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Home Range, Site Fidelity, and Movement Patterns of the Wood Turtle (Glyptemys insculpta) at the Southwestern Edge of Its Range

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ABSTRACT. – Wood turtles (Glyptemys insculpta) are considered rare or threatened throughout their range. Populations in Iowa occur at the western periphery of the species' range and may be particularly vulnerable to extirpation due to low population density, geographic isolation with restricted opportunities for gene flow, a small range, and a high percentage of land that has been converted for agriculture. To improve our understanding of the ecological needs of the species and to provide targeted conservation of required habitat, determining home range size, site fidelity, and movement patterns is needed. We conducted a 2-yr radiotelemetry study on wood turtles in Iowa to provide baseline data on movement patterns (including estimated total distance moved in an active season and mean daily movement) and home range size and site fidelity between years of survey. Home range size of adult male and female wood turtles differed significantly for 100%, 95%, and 50% minimum convex polygon home range, with male mean home range being nearly 3 times the mean size of female home range. Stream home range length also differed significantly between males and females, with males utilizing a larger portion of lotic habitat. Both sexes showed a high degree of site fidelity to annual home ranges but not to specific overwintering locations. Our study provides important data on home range size, degree of site fidelity, and movement patterns of wood turtles from an isolated population in Iowa at the southwest periphery of the species' range. These data will inform conservation agencies on relevant habitat protection and management strategies of riparian areas that are necessary for the continued survival and protection of the species in the state.

KEY WORDS. – Reptilia; Testudines; Emydidae; *Glyptemys insculpta*; home range; site fidelity; stream home range; movement; Midwest; Iowa

Understanding a species' spatial and temporal requirements is critical to maximizing future conservation efforts. The way animals move and use space in their environment is an important life-history component that is inherently tied to survivorship. Studies assessing patterns of movement and home range size may help determine the distribution and spatial dynamics of populations while also identifying critical habitat and dispersal patterns (Bowler and Benton 2005). Knowledge of home range size (i.e., the area an animal regularly travels in search of food, mates, and shelter; Burt 1943), site fidelity (i.e., the tendency an animal has to remain in and/or return to its ''home'' area where its ecological needs are met; Greenwood 1980; Piper 2011), and movement patterns (Allen and Singh 2016) are essential in determining whether a species will benefit from the protection or restoration of currently used habitat, the area needed to protect individuals, and the extent to which habitat management practices may influence movement patterns and usage (e.g., whether an individual alters its home range in response to the creation of suitable habitat; Parnell et al. 2006).

Home range estimation methods have varied greatly between species and studies, resulting in different methods employed among studies on the same species (Powell 2000), often making comparisons difficult. While there is no single best estimator, it is important to select the most suitable method based on study species, habitat, and goals of the study. The home range estimation method used should delimit where an animal can be found with some level of predictability (Powell 2000) while considering whether locations that are used very little or not at all should be included or whether areas that may serve as travel corridors between known locations should be considered (Gregory et al. 2017). The use of multiple methods to describe the data helps avoid misinterpretation while providing the ability to compare results across studies. In addition, conducting a home range study over an entire year or multiple years is important because feeding resources may shift with phenological cycles, habitat requirements may change based on time of year, or availability of suitable habitat may be altered depending on

season (e.g., wetlands drying in summer months) or year (e.g., flood events).

The most frequently used methods for estimating home range size are the kernel density estimator (KDE) and minimum convex polygon (MCP) methods. Although KDE home range methods are becoming more widely used, the number of sampling points (Seaman and Powell 1996) and appropriate smoothing factor selection cause inconsistencies in determining home range size in herpetofauna (Row and Blouin-Demers 2006; Boyle et al. 2009). Meanwhile, the majority of wood turtle home range studies have used MCP methods, allowing for easy, accurate comparisons (Kaufmann 1995; Arvisais et al. 2002; Saumure 2004; Sweeten 2008; Jones 2009). The MCP home range is defined as the home range in which a polygon having all interior angles less than 180° is drawn around a specified percentage of location points (Hayne 1949). Although widely used, the MCP provides a crude outline of home range, often including large areas never used by the animal (Powell 2000). Therefore, 3 metrics of MCP are commonly calculated: the 100% MCP, the entire, integral home range including all location points sampled (Powell 2000; Saumure 2004); the 95% MCP, the statistical home range, excluding the most peripheral outlier points, under the assumption that these points may represent exploratory locations only (White and Garrot 1990; Silva et al. 2020); and the 50% MCP, the core home range area in which an individual spends 50% of its time (Anderson 1982).

In species that have limited movements outside of aquatic environments or move from one place to another through the stream channel, additional methods of home range estimation have been used to determine the length of home range and locate important travel corridors (Jones 2009; Ouellette and Cardille 2011). The simplest method is the stream home range (SHR) estimation, also referred to as the home range length or linear home range (Ouellette and Cardille 2011). The SHR estimation is most useful in a single-channel lotic environment; this metric calculates the shortest straight-line distance between the farthest upstream and downstream locations recorded when the animal is located within the stream banks (Plummer et al. 1997). This measure has been used to characterize movement patterns of turtles in a variety of aquatic habitats (Doody et al. 2002; Riedle et al. 2006; Chen and Lue 2008; Sterrett et al. 2015).

Home range site fidelity has been observed in species from all major vertebrate clades, including turtles and other reptiles that display low dispersal capabilities (Bock et al. 1985; Sinsch 1990; Arvisais et al. 2002; Tuberville et al. 2005; Refsnider and Linck 2012). In turtles, ecological needs are met through acquiring food resources, finding mates, and locating suitable nesting and overwintering locations while reducing inter- and intraspecific competition and avoiding mortality resulting from predators and vehicles (Lovich et al. 2018). Because turtles are not highly mobile like large mammals, birds, and large fish, they must maximize resource utilization within a smaller home range area, which they can accomplish by having a strong degree of site fidelity and remaining within the same general area or by returning to previously occupied areas (Merkle et al. 2014). Having familiarity with a site, including prior knowledge of the distribution of food resources, refugia, and effective thermoregulation locations, plays an important role in efficient habitat and resource utilization (Switzer 1993).

Characterizing patterns of site fidelity is important for understanding the structure and dynamics of animal populations (Benhamou 2006; Rich et al. 2006) and in determining feeding and mating strategies (Pratt and Carrier 2001; Loher 2008), determining parturition and nesting behavior (Gauthier 1990; Freedberg et al. 2005), and defining the potential costs and benefits associated with using specific areas and habitats (Greenwood 1980). Revealing site fidelity patterns is also necessary to gauge the impact of human development on species movement (White and Garrott 1990), ultimately providing insight into how animals respond to habitat loss, alteration, fragmentation, or translocation and how anthropogenic changes may influence survival, dispersal, and gene flow.

While home range provides a general description of the area used, movement provides a framework of how far and often individuals move. Intersexual differences in turtle activities and movements are presumably related to reproductive ecology (Rowe and Dalgarn 2009). Females may increase basking and decrease long-distance movements in the spring to allocate energy to ovaries for egg production (Huey 1982). Females in some species may move more often and farther during the nesting season to locate suitable nesting habitat (Litzgus and Mousseau 2004), while male movement is associated with searching for mates (Morreale et al. 1984; Hall and Steidl 2007). Increasing frequency of movements and distances traveled in turtles increases the chances of being exposed to many hazards, including roads (Gibbs and Shriver 2002; Steen and Gibbs 2004; Dorland et al. 2014). To quantify movement, total distance (TD) moved during an active season can be calculated to provide an overall assessment of the distance individuals are moving through their home range during the active season (Jones 2009), while mean daily movement (MDM) provides an estimation of the distance turtles move through their habitat each day during an active season (Jones 2009; Rowe and Dalgarn 2009).

Wood turtles (Glyptemys insculpta) exhibit some degree of site fidelity (Harding 1991; Arvisais et al. 2002; Jones 2009). They are undergoing population declines across their range due to both direct and indirect anthropogenic causes (Garber and Burger 1995; Saumure and Bider 1998; Daigle and Jutras 2005; Saumure et al. 2007; Spradling et al. 2010; Parren 2013; Willoughby et al. 2013; Cochrane et al. 2018). Wood turtles are semiaquatic freshwater turtles found in northeastern North America; their distribution is limited to areas with the appropriate combination of aquatic (streams with sand or gravel substrates) and terrestrial habitats (forested riparian areas with suitable nesting areas; Harding 1991; Ernst and Lovich 2009). They are listed as globally endangered by the International Union for Conservation of Nature (van Dijk and Harding 2011) and are state listed as endangered (Iowa), as threatened (Minnesota, New Jersey, Virginia, and Wisconsin), or of special conservation concern throughout their range. This status is a result of habitat loss and degradation, fragmentation, overcollecting, road mortality, and predation (Garber and Burger 1995; Ernst 2001; Gibbs and Shriver 2002; Saumure et al. 2007; Harding 2008; Lapin et al. 2019).

Wood turtle populations in Iowa may be particularly vulnerable due to limited distribution, lack of detectable gene flow with other populations, high adult mortality, high nest destruction rates, and low numbers of juveniles (Spradling et al. 2010; Tamplin 2016, 2019; Lapin et al. 2019). Although voucher records from southeastern Minnesota indicate that the species' distribution may be contiguous across the Iowa–Minnesota border (Moriarty and Hall 2014), Spradling et al. (2010) detected no evidence of gene flow between turtles sampled at the extreme southern edge of their distribution in Iowa and several specimens from southeastern Minnesota. Wood turtle populations in Iowa may be unique in that they are one of the few populations that are found within a historical prairie-forest ecotone of the Great Plains ecoregion (Omernik 1987), appearing to be near the leading edge of the species' post-Pleistocene range expansion (Amato et al. 2008; Spradling et al. 2010). Populations in Iowa are likely perturbed by extensive land conversion to agriculture coupled with recent changes in precipitation patterns and the resulting negative effects of flooding on recruitment (Spradling et al. 2010). In addition, Iowa wood turtles typically occur in small patches of isolated or fragmented riparian habitat that are threatened by agricultural encroachment and road bisection (Tamplin 2016, 2019; Otten 2017).

The primary objective of our study was to collect baseline data using a variety of metrics of home range size and movement patterns from wood turtles in Iowa, a population at the southwestern periphery of its range. Specifically, to compare home range size of Iowa wood turtles with those from other regions, we investigated the differences in 100%, 95%, and 50% MCP home range and SHR between the sexes and between juveniles and adults. We hypothesized that home ranges would be larger in adult males compared with females if males were the predominant sex that actively sought out mates and maintained social hierarchy (Kaufmann 1992; Ernst and Lovich 2009).

In addition, we compared movement through 2 metrics, annual TD and overall MDM, between the sexes and between adults and juveniles, hypothesizing that if males were searching for mates and had larger home ranges, they would move more often and move longer distances than females. Finally, we investigated differences in home range size between years of study and the degree of site fidelity as a function of annual 95% MCP overlap and distance between overwintering locations, hypothesizing that wood turtles would have a high degree of site fidelity between years to reduce energy expenditure while utilizing similar habitats between years for foraging, mating, basking, and hibernating. The knowledge gained from this study will inform conservation planning and practices within the state or for other populations experiencing similar conditions.

METHODS

Study Sites. — During 2014 and 2015, we studied 2 populations of wood turtles at 2 locations in riparian woodland habitat, incorporating an area within a 300-m buffer surrounding 2 second-order streams, 1 in Black Hawk County (Black Hawk) and 1 in Butler County (Butler), Iowa. Exact site locations are withheld due to the sensitive nature of the species. The 2 sites are approximately 23.0 km straight-line distance apart and are separated by numerous county highways, gravel roads, and agricultural fields. Although a continuous waterway connects both sites (approximately 45.0 river channel km), they are distinct from one another, and no movement of turtles occurred between locations.

The Black Hawk site (299 ha) is located in a suburban area, centered on a 3.5-km stretch of lotic habitat that ranges in width approximately 10–50 m, with a depth of 0.5–2.0 m. The majority of the site (193 ha; 65%) contains moderately mature to mature riparian floodplain forest that is dominated by tree species such as silver maple (Acer sacchariunum), eastern cottonwood (Populus deltoides), American elm (Ulmus americana), and mulberry (Morus spp.). Agricultural fields (26 ha; 9%) and open-canopy clearings containing a mixture of grasses and forbs (13 ha; 4%) are also prominent landscape features of the site (Otten 2017).

The Butler site (434 ha) is centered on a 3.5-km stretch of lotic habitat that ranges in width approximately 10–60 m with a depth of 0.5–2.5 m. The majority of the site (253 ha; 58%) contains moderately mature to mature riparian woodlands with shrubby young woodland species found along the periphery. The dominant tree species include silver maple, eastern cottonwood, American elm, box elder (Acer negundo), and oak trees (Quercus spp.). Open-canopy grassland forb areas (58 ha; 13%) are found scattered along the river, the majority of which are ≤ 1 ha in size. Four areas of larger grassland areas $($ > 5 ha) are found at the site; these areas are dominated by reed canary grass (Phalaris arundinacea), crown vetch (Coronilla varia), and orchard grass (Dactylis glomerta). The Butler site is located in a rural area and contains 26 ha (9%) of agricultural fields (Otten 2017).

Both study sites contain a mixture of public land (Black Hawk = 129 ha, 43%; Butler = 238 ha, 55%) and private land, and both sites contain at least a small degree

of human nonagriculture development (Black Hawk = 28 ha, 9%; Butler = 5 ha, 1%; Otten 2017). Numerous piles of flood-deposited woody debris are found at each site and are used by adult and juvenile wood turtles as terrestrial basking and aquatic or terrestrial hiding locations. In recent decades, both river drainages have experienced a substantial increase in the frequency, amplitude, and duration of flooding events, potentially due to the effects of climate change and altered agricultural practices in the surrounding landscape (Spradling et al. 2010).

Turtle Surveys. — Turtles were initially located and captured by hand during visual encounter surveys in April and May 2014 and 2015; however, 15 adult turtles (7 females and 8 males) at Black Hawk captured and affixed with radio transmitters during prior surveys (Williams 2013) were employed for the current study. Visual encounter surveys occurred by searching streams, rivers, riverbanks, and adjacent habitat within the 300-m buffer zone; however, the majority of new captures were opportunistic and occurred during biweekly radiotelemetry surveys.

All turtles were photographed, sexed using secondary sex characteristics (Harding and Bloomer 1979), measured (maximum straight-line carapace length, SCL_{max}) with digital calipers to the nearest 0.1 mm, weighed to the nearest 0.1 g, and marked with a unique combination of holes drilled into the marginal scutes (modified from Cagle 1939). All captured turtles were aged by counting growth annuli on carapace and plastron scutes or, for older individuals, estimated in 5-yr increments due to shell wear. Turtles were classified as juveniles if they had new annuli growth visible, were aged to < 18 yrs, and had a SCL_{max} $<$ 140 mm (Ernst and Lovich 2009). Initial and all subsequent capture and radiotelemetry locations were recorded with a handheld Global Positioning System unit (Garmin GPSMap 60CSX; NAD 83; accuracy \leq 3.66 m).

Radiotransmitters from Advanced Telemetry Systems (ATS; adult model R2220 and juvenile model R2222; 35 and 25 g, respectively) were affixed to the right third and fourth costal scutes of turtles using marine epoxy (PC-7; Protective Coatings, Inc) and totaled $\leq 5\%$ of body mass. All turtles were held overnight to allow the epoxy to cure and were released at the point of capture within 48 hrs.

From the initial capture date through December 2015, each transmitter-equipped turtle was located via groundbased VHF radiotelemetry (ATS R410 receiver and 3 element Yagi antenna) at least once a week when possible. Individual turtles were tracked at various, arbitrary times of day (usually between 1100 and 2000 hrs) and various days of the week to minimize diel effects on locations of individuals. Locations of turtles were confirmed visually except when individuals were under banks, in swift currents, or in water too deep to safely be observed. In these instances, location was triangulated and estimated within 3 m.

Home Range Analysis. — For home range analyses, data were restricted to telemetry locations recorded during the active season (generally April–November) of 2014 and 2015, including the first location during hibernation for each year (i.e., the time a turtle was found exclusively in aquatic habitat and did not move between subsequent tracking events and water temperature was \lt 8°C) and the last hibernation location before an animal became active for each year (i.e., first field observation of movement > 10 m between tracking events and water temperature $> 8^{\circ}$ C). Based on previous wood turtle home range studies, turtles with ≤ 20 radiotelemetry locations were excluded from home range analysis (Arvisais et al. 2002; Sweeten 2008; Jones 2009). Data points were collected at least once a week, separated by at least a 72-hr period.

Radiotelemetry locations for each year were pooled and plotted in ArcGIS 10.3, and MCPs and SHR were calculated. All MCP home range analyses were calculated using the GME extension in ArcGIS 10.3, with the 100%, 95%, and 50% MCP calculated for each individual. SHR was calculated by determining the shortest linear distance between the farthest upstream and downstream radiotelemetry location of each individual along a lotic corridor, a method similar to that of Ouellette and Cardille (2011).

Movement Analysis. — Two movement metrics were calculated: the annual TD moved during each active season and the overall MDM. Only individuals with at least 20 telemetry locations during an active season had an annual TD calculated. For individuals with at least 20 telemetry locations during the active season of each year of survey, 2 TDs were calculated: 1 for 2014 and 1 for 2015. For each year, the Euclidean distance between 2 successive telemetry locations was calculated in Microsoft Excel using the Pythagorean theorem, and the sum of all locations found during each active season was calculated, including the first and last hibernation locations. This resulted in some individuals having a TD for 2014 or a TD for 2015 as well as some individuals having a TD for both 2014 and 2015. Because we used VHF radiotelemetry and collected location data from weekly site visits, we calculated MDM to estimate MDM; the MDM was determined by dividing annual TD by the total number of days each individual was tracked during that season, not including hibernation days. For individuals in which TD was calculated for both years of survey, the sum of the TD for both years was divided by the sum of the total number of days the individual was tracked in 2014 and 2015.

Site Fidelity Analysis. — Site fidelity was estimated for individuals with ≥ 20 active-season telemetry locations during both years of the study and was measured as the percent overlap of annual 95% MCP home range; these values and the area of overlap were calculated in ArcGIS 10.3, and the overlapping measure used the Minta Index (Minta 1992), which is percent overlap $=$ [(area overlap/ area of year 1) \times (area overlap/area of year 2)]^{0.5}. Finally, distance between overwintering locations was calculated by measuring the straight-line distance between overwintering locations of each individual whose location was determined during both years. Although persistent flood-

Table 1. Mean home ranges $(\pm SD)$ of female, male, and juvenile wood turtles in Iowa calculated from radiotelemetry points collected during 2014 and 2015. Home ranges calculated include the 100%, 95%, and 50% minimum convex polygon (MCP) as well as stream home range (SHR). Additional movement calculations include the total distance (TD) moved during 2014 and 2015 as well the mean daily movement (MDM).

	No. of	Average no.	100% MCP	95% MCP	50% MCP	SHR	Annual TD	MDM
	individuals	of locations	(ha)	(ha)	(ha)	(km)	(km)	(m)
Females Males Juveniles	22. 18	$54.4 + 16.21$ $41.4 + 17.90$	$8.7 + 5.50$ $48.6 + 15.68$ $24.7 + 21.04$ $5.9 + 3.12$	$6.3 + 4.49$			1.4 ± 1.51 0.7 ± 0.52 2.49 ± 0.79 20.7 ± 18.42 5.4 ± 7.31 1.6 ± 0.71 5.53 $\pm 3.33^{\circ}$ 27.6 $\pm 12.79^{\circ}$ $5.1 + 3.52$ $1.1 + 1.24$ $0.6 + 0.18$ $2.24 + 0.56$	$12.3 + 3.45$ $16.3 + 5.83$

^a One fewer male was sampled for annual TD and MDM due to the fewer than 20 telemetry locations found in 2014 and 2015.

ing at these sites and river dynamics may alter potential and specific hibernation locations annually, we used satellite images and ground-based knowledge of the sites to determine if a given hibernation location was considered to be the same or a different location from one previously used. We considered locations within 20 m of previous hibernacula and along the same bank as evidence of hibernacula fidelity.

Statistical Analysis. — All statistical tests were performed in R 3.6.3 (R Core Team). We used type III analyses of covariance to test the effects of sex, study, body size (SCL_{max}) , and number of telemetry locations on home range analysis and movement, including the 100%, 95%, and 50% MCP home range size, SHR size, annual TD, and MDM calculated from pooled 2014 and 2015 data. Based on visual inspection of residuals and Levene's tests, the assumption of homogeneity of variance was violated for 100%, 95%, and 50% MCP, TD, and MDM between the sexes; therefore, we log-transformed each variable for statistical analyses to meet the assumption of homogeneity of variance (Qian 2010; Slavenko et al. 2015).

We used paired *t*-tests to determine if there were differences in home range sizes of individuals between years. The percentage of 95% MCP overlap and distance between hibernation locations of sexes between years were compared using 1-way analyses of variance.

RESULTS

Turtle Surveys. — Between February 2014 and November 2015, 50 wood turtles (25 females, 20 males, and 5 juveniles) were tracked during radiotelemetry surveys; however, only 45 (22 females, 18 males, and 5 juveniles) had > 20 locations for home range analysis. Three female and 2 males were censured: 1 as a result of a depredation event, 1 due to transmitter loss from agricultural equipment (the transmitter was found dislodged from the turtle in a recently mowed field, but no turtle was located), and 3 due to transmitter failure or the individuals traveling outside the study area so that enough locations for analysis were not recorded.

Of the 45 individuals used for analysis, we collected 2277 active-season radiotelemetry locations, with individuals ranging from 20 to 76 locations (mean = 50.6 ± 16.4) SD) over the course of the study. Totals represented 17 females, 15 males, and 3 juveniles in 2014 and an additional 5 females, 3 males, and 2 juveniles in 2015. A total of 33 individuals (16 females, 14 males, and 3 juveniles) had > 20 locations during both years for site fidelity analysis. Of these, 26 individuals (14 females, 10 males, and 2 juveniles) were located at hibernacula during both winter periods.

Home Range. — Female and male home range size for each MCP (100%, 95%, and 50%) differed significantly between sexes ($p < 0.001$), with females' home ranges being nearly 3 times smaller than males' home ranges (Tables 1 and 2; Fig. 1A–B). Females' 100% MCPs ranged from 1.66 to 23.24 ha, while males' ranged from 3.39 to 93.69 ha; females' 95% MCP ranged from 1.52 to 16.93 ha, while males' ranged from 2.99 to 80.56 ha; and females' 50% MCP ranged from 0.12 to 6.78 ha, while males' ranged from 0.32 to 32.57 ha.

SHR also differed significantly between the sexes $(p < 0.001$; Table 2), with males utilizing twice the length of lotic habitat compared with females. SHR ranged from 0.19 to 2.28 km for females and from 0 to -3.25 km for males. Although sample size of juveniles was small

Table 2. Results from type III analyses of covariance of variable effects on 100% minimum convex polygon (MCP), 95% MCP, 50% MCP, stream home range (SHR), total distance (TD), and mean daily movement (MDM) for adult wood turtles comparing sex, study site, body size (SCL), and total locations. Bold indicates significant values ($p < 0.05$).

	100% MCP		95% MCP		50% MCP		SHR		TD		MDM	
	$F_{1,35}$		$F_{1,35}$		$F_{1,35}$		$F_{1,35}$		$F_{1,35}$		$F_{1,35}$	
Sex Study site Size (SCL) Total locations	18.90 0.19 1.26 0.54	< 0.01 0.57 0.15 0.34	1.97 1.08 1.06 0.05	< 0.01 0.31 0.31 0.82	13.42 2.53 0.19 0.04	$<\,0.01$ 0.12 0.67 0.84	17.81 0.05 1.11 0.13	< 0.01 0.82 0.30 0.72	15.77 0.02 0.03 6.29	< 0.01 0.88 0.85 0.02	30.99 3.55 0.03 77	< 0.01 0.07 0.87 0.19

Figure 1. Representative example of home ranges (100% minimum convex polygon [MCP], 95% MCP, 50% MCP, and stream home range) calculated for a female (A) and male (B) wood turtle located at the Butler study site.

 $(n = 5)$ and not compared statistically with either sex, they appeared more similar to females for each metric (Table 1).

Movement. — A total of 44 individuals (22 females, 17 males, and 5 juveniles) were used for movement calculations. Of these, 16 females, 11 males, and 3 juveniles had TD calculated for both 2014 and 2015. Although females were located more frequently than males, results of the 2 metrics characterizing the movements of individuals were similar to those for home range size: males moved significantly farther, more than twice the TD and MDM of females ($p < 0.001$; Tables 1 and 2). Annual TD ranged from 0.94 to 4.46 km for females and from 1.02 to 13.35 km for males. Female MDM ranged from 4.90 to 17.63 m, and male MDM ranged from 11.20 to 47.61 m. Juvenile TD was slightly less than adult TD, and their movement patterns most closely resembled those of females (Table 1). The number of telemetry locations significantly influenced TD $(p = 0.02;$ Table 2); for every 10 additional telemetry locations, TD increased by 17.6% (95% confidence level $7.5\% - 17.6\%$).

Site Fidelity. — There was no significant difference in sizes of 95% MCP home ranges of all individuals (including 3 juveniles) between 2014 and 2015 $(t_{32} = -0.53; p = 0.60)$. The mean 95% MCP home ranges calculated in 2014 were nearly identical to those calculated in 2015 for both sexes (Table 3). Similarly, the percentage of home range overlap between years was not significantly different between the sexes ($t_{29} = 1.21$; $p = 0.24$). Females ranged from 56.2% to 87.4% in overlap, while males ranged from 23.1% to 84.4% in overlap. Only 1 individual had a home range overlap of $<$ 50%, a male from the Black Hawk study site. Although sample size was small, juveniles appeared to show site fidelity similar to that of males (Table 3).

Between years, females utilized hibernation locations that were significantly closer to the previous overwintering location than those of males ($t_{23} = 2.08$; $p = 0.003$), with an average distance between overwintering locations of 75.2 ± 89.0 m SD for females and 313.3 \pm 233.7 m SD for males. Females ranged from 1.3 to 307.0 m between overwintering sites, while males ranged from 45.7 to 735.4 m. Over 50% of the females tracked $(n = 9)$ but only 1

Table 3. Mean 95% minimum convex polygon (MCP) home range size calculated for wood turtles in Iowa during 2014 and 2015. The percent overlap (site fidelity) was calculated from the 95% MCP home ranges in 2 subsequent years of radiotelemetry surveys of turtles that had at least 20 locations determined per active season.

		2014		2015		
	No. of individuals	Average no. of locations	95% MCP	Average no. of locations	95% MCP	$%$ Overlap
Female Male Juvenile	16 14	28.5 ± 3.85 24.1 ± 4.24 22.3 ± 2.08	4.2 ± 3.00 14.9 ± 12.96 3.8 ± 3.87	34.6 ± 5.10 29.5 ± 8.00 30.7 ± 9.29	4.9 ± 3.71 14.6 ± 12.27 5.8 ± 3.75	71.9 ± 10.13 65.9 ± 15.88 66.3 ± 24.06

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male were found within 50 m of their previous hibernaculum.

DISCUSSION

Home Range. — Our results indicate that wood turtles from Iowa and the Great Plains ecoregion at the southwestern periphery of their distribution have home range sizes similar to those found at other locations (Ross et al. 1991; Foscarini 1994; Arvisais et al. 2002; Saumure 2004; Sweeten 2008; Jones 2009; McCoard et al. 2018; Drescher-Lehman 2019). Males used significantly more area than females for each home range metric (100%, 95%, and 50% MCP and SHR) examined during the present study. Although methods and timing of data collection differ, these results are similar to studies conducted in Massachusetts (Jones 2009), Quebec (Saumure 2004), and Virginia (Sweeten 2008); however, these results differ from studies in New Hampshire (Jones 2009) and Ontario (Foscarini 1994), where females had larger home ranges than males, and Quebec (Arvisais et al. 2002) and Wisconsin (Ross et al. 1991), where home range size of both sexes were nearly equal.

During the present study, males on average had nearly 3 times the MCP area than females and about twice the SHR. In males, maintaining a larger home range size where extensive suitable habitat is available and traveling greater distances may increase the frequency of mating opportunities (Morreale et al. 1984; Rowe and Moll 1991; Piepgras and Lang 2000) and help maintain social hierarchy (Kaufmann 1992).

Female home ranges were centered on suitable nesting habitat and often encompassed 1 or 2 confirmed nest sites (Tamplin 2016). Confirmed nest sites located during and outside the study period were areas with a slightly elevated bank at or near a bend in the river, composed of sandy soils largely free of vegetation (Tamplin 2016, 2019). Six female nest sites from 2014 and 2015 were confirmed, with individual females not moving more than 500 m from them during any part of the year. Female turtles are known to conserve energy prior to nesting to facilitate egg development (Krawchuk and Brooks 1998), which may explain the difference in size of home ranges between males and females; however, some turtle species have been known to move long distances to lay eggs in suitable nesting locations (Refsnider and Linck 2012), inflating a female's home range size. At our study sites, suitable nesting habitat was found throughout both sites at numerous locations along lotic habitat, minimizing the need for females to make long-distance nesting forays.

Although only a small number of larger ($>$ 500 g) juveniles were tracked during this study $(n = 5)$, they behaved more similarly to females than to males. Juveniles were not observed during the study to move long distances, to actively associate with other turtles, or to participate in establishing a social hierarchy; instead, their

small home range size may be influenced by selection for predator avoidance.

Wood turtles have a moderate tolerance to human perturbations (Harding and Bloomer 1979; Harding 1991; Garber and Burger 1995) and disturbance (e.g., forest exploitation, habitation) that may explain interindividual variability in home range size (Arvisais et al. 2002). Our study found that wood turtles of both sexes tended to use areas away from roads, agricultural fields, or residential areas; however, 10 individuals moved distances greater than 500 m between tracking surveys to utilize suitable basking and foraging habitat in roadside ditches and presumably passed under bridges to access these areas and to avoid crossing roads, as only a few turtles were observed on roads at these sites, even when documented turtle locations were ≤ 1 m from the roadway. Only a single vehicular mortality (a gravid female during the nesting period of 2019) has been documented at these sites over the past decade (Lapin et al. 2019). Roadways at the study sites had a large volume of traffic throughout both years of survey.

Movement. — Mean TD measurements in this study were directly influenced by the number of times an individual was tracked during the active season. Weekly observations utilizing VHF telemetry may not always be an accurate metric into how much an animal moves, but they do provide an insight into behavior and habitat usage patterns with potential conservation implications. Because our study sites are surrounded by suburban and agricultural development, we believe that those individuals that move farther and more often may be at a higher risk to be directly impacted by human disturbance at these sites. Although road mortalities and strikes by agricultural implements are apparently rare at these sites, despite the close proximity of turtles to high-traffic roadways and the abundance of adjacent habitat utilized for agriculture, anthropogenic changes to habitat utilized by wood turtles are known to increase mortality risk (Saumure and Bider 1998; Saumure et al. 2007; Wallace et al. 2020). Males on average moved twice as far as females during the entire active season; however, they remained closely tied to lotic habitat, often utilizing rivers and streams to move while mitigating their encounters with anthropogenic disturbances. Females have been found to be at a greater risk of mortality during the nesting season (Steen et al. 2006), but no anthropogenic female mortalities were observed during the study period.

Site Fidelity. — The high percentage of home range overlap and nearly identical sizes of 95% MCP home ranges between 2014 and 2015 indicate that both male and female wood turtles exhibited a high degree of site fidelity and generally utilized the same geographic locations and similar habitats from one year to the next. This finding has been documented in some freshwater turtle species (Standing et al. 1999; Freedberg et al. 2005; Attum et al. 2013), including other wood turtle populations (Arvisais et al. 2002). Wood turtle individuals utilize the same

locations between years (Harding and Bloomer 1979), return to an initial capture site when moved to a previously unknown location (Carroll and Ehrenfeld 1978), and may use the same nesting site between years (Walde 1998). Utilizing known areas to meet ecological needs may increase fitness by augmenting familiarity with effective foraging sites, providing prior knowledge of seasonal food sources (e.g., location of fruiting plants), location of shelter, basking habitat, and overwintering locations. Although the majority of site fidelity studies have occurred over a short period of time (2–3 yrs), these may not be reflective of long-term trends (Otten 2017). Further studies evaluating long-term site fidelity may be important for long-lived species such as wood turtles.

Although our sample size was small $(n = 3)$, juvenile wood turtles had a high degree of site fidelity between years (66%). This observation suggests that home range development occurs before sexual maturity and potentially develops before 8 yrs of age, the approximate age of the youngest turtle tracked during our surveys.

For our study, we determined hibernaculum fidelity between subsequent years for 26 individuals. Although Sweeten (2008) found that 22% of wood turtles (all female) in Virginia returned to the same hibernacula between years, only 1 female (2% of all females) in our study returned to the same hibernaculum (i.e., found within 20 m of previous hibernacula and located on the same bank); however, 4 additional females were within 30 m of their previous hibernacula. No males returned to the same hibernacula, with the nearest being 46 m from the previous year. The majority of males (80%) were found greater than 100 m from the previous location, suggesting that male wood turtles in these 2 Iowa populations do not exhibit site fidelity to overwintering location. Turtle hibernation locations were characterized by areas in lotic habitat with low current flow (turtle location = $0.01 - 0.06$ m/sec, channel = $0.20 - 0.60$ m/sec; J.W.T., pers. obs.) and that were approximately 1.0–1.5 m deep and 1.0–3.0 m from the bank. Turtles were observed resting mostly exposed on the bottom on sandy flat substrate, wedged under submerged logs and tree root balls, or in forms in undercut banks, similar to hibernacula reported from Ontario and West Virginia (Greaves and Litzgus 2007; McCoard et al. 2018). Although most individuals in this study did not use the same hibernacula during both years, the locations used were within the estimated active-season home range, suggesting that individuals are not moving large distances to locate specific hibernacula.

In conclusion, our findings have several important implications for planning effective conservation strategies for wood turtles and managing their habitat. First, the overall lack of year-to-year variation in size and location of home ranges and the high degree of site fidelity exhibited imply that short-term data (i.e., data collected over 2–3 yrs of activity) may be sufficient for inferring space use patterns in a given population. However, it is

important to collect enough locations to adequately assess use during various wood turtle activity periods, and future studies utilizing long-term (decades-long) comparisons may alter this conclusion or provide additional insight. Second, it is important to utilize large sample sizes in different geographic areas, as individual variation occurs within and between populations of turtles regardless of any inherent sex, age class, location, and geographic factors. In addition, within the 300-m buffer defining our site boundaries, our study sites are moderately impacted by human encroachment and development: a rail line bisects the Black Hawk site, a heavily traveled paved road and several bridges cross through each site, and managed road banks that are frequently used as open-canopy basking and foraging sites are disrupted by periodic mowing activities. Thus, our data serve as a critical baseline to which the habitat and space usage and movement patterns of other imperiled wood turtle populations can be compared, especially those that may be impacted by human development and the alteration of habitat.

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