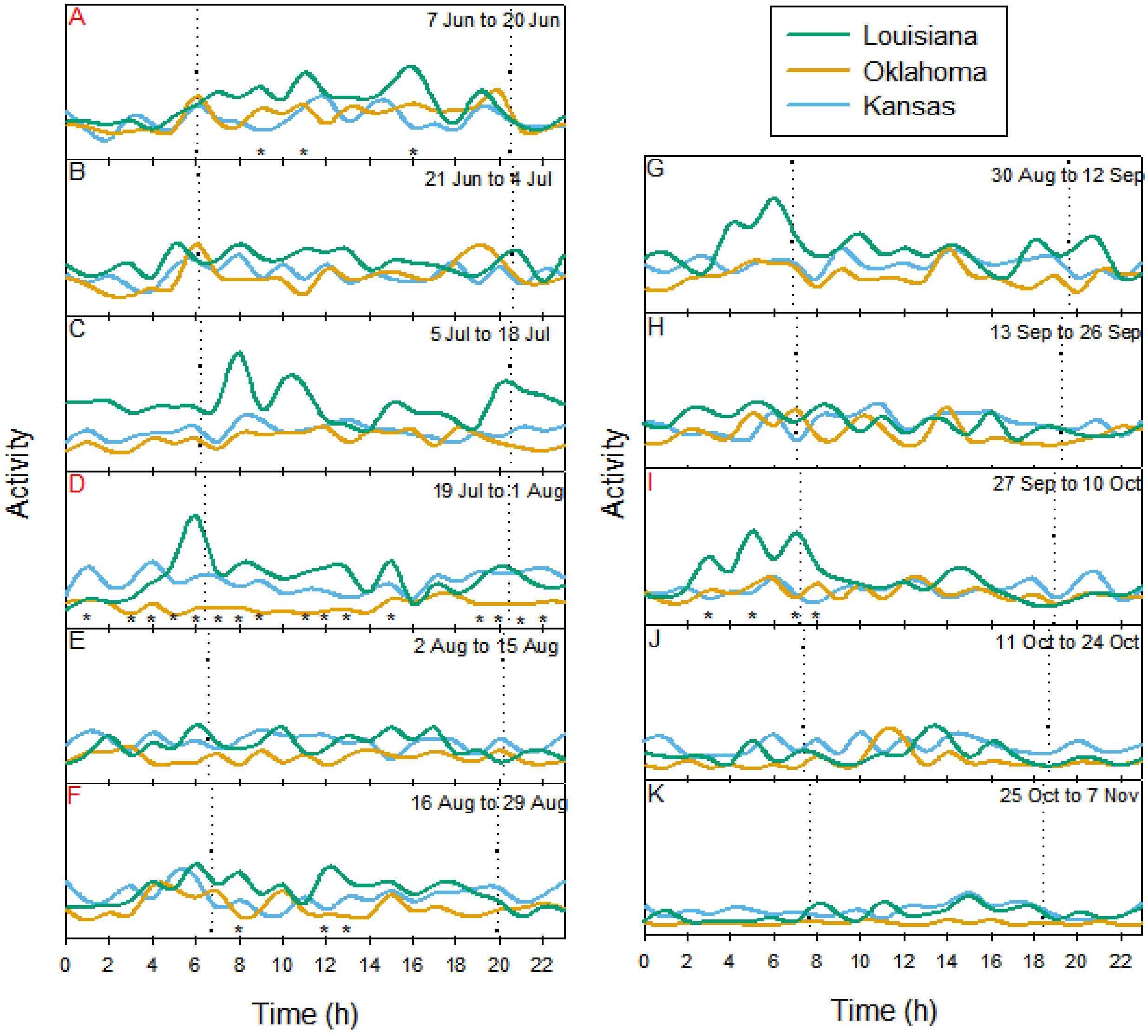

Figure 5. Mean hourly activity of Alligator Snapping Turtles (*Macrochelys temminckii*) occupying three sites located in Louisiana, Oklahoma, and Kansas from 7 June to 7 November. Dotted lines represent mean sunrise and sunset times for each time period. Time periods where activity differed among groups are denoted by a red label, and asterisks (*) indicate hours when activity levels differed among sites as determined by repeated-measures ANOVA. The y-axis units are not noted as the activity scores calculated by transmitters were reported in arbitrary units.

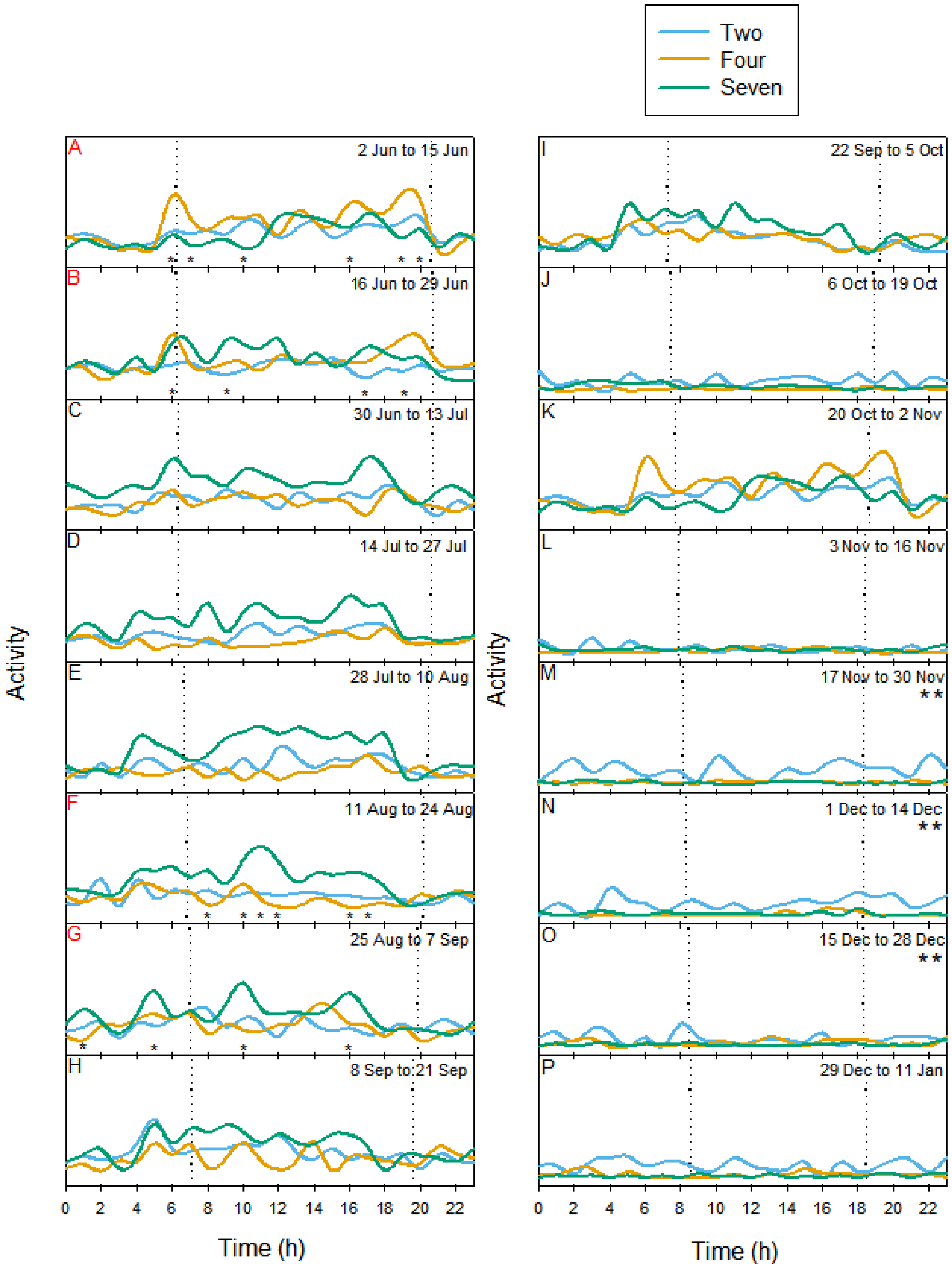

Figure 6. Mean hourly activity of 2-, 4-, and 7-year-old Alligator Snapping Turtles (*Macrochelys temminckii*) from 2 June 2019 to 11 January 2020. Dotted lines represent mean sunrise and sunset times for each period. Time periods in which activity differed among ages are denoted by a red letter. Single asterisks (*) indicate hours in which the interactions between age and hour of day were significant, and double asterisks (**) denote times when 2-year-olds exhibited significantly higher levels of activity than the two older age groups as determined by repeated-measures ANOVA. The y-axis units are not noted as the activity scores calculated by the transmitters were reported in arbitrary units.

DISCUSSION

Although all turtles grew over the duration of the study, I did not find support for consistent differences in growth among year classes of young juvenile Alligator Snapping Turtles. Somewhat surprisingly, I also found no support for an effect of latitude on growth. Differences in growth have previously been observed between hatchling Alligator Snapping Turtles housed at Tishomingo National Fish Hatchery in Oklahoma and Natchitoches National Fish Hatchery in Louisiana (B. Fillmore, unpublished data); however, those differences were observed after a full year of observations, whereas my size comparisons spanned just 153 days. Additionally, the previous study had much larger sample sizes, with 100 hatchlings housed in Louisiana and more than 200 housed in Oklahoma. Had my study run longer, allowing for changes in growing season due to difference in overwintering periods, or had similarly large sample sizes then treatment differences might have become evident.

Latitudinal Temperature

Consistent with predictions, mean hourly water temperatures correlated inversely with latitude. Summertime temperatures were more similar among sites than autumn or winter temperatures, and temperatures declined dramatically at all sites in October. Latitude likely accounts for most temperature differences among sites, but it should be noted that the emergent vegetation and water depth varied among sites and may have subtly influenced the temperatures that turtles experienced.

Effects of Latitude on Seasonal and Daily Activity Patterns

The effects of latitude on diel activity patterns of 4-year-old Alligator Snapping Turtles were surprisingly inconsistent. However, during intervals when activity differed significantly among treatments, the animals that were reared at the southernmost site in Louisiana tended to be more active during pre-dawn hours (two time periods) or daylight hours (two time periods) than those reared in Oklahoma or Kansas. Had I obtained a full year of data that spanned all seasons, it is possible that greater differences would have become apparent in spring as southerly latitudes likely would have warmed earlier in the year than more northerly sites.

On a seasonal scale, juvenile Alligator Snapping Turtles reared in Louisiana were more active than those at more northerly latitudes in late September and early October, and subsequently decreased to levels comparable to turtles reared in Oklahoma and Kansas, suggesting that water temperatures at my study site in Louisiana remained warm enough to support activity later into autumn.

While I found temperature to be a significant predictor of activity (Fig. 4) other variables not accounted for must play a factor in activity as Kansas activity levels where comparable or higher to those of turtles in Oklahoma, which experienced higher temperatures on average.

Differences in the ponds at each site may account for some degree of difference in activity patterns (Table 1). The pond in Louisiana was by far the largest of the three, which may have resulted in a lower density of prey items than at the other two locations. With that said, I noted while in the field that turtles in Louisiana tended to stay near the kettle, which is a concrete lined structure where water enters the pond and is the deepest point. Vegetation was by far the densest in the Kansas pond, which was also the shallowest. Turtles in Kansas where often recollected amongst the vegetation on the edge of the pond, similar to how turtles in Oklahoma utilized the shade mats. These differences in cover and depth may variables for which future researchers want to control for. Alligator Snapping Turtles have previously been shown to change their use of depth with season (Riedle et al., 2006) meaning that the activity associated with that change may have been influenced by the difference in available deep-water habitat. Another potentially confounding variable is the use of supplemental feedings. While these feedings were irregular and in small amounts, ensuring that hatchery staff at all sites are using a similar supplemental feeding regiment at each site would ensure that any potential impact of this action would be able to clearly be explained.

Effects of Age Class on Seasonal and Daily Activity Patterns

Activity patterns varied seasonally among 2-, 4-, and 7-year-old Alligator Snapping Turtles that were reared in Oklahoma. Unsurprisingly, generally higher levels of activity occurred during summer and early autumn intervals and much lower levels of activity during late autumn and winter. Diel cycles varied among age classes, but in general, activity tended to be higher during predawn and daylight hours and lower in the evening and nighttime. During most 2-week time intervals, activity tended to decrease at or before dusk and increase at or before dawn, suggesting a diurnal activity pattern that is biased toward more early morning and less evening activity.

Where age-specific differences occurred, 7-year-olds tended to be more active during summer months when overall activity was comparatively higher. However, during late autumn and winter, 2-year-old Alligator Snapping Turtles consistently exhibited higher levels of activity than did older conspecifics. This result is surprising for several reasons. First, a recent study demonstrated that hatchling Alligator Snapping Turtles adhere to a distinctly diurnal activity pattern (Spangler, 2017). Based upon my results, it appears that unimodal daytime activity may be unique to hatchlings, with transitions to uni- or bimodal crepuscular activity patterns occurring within two years of hatching. Reasons for these early shifts in activity are unclear, but it is possible that hatchlings follow patterns of activity that minimize interactions with potential predators, including large conspecifics. Previous research of the activity of both hatchling and adults have shown Alligator Snapping Turtles reduce activity in winter months (Spangler, 2017; Van Den Bussche et al., 2018). This makes the discovery of the elevated wintertime activity levels that I observed in 2-year-olds surprising, and the reasons underlying this result remain enigmatic.

Conclusion

To date, no empirical studies of the activity of Alligator Snapping Turtles indicate that the species consistently conforms to a predominantly nocturnal pattern, although such a pattern does occasionally arise during certain seasons and among a demographic subset of individuals (Van Den Bussche et al., 2018). My results, in combination with previous studies of hatchlings and adults, indicate that overall activity levels and patterns vary with season and life stage. Furthermore, my southernmost population in Louisiana showed a modest and inconsistent tendency toward higher activity levels than populations maintained farther north, a pattern consistent with activity correlating positively with temperature.

Alligator Snapping Turtle activity is likely influenced by variables beyond those associated with latitude (i.e., temperature and photoperiod) and age that may influence changes in these patterns. Alligator Snapping Turtles are uniquely adapted to sit-and-wait foraging, although the proportion of food that are obtained passively versus by active searching is unknown. Nonetheless, this tendency for passive foraging suggests that movement, as measured in this study, may miss ecologically important behaviors that are indistinguishable from true inactivity. Furthermore, it is possible that seasonal fluctuations in available forage influences activity patterns (Collier et al., 1990; Thies et al., 2006). As different prey become more abundant, Alligator Snapping Turtles may adjust foraging tactics to maximize prey acquisition rates.

In conclusion, my results suggest that activity patterns of Alligator Snapping Turtles vary with latitude and age but are likely also influenced by other variables that were not accounted for in this study. Future studies should focus on pairing acceleration-derived measures of activity with specific behaviors to provide a more detailed accounting of time and energy budgets. Understanding why and when a species may be active is helpful in both allowing a better understanding of the niche of that species, while also allowing researchers to better plan potential projects to maximize observations or captures.

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APPENDIX: IACUC APPROVAL LETTER

Missouri State
UNIVERSITY

June 4, 2020

RE: IACUC protocol 2020-03

Hello Dr. Ligon,

Your IACUC protocol #2020-03 entitled "Alligator Snapping Turtle Activity Patterns" has been approved.

The final approval date is 6/4/2020.

Thank you and if you need anything in the future regarding this protocol please contact me either via email (janeneproctor@missouristate.edu) or at 417-836-8419.

Sincerely,

Janene Proctor

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