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Home Range, Seasonal Movement Patterns, And Overwintering Ecology in Two Spotted Turtle (*Clemmys guttata*) Populations in Northwestern Indiana

Jessica R. Lindberg[1], Marlen Terrazas[1,2], Haydn G. Notario[1], Trang Nguyen[1], Ella Janson[1], Leigh Anne Harden[3], and Joseph R. Milanovich[1]

[1]Department of Biology, Loyola University Chicago, Chicago, Illinois 60076, USA (jmilanovich@luc.edu)
[2]School of the Environment, Washington State University, Pullman, Washington 99163, USA
[3]Department of Biological Sciences, Benedictine University, Lisle, Illinois 60532, USA

Abstract.—Land-use change has resulted in natural habitats becoming fragmented and disjunct. Wetland ecosystems in the United States are one example that has impacted wetland-adapted species. One species, the Spotted Turtle (*Clemmys guttata*), lives and relies on freshwater wetland habitats. Unfortunately, relatively little is known about the spatial and habitat requirements for *C. guttata*, especially in fragmented habitats. Using ground-based radio-telemetry and thermal ecology, we calculated seasonal home ranges and examined overwintering ecology for 30 adult turtles from April 2022 to January 2023 at two sites in northern Indiana. We then calculated annual and seasonal (seasonal movement areas, SMA) home ranges using 100% Minimum Convex Polygons (MCP) and annual 95%, 90%, and 50% kernel density estimates (KDs). Our results show MCPs were not significantly different between sexes or sites but differed significantly across seasons (highest in spring). Annual KDs (95%, 90%, and 50%) did not differ between sites. Daily mean air temperatures prior to overwintering were 12.01 °C and no turtle was recorded to have a carapacial temperature below 0.5 °C. Results of this study show that even in these highly fragmented areas Spotted Turtles can operate similar to other populations in more natural habitats. These data can be used to help develop management plans for Spotted Turtle populations in disjunct and/or urban areas.

Turtles are among the most endangered vertebrate groups, with only 19% classified as not threatened or of least concern by the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species in 2019 (McCallum 2021). Climate change, collection for the pet trade, pollution, road mortality, introduction of invasive plants, increased predation, and habitat loss all play a role in the decline of turtles (Lewis et al. 2004; Beaudry et al. 2009; Howell and Seigel 2019). The impact of habitat loss and fragmentation is especially threatening for aquatic and semi-aquatic turtles that rely on the connectivity of several habitat types (Gibbons 1970; Beaudry et al. 2009; Howell and Seigel 2019). In addition to anthropogenic factors, threats based on turtles' life history traits such as low reproductive output and late sexual maturity make them particularly susceptible to extinction (Browne and Hecnar 2007). Therefore, studying how these long-lived animals interact with their environment is crucial to the development of species-management plans.

Spotted Turtles (*Clemmys guttata*; Fig. 1) are small, semi-aquatic, freshwater turtles native to the coastal plain of the eastern U.S. and remnant wetland habitats of the eastern Great Lakes (Beaudry et al. 2009; Rasmussen and Litzgus 2010; Powell et al. 2016; Lassiter 2022). The northern range limit extends to Ontario and the southern limit reaches into Florida (Litzgus et al. 1999; Boykin 2018). Compared to other turtle species' life histories, Spotted Turtles are more susceptible to threats due to smaller body size, slower growth rates, nonaggressive behavior, smaller clutch sizes, low survival rates for juveniles, and highly delayed sexual maturation (Ernst and Zug 1994; Litzgus and Brooks 1998; Litzgus and Mousseau 2006; Feng et al. 2019). In addition, populations of Spotted Turtles are at risk of habitat loss and fragmentation due to roads, development, habitat conversion, and industrialization (Lewis et al. 2004). Spotted Turtles are listed as endangered in Indiana (Indiana Division of Fish & Wildlife 2020) and on the IUCN Red List of Threatened Species (van Dijk 2011).

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Figure 1. A Spotted Turtle (*Clemmys guttata*) at Site 1 of the study site in northwestern Indiana. Photograph by Dr. Leigh Anne Harden.

Northwestern Indiana is a prime example of a fragmented landscape. In the late 1800s to 1920s, the region's steel mills, oil refineries, and landfills resulted in considerable habitat conversion and development of roads. In 1991, 85% of Indiana's native wetlands had been lost due to industrialization, and the status of wetland loss or gain since then remains understudied (Dahl 1990; Seng and Case 1996). Consequently, populations of Spotted Turtles in the broader Midwest and Indiana are disjunct, and movement between wetlands is a high-risk endeavor (Beaudry et al. 2009). Habitat fragmentation thus creates several challenges when attempting to conserve this species in the region, and studying the spatial ecology of these Spotted Turtle populations can better inform management plans of this species in fragmented landscapes.

To implement conservation efforts that mitigate habitat loss and promote survival of native Spotted Turtle populations, a better understanding of the species' spatial ecology is needed. This involves defining home ranges and seasonal-movement areas, as well as describing habitat use throughout the year (Seaman and Powell 1996; Beaudry et al. 2009; Rasmussen and Litzgus 2010; Chandler et al. 2019). Semi-aquatic turtles move among wetland and terrestrial habitats to bask, forage, mate, nest, aestivate, and overwinter (Gibbons 1970; Milam and Melvin 2001; Bowne et al. 2006; Beaudry et al. 2009; Rasmussen and Litzgus 2010), with initiation of such movements likely triggered by phenological changes. Thus, studying thermal ecology further increases our understanding of how Spotted Turtles use habitat in response to changing environmental conditions.

Typically, Spotted Turtles emerge in early spring, often before other semi-aquatic turtles in their range (Litzgus and Brooks 1998; Ultsch 2006). As temperatures rise and wetland pools dry up during the summer, Spotted Turtles aestivate by taking cover under leaf litter in terrestrial upland habitats near wetlands (Litzgus and Brooks 1998; Milam and Melvin 2001; Ultsch 2006; Beaudry et al. 2009; Ernst and Lovich 2009). In late summer and early fall, Spotted Turtles begin moving toward hibernacula, sometimes moving back and forth between upland and wetland habitats (Litzgus et al. 1999; Beaudry et al. 2009). Spotted Turtles generally overwinter in deep wetland pools, although terrestrial hibernacula have been documented (Litzgus et al. 2004; Beaudry et al. 2009; Rasmussen and Litzgus 2010). They also have been observed moving deeper into substrates to avoid freezing temperatures and aggregating in hibernacula, with as many as 34 turtles sharing an overwintering site (Lewis and Ritzenhaler 1994; Litzgus et al. 1999; Rasmussen and Litzgus 2010).

Many studies have investigated Spotted Turtle home ranges, movements, habitat use, and overwintering in other parts of their range (Table 1; e.g., Litzgus et al. 1999; Beaudry et al. 2009; Rasmussen and Litzgus 2010; Feng et al. 2019), and small, disjunct Midwestern populations have been studied in Illinois (Wilson 1994; Feng et al. 2019) and southwestern Michigan (Coury 2022). However, no published studies have examined populations in Indiana. We examined annual home ranges, seasonal movement patterns, and overwintering ecology of two populations of Spotted Turtles in northwestern Indiana with the intent of providing new information to facilitate local conservation decisions.

Methods

This study spanned all seasons from 21 March 2022 through 8 April 2023 in two urbanized and post-industrial sites in northwestern Indiana (Lake County). Site 1 is a 91-ha state nature preserve dominated by tall grasses, ferns, and forbs, with small ephemeral ponds often invaded by common reeds (*Phragmites* spp.), that is surrounded by a heavily urbanized and industrial area. Site 2 is a 258-ha marsh-like preserve that consists of native sedges, wetland forbs, Rough Horsetail (*Equisetum hyemale*), Buttonbush (*Cephalanthus occidentalis*), and bulrushes (*Schoenoplectus* spp.), although invasive species such as Cattails (*Typha* spp.) and Common Reeds (*Phragmites* spp.) were present in pockets throughout the preserve. Site 2 also is located in an urbanized and industrial area.

We trapped turtles between 21 March and 8 April 2022 by deploying collapsible, 12-inch hoop-net traps baited with sardines at both sites. For each turtle captured, we measured carapace length (mm), carapace width (mm), plastron length (mm), shell height (mm), and mass (g) before and after hardware attachment. Unique notch codes and identification numbers based on radio-transmitter frequencies painted on each carapace with non-toxic paint markers were used to identify each individual. We affixed transmitters (Advanced

Table 1. A comparison of studies of Spotted Turtle (*Clemmys guttata*) annual home range sizes (ha) with this study. Studies are listed in descending order based on the mean minimum convex polygon (MCP) estimates of home range sizes (ha). Studies that compared home range sizes of males (m), females (f), or gravid females (gf) are specified.

Reference (location)	Site Size (ha)	MCP (ha)	95% KD (ha)	50% KD (ha)
Litzgus et al. 2004 (South Carolina)	4500	5.15 (m); 19.06 (gf)	4.67 (m); 10.36 (gf)	0.92 (m)
Haxton and Berrill 1999 (Ontario)	120	3.7	—	—
Milam and Melvin 2001 (Massachusetts)	89.7	3.5	—	—
O'Dell et al. 2021 (Massachusetts)	43	1.99	—	—
Kaye et al. 2001 (Massachusetts)	29.2	1.95 (m); 0.95 (f)	—	—
This study (Indiana)	91; 80	1.79; 1.97	1.78; 1.99	0.29; 0.28
Wilson 1994 (Illinois)	101	1.36	—	—
Coury 2022 (Michigan)	53	1.31; 1.26	3.63; 2.53	0.90; 0.54
Graham 1995 (Massachusetts)	607	0.7	—	—
Ernst 1970 (Pennsylvania)	10.1	0.5	—	—
Rowe et al. 2013 (Michigan)	13.6	~0.5	~0.3	~0.05

Telemetry Systems, R1680; 3.6 g) on 30 adult turtles (21 males and 9 females) from both sites, ten at Site 1 (9 males, 1 female) and 20 at Site 2 (12 males and 8 females). To prevent interference with mating, we affixed transmitters to the lower right posterior end of the carapace using a quick-dry epoxy (Devcon 5 Minute Epoxy®) and steel-reinforced putty (JB Weld SteelStick®).

We began tracking turtles using ground-based telemetry on 5 April 2022. We used a receiver (Advanced Telemetry Systems, Model R410) attached to 3-yagi antenna one to three times per week during the active season (April–November; Table 2). We took global positioning system (GPS) points within one meter of each encounter, recorded these in the field, and noted behavior and habitat use. Tracking effort mirrored turtle-activity levels. As activity declined during late summer, we reduced our tracking efforts to once per week. We tracked turtles once per month during the winter to gain insight into overwintering behavior. Trackers were removed in March through April of 2023 before the transmitters lost power. We divided the active season into spring (April, May, June), summer (July, August), and fall (September, October, November) periods.

Spatial Ecology.—To assess annual home ranges (AHRs), we calculated 100% minimum convex polygons (MCPs) (Ernst 1970; Row and Blouin-Demers 2006; Struecker et al. 2023) as well as 95%, 90%, and 50% kernel density estimates (KDs) to characterize size and intensity of use (Seaman and Powell 1996). We also calculated spring, summer, and fall seasonal movement areas (SMAs) to assess differences in spatial use across the active season. To estimate SMAs, we calculated 100% MCPs. We did not calculate KDs for SMAs because we had fewer than 20 points per season per turtle (Paterson et al. 2012; Coury 2022).

Although minimum convex polygons are commonly used to characterize home range sizes and their simplicity is useful, MCPs outline the individual's home range or SMA without emphasizing where individuals are most frequently located (Row and Blouin-Demers 2006). Consequently, MCPs often include areas not used by an individual but may nonetheless be vital to their survival (Kaufmann 1995; Milam and Melvin 2001; Litzgus et al. 2004). We calculated 100% MCPs using the "adehabitatHR" package in R (R version 4.3.2 "Eye Holes"), and code in Paterson (2019).

KDs are controversial for assessing home ranges of herpetofauna because they tend to overestimate home-range size; however, we wanted to use multiple indices to characterize habitat use within each home range (Row and Blouin-Demers 2006). KDs provide a gradient of predicted location data, concentrating on areas within the home range that are more likely to be used; 95%, 90%, and 50% KDs estimate where individuals are located 95%, 90%, and 50% of their time, respectively (Seaman and Powell 1996). This prediction is based on the frequency of data points recorded in particular locations and is sensitive to autocorrelation due to sampling effort, site fidelity, and reduced dispersal during low-activity periods (Worton 1987; Row and Blouin-Demers 2006). However, if sampling intervals are consistent, then autocorrelation should not invalidate estimates of home ranges (de Solla et al. 1999) The most difficult part of using KDs is choosing the correct smoothing factor (h), which may overestimate area used or place too much value on clusters of proximate localities (Seaman and Powell 1996; Row and Blouin-Demers 2006). We used several spatial ecology R packages (adehabitatHR, sp, sf) and code published on GitHub by Paterson (2019) to generate 95% KDs for each turtle's AHR (Pebesma 2018; Pebesma and Bivand 2023). This R code

Table 2. Number of GPS points for each Spotted Turtle (*Clemmys guttata*) at Sites 1 and 2 in spring, summer, fall, and annual total, as well as dates of descent into hibernation and habitat type at descent.

Turtle ID	Site	Spring Points	Summer Points	Fall Points	Annual Points	Entry into Hibernation	Habitat
T8592	Site 1	12	0	0	12	—	—
T8620	Site 1	12	8	10	30	28 Oct. 2022	Underwater/vegetation
T8650	Site 1	13	7	10	30	28 Oct. 2022	Terrestrial
T8799	Site 1	10	11	10	31	28 Oct. 2022	Underwater/mud
T9212	Site 1	14	1	10	25	16 Oct. 2022	Underwater/vegetation
T9244	Site 1	15	0	0	15	—	—
T9332	Site 1	14	11	11	36	15 Oct. 2022	Underwater/vegetation
T9440	Site 1	14	10	11	35	15 Oct. 2022	Underwater/vegetation
T9503	Site 1	12	9	11	32	15 Oct. 2022	Vegetation
T9571	Site 1	13	9	11	33	15 Oct. 2022	Underwater/vegetation
T8573	Site 2	15	12	11	38	15 Oct. 2022	Underwater/mud
T8680	Site 2	11	10	11	32	21 Oct. 2022	Underwater/vegetation
T8710	Site 2	14	11	10	35	15 Oct. 2022	Underwater/mud
T8740	Site 2	17	12	11	40	15 Oct. 2022	Mud/vegetation
T8770	Site 2	14	12	11	37	15 Oct. 2022	Underwater/vegetation
T8831	Site 2	10	11	11	32	21 Oct. 2022	Underwater/vegetation
T8859	Site 2	10	8	11	29	16 Oct. 2022	Underwater/mud/vegetation
T8890	Site 2	9	12	11	32	15 Oct. 2022	Underwater/mud
T8953	Site 2	5	7	7	19	21 Oct. 2022	Underwater/mud/vegetation
T8982	Site 2	8	12	11	31	16 Oct. 2022	Underwater/vegetation
T9002	Site 2	9	7	11	27	16 Oct. 2022	Terrestrial/buried/vegetation
T9262	Site 2	14	12	11	37	16 Oct. 2022	Underwater/vegetation
T9290	Site 2	13	12	12	37	16 Oct. 2022	Terrestrial/mud
T9363	Site 2	11	11	9	31	15 Oct. 2022	Underwater/mud
T9380	Site 2	17	10	8	35	16 Oct. 2022	Terrestrial/mud
T9391	Site 2	13	12	10	35	16 Oct. 2022	Mud/vegetation
T9422	Site 2	7	0	0	7	—	—
T9481	Site 2	15	10	10	35	16 Oct. 2022	Underwater/mud
T9533	Site 2	8	2	0	10	—	—
T9552	Site 2	10	11	11	32	16 Oct. 2022	Underwater/vegetation

adjusts *h* until the 95% KD area equals 100% MCP area as MCPs characterize the entirety of a home range (Row and Blouin-Demers 2006). This code generates a different *h* value for each individual turtle's 95% KD. We then used this same *h* to estimate each individual turtle's 90% and 50% KDs for all SMAs (Paterson 2019). This prevented the severe overestimation of home range size that occurs in the more commonly used ad hoc and least-squares cross validation methods of calculating KDs (Worton 1989; Row and Blouin-Demers 2006). Although these methods are commonly used, they work better for animals with large home ranges, larger sample sizes, and/or daily sampling efforts (Worton 1989; Paterson 2018).

We calculated home ranges for 30 turtles (10 at Site 1 and 20 at Site 2) and SMAs depending on the number of points per season (Table 3). All statistical analyses were done in RStudio (R version 4.3.2 "Eye Holes"). Because of our small sample size (21 males and 9 females), we conducted Mann-Whitney *U*-tests and determined that no significant differences existed between sexes for MCPs across SMAs as well as AHRs across all KD levels. We used two-way ANOVAs to test for variation in MCPs across seasons, between sites,

Table 3. Mean (SD) areas (ha) of annual home ranges (AHR) and seasonal movement areas (SMA) of Spotted Turtles (*Clemmys guttata*) at Sites 1 and 2 across the active season. Points are the mean number of GPS points used to calculate home ranges for individuals during each season.

Season	n	Points	MCP (ha) AHR	95% KD (ha) SMA	90% KD (ha) SMA	50% KD (ha) SMA
Site 1						
Spring	10	12.9	1.30 (1.50)	—	—	—
Summer	7	6.6	0.04 (0.05)	—	—	—
Fall	7	8.4	0.07 (0.04)	—	—	—
Annual	10	27.9	1.79 (1.51)	1.78 (1.53)	1.36 (1.16)	0.29 (0.29)
Site 2						
Spring	20	11.5	1.40 (0.97)	—	—	—
Summer	18	9.7	0.16 (0.19)	—	—	—
Fall	18	9.4	0.11 (0.10)	—	—	—
Annual	20	29.6	1.97 (1.47)	1.99 (1.56)	1.48 (1.18)	0.28 (0.17)

and the interaction of both; and significant ANOVAs were followed by Tukey's Honest Significant Difference (HSD) Tests. To compare AHRs between sites, we conducted two-tailed t-tests for MCPs and across all KD levels.

Overwintering Ecology.—We used carapace temperature (T_c) to assess phenology and hibernation behavior, measuring T_c using Thermochron iButton dataloggers (model DS1921G, Dallas Semiconductor) coated in rubber (Performix Plast-dip) to prevent water damage. This coating can cause minor discrepancies in temperature readings, but the differences are insignificant and vary only 0.0–1.3 °C from uncoated iButtons (Roznik and Alford 2012; Harden et al. 2015; Cann et al. 2023). To prevent adverse effects of equipment on their shells, we placed transmitters and iButtons only on adult turtles weighing more than 105 g (both items weighed < 5% of turtles' initial masses).

iButtons measured temperatures every 4 hours. Rubber-coated iButtons also were inserted into a section of PVC pipe placed vertically in the water and sediment at Site 2 to measure environmental temperatures (T_e) 15 cm above water level (air), at water level, and at depths of 25 cm, 50 cm, 100 cm, and 122 cm below the underwater substrate level. This pole was deployed on 27 March 2022 and removed on 10 August 2023. We compared environmental temperatures to T_c to evaluate thermoregulatory behavior throughout the season, including changes in water or substrate depths during hibernation.

Results

At Site 1, we captured and tracked nine males and one female, but recorded the entire active season for only seven turtles as two transmitters were not recovered; also, one additional transmitter was not recovered during winter tracking (Table 3). While we observed one instance of road mortality of an unmarked individual, we did not encounter any of the turtles we tracked crossing the road. At Site 2, we attached transmitters to 20 turtles and were able to track 18 throughout the active season (Table 3).

Table 4. Analysis of variance (ANOVA) table for site, season, and interaction between site and season for minimum convex polygon estimates of annual home ranges (AHR) of Spotted Turtles (*Clemmys guttata*).

Effect	df	MS	F	P
Season	2	14.54	28.05	9.17e-10
Site	1	0.13	0.25	0.62
Season x Site	2	0.01	0.02	0.98

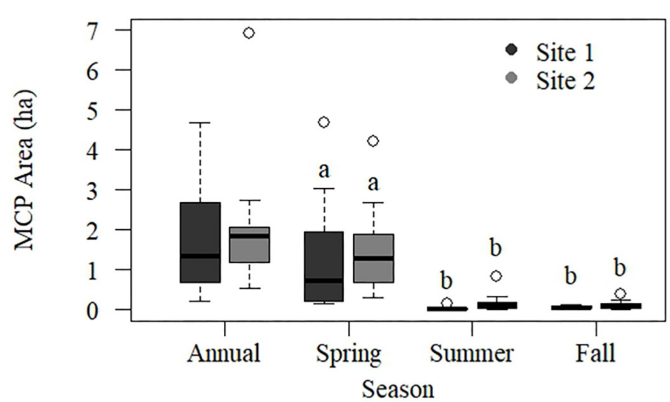

Figure 2. Boxplot of annual home range and seasonal movement area size (ha) for minimum convex polygons. Line represents mean, boxes equal standard error and whiskers are 95th percentile confidence intervals). Letters above whiskers indicate results from Tukey's Honest Significant Difference test.

Table 5. Results of T-tests comparing mean annual home range sizes of Spotted Turtles (*Clemmys guttata*) for 95%, 90%, and 50% kernel density estimates at Sites 1 and 2.

	t	df	p-value	Mean Difference	95% Confidence Interval Lower	Upper
95% KD	-0.312	14.326	0.760	0.208	-1.634	1.218
90% KD	-0.236	14.334	0.817	0.119	-1.202	0.964
50% KD	0.113	9.362	0.912	0.124	-0.235	0.260
MCP	-0.284	13.729	0.781	0.184	-1.580	1.211

Spatial Ecology.—Mann-Whitney *U* tests revealed no significant differences between sexes for MCPs across SMAs or for AHRs across MCPs and all KD levels (all $P \leq 0.05$). Consequently, we did not consider sex a covariate, nor did we consider it when using ANOVAs or t-tests. Two-way ANOVAs determined that MCPs differed significantly across seasons, did not differ between sites, and that no significant interaction existed between site and season (Table 4; Fig. 2). Tukey's HSD tests showed that spring MCPs were significantly larger than fall and summer, and summer and fall MCPs did not differ significantly (Fig. 2). Combining sites, mean spring MCPs were 1.33 ha, mean summer MCPs 0.12 ha, and fall MCPs 0.10 ha. Thus, spring MCPs were approximately 10 times larger than both summer and fall MCPs. AHRs were assessed using MCPs as well as 95%, 90%, and 50% KDs (Table 3). T-tests revealed no significant differences between sites for all KD levels (Table 5). Combined means for both sites were 1.91 ha for MCPs, 1.92 ha for 95% KDs, 1.44 ha for 90% KDs, and 0.28 ha 50% KDs.

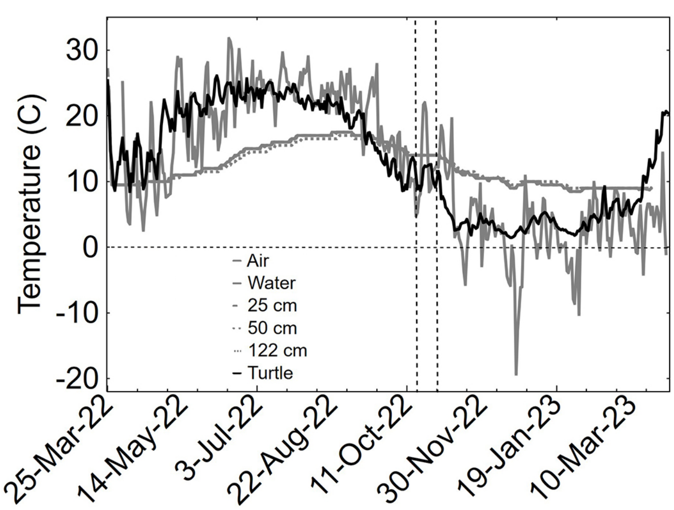

Figure 3. Mean daily carapace temperature (T_c = Turtle) of Spotted Turtles (*Clemmys guttata*) and environmental temperatures (air, water, and underwater substrate depths of 25, 50, and 122 cm). Substrate depths did not significantly differ and overlapped across the season. Dotted vertical lines estimate the entrance period into hibernation based on observations during tracking events.

Overwintering Ecology.—We recovered 18 iButtons (7 at Site 1 and 11 at Site 2) and found that carapace temperatures (T_c) followed similar trends as air temperatures compared to water or underwater substrate temperatures (Fig. 3). Turtles entered hibernation from 15–28 October 2022. During this period, daily mean T_c for all turtles was 11.33 ± 2.88 °C. Mean daily air temperature during this time was 12.01 ± 9.30 °C. During the seven days prior to hibernation, mean daily T_c of all turtles was 10.38 ± 3.60 °C and mean daily air temperature was 11.94 ± 8.55 °C. Unlike air temperatures, we never recorded T_c below 0 °C.

Discussion

Our results show Spotted Turtle ranges at both Sites 1 and 2 were within the range sizes of other Spotted Turtle spatial ecology studies (Ernst 1970; Haxton and Berrill 1999; Milam and Melvin 2001; Litzgus et al. 2004; Rowe et al. 2013). These studies suggest that larger home ranges occur in higher-quality habitats in contiguous landscapes removed from heavy development (Haxton and Berrill 1999; Milam and Melvin 2001; Litzgus et al. 2004). This conclusion is supported further by other turtle studies that describe larger home ranges of turtles in large, contiguous landscapes and smaller home ranges in fragmented landscapes (Litzgus et al. 2004; Iglay et al. 2007; Blake et al. 2023). For example, Litzgus et al. (2004) estimated the largest home range MCPs of Spotted Turtles (5 ha for males and >16 ha for gravid females) in a 4,500-ha unaltered forest site. This contrasts with one of the smaller Spotted Turtle home range estimates in a 13.6-ha site with less suitable habitat surrounding the site (Rowe et al. 2013). In some studies, animals in lower quality, less productive sites may expand their home range sizes in search of more suitable habitat (Ims et al. 1993; Morrow et al. 2001). For example, Morrow et al. (2001) compared Bog Turtle (*Glyptemys muhlenbergii*) home range sizes before and after encroachment of invasive Multiflora Rose (*Rosa multiflora*) at the same site. In that study, turtles expanded their mean home range sizes nearly tenfold in search of more suitable habitat. Conversely, O'Dell et al. (2021) examined Spotted Turtle habitat selection before, during, and after a salt-marsh restoration project and found home range sizes were not significantly different despite the changes in habitat selection and location pre-, mid-, and post-restoration. We did not observe any tracked turtles migrating from the preserves, likely due to adjacent land primarily comprised of heavily altered, unsuitable habitat.

We found variation in SMAs calculated with minimum convex polygons across both sites and seasons. Spring SMAs were approximately 10 times larger than summer and fall SMAs, but summer and fall SMAs did not differ significantly. This aligns with other Spotted Turtle studies that described significantly greater movement during the spring when Spotted Turtles emerge from overwintering sites to forage and search for mates (Lassiter 2022; Rasmussen and Litzgus 2010). Rasmussen and Litzgus (2010) defined three active seasons: emergence, nesting, and post-nesting, all of which differed significantly, with emergence (early spring) demonstrating the greatest average daily distance moved.

Daily distance moved is another spatial-ecology metric that, in this case, showed that Spotted Turtles are most active following emergence. In the summer months, Spotted Turtles reduce activity and seek refugia as daily maximum temperatures climb and vernal pools dry up (Wilson 1994; Graham 1995; Litzgus et al. 1999). We found Spotted Turtles aestivating in both aquatic and terrestrial habitats: under leaf litter, in shaded pools, and burrowed into sediment and along the banks of larger wetlands. During aestivation, Spotted Turtles often seek concealed aquatic and terrestrial habitats like floating sphagnum mats, muskrat burrows, dried wetland beds, leaf litter, and woody debris (Ernst 1982; Lovich 1988; Litzgus and Brooks 2000; Milam and Melvin 2001; Litzgus et al. 2004; Beaudry et al. 2009; Lassiter 2022).

Conjecture in the literature questions whether this justifies "true" aestivation as Spotted Turtles do not seek refugia with cooler temperatures but simply limit their movement and exposure (Litzgus and Brooks 1998). Regardless, this period of concealed inactivity has been proposed to reduce predation risk, conserve energy during times of lower food availability, and minimize detrimental effects of hot and dry summer climates (Ward et al. 1976; Ernst 1982; Litzgus and Brooks 2000; Haxton and Berrill 2001; Kaye et al. 2001; Milam and Melvin 2001). Following late summer and fall rains, Spotted Turtles move to overwintering sites (Rowe et al. 2013; Lassiter 2022). Like our study, Beaudry et al. (2009) found that variance in Spotted Turtles was highest in spring and lowest in fall. Once Spotted Turtles locate overwintering sites, they again reduce their activity as they enter hibernation.

Spotted Turtle seasonal movement trends may be similar but not necessarily the same as those of other species of freshwater turtles with overlapping ranges. Beaudry (2009) compared seasonal movements between Spotted and Blanding's Turtles (*Emydoidea blandingii*) in Ontario. They defined four seasons for Spotted Turtles: spring (late April–May), early summer (late May–June), late summer (late June–mid-August), and fall (late August–October) and three active seasons for Blanding's Turtles: spring (early April–May), early summer (late May–July), and late summer/early fall (late July–October). While nesting periods overlapped between the two species, Spotted Turtles aestivated in late summer, whereas Blanding's Turtles did not change activity between summer and fall and did not aestivate. Additionally, gravid female Blanding's Turtles had significantly larger summer seasonal movement areas as they searched for suitable nesting habitat (Millar and Blouin-Demers 2011; Cann et al. 2023), whereas Spotted Turtles in our study had the largest SMAs in the spring. In a study of Wood Turtles (*Glyptemys insculpta*) in Quebec, Arvisais et al. (2002) found that activity was highest during the nesting period (mid- to late-June) and then decreased continuously through mid-September during a period of terrestrial inactivity. During prehibernation, Wood Turtles experienced a small activity peak associated with mating before returning to aquatic hibernacula and ceasing movement in November, seasonal movement patterns similar to those of Spotted Turtles in our study.

Spotted Turtles in our study began preparation for hibernation in October. In the northern part of their range, Spotted Turtles begin hibernation in September and early October while those in the southern parts of the range became inactive as late as November and December (Litzgus et al. 1999; Litzgus et al. 2004). Overwintering may last as short as two months in the south and as long as eight months at the northern range limits (Litzgus et al. 1999; Haxton and Berrill 2001; Litzgus et al. 2004; Ultsch 2006). In the south, Spotted Turtles emerge around late February, whereas at the northern limits of the range, Spotted Turtles may not emerge until mid-April (Litzgus et al. 1999; Haxton and Berrill 2001; Litzgus et al. 2004; Ultsch 2006).

During hibernation, Spotted Turtles at both Sites 1 and 2 had daily average T_c = 11.24 °C, which is within the observed range of other Spotted Turtle studies in which cloacal temperatures of 4.0–15.0 °C have been recorded during hibernation (Ernst 1982; Litzgus et al. 1999; Litzgus and Brooks 2000). Although fluctuations in T_c resembled air temperature trends at both sites, T_c never dipped below 0 °C. When air temperatures fell below freezing, mean T_c hovered between air and water temperatures, implying that the turtles did not bury themselves under sediment or stay on land. Turtles appeared to have stayed closer to the surface for basking but near the thermal stability of seasonal pools when air temperatures became too extreme. This is similar to Spotted Turtles in South Carolina that have been seen basking on sunny winter days (Litzgus et al. 2004).

Our results, however, differed from other studies, which found that Spotted Turtle body temperatures typically matched water temperatures. Wilson (1994) found that

Spotted Turtle cloacal temperatures were more closely related to water temperature during hibernation in Illinois. Eastern populations in Maine, Maryland, and Pennsylvania hibernated underwater at depths of 10–25 cm (Ward et al. 1976; Ernst 1982; Joyal et al. 2001). Litzgus et al. (1999) found that Spotted Turtles in Ontario did not use muskrat burrows or lodges for hibernacula as had been observed in other studies (Ernst 1982); instead, body temperatures suggested that they hibernated in seasonal pools just above freezing. Although we did not track turtles regularly throughout the winter months (once a month from November through February), we typically observed Spotted Turtles under water, and often below a layer of ice. Several areas were occupied by groups of turtles, which is common in hibernating Spotted Turtles (Litzgus et al. 1999; Milam and Melvin 2001; Ultsch 2006).

Spotted Turtle overwintering behavior differed from many other freshwater turtle species sharing this part of the range. Blanding's Turtles thermoregulate by shifting depth below the surface, sometimes as much as 45 cm to avoid freezing surface temperatures (Cann et al. 2023). Map Turtle (*Graptemys geographica*) hatchlings will overwinter in terrestrial nests as much as 12 cm below the surface (Baker et al. 2003). Painted Turtle (*Chrysemys picta*) hatchlings are well-known for their freeze tolerance at temperatures below -4 °C, and they overwinter in terrestrial nests that can reach temperatures below -8 °C (Packard 1997; Packard et al. 2002; Riley et al. 2014; Murphy et al. 2020). While Spotted Turtle freeze tolerance has not been studied, we did not find any T_c recordings below 0 °C. Instead, Spotted Turtles likely thermoregulate between basking and utilizing stable temperatures at the edges of bodies of water, overwintering in a fashion most similar to that of Wood Turtles (*Glyptemys insculpta*), whose body temperatures remain near 0 °C throughout winter despite large fluctuations in air temperatures, which is indicative of hibernation below the water's surface (Greaves and Litzgus 2007).

Understanding how Spotted Turtles navigate their habitat throughout the active season is essential for creating well-informed management plans. Based on our findings, Spotted Turtles at both Sites 1 and 2 use an area of nearly 2 ha. Our home-range estimates likely are lower than those documented in other studies due to confinement in an isolated, heterogenous landscape. Spotted Turtles require permanent water for daily activity and hibernation, vernal pools for travel between wetlands, and upland habitat during aestivation and for other purposes throughout the active season (Joyal et al. 2001; Milam and Melvin 2001; Rasmussen and Litzgus 2010). Studies suggest creating 275-m buffers around isolated wetlands to conserve upland habitat for freshwater turtle life history requirements (Burke and Gibbons 1995; Milam and Melvin 2001). Protecting habitat from further fragmentation and destruction is a first step. However, Browne and Hecnar (2007) warned that this alone might not be enough to sustain a population of endangered turtles. Nest and hatchling depredation is a common deterrent to turtle survival and recruitment (Browne and Hecnar 2007; Cann et al. 2023), and environmental contamination in the Great Lakes region poses additional risks (Mason and Sullivan 1997; Smith et al. 2016; Dietrich et al. 2019). Additional studies of spatial ecology spanning several consecutive years would further illuminate the seasonal movements of Spotted Turtles in post-industrial Indiana to help create well-informed conservation plans for these disjunct populations.

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