Chelonian Conservation and Biology, 2021, 20(2): 281–289
doi:10.2744/CCB-1490.1

Movement Ecology of the Imperiled Wood Turtle (*Glyptemys insculpta*) in a Lower Hudson River Watershed

Jason S. Hagani[1,7,*], **Suzanne K. Macey**[2,3,7], **John D. Foley**[4], and **Chad L. Seewagen**[4,5,6]

[1]*Department of Earth and Environmental Sciences, Columbia University, 557 Schermerhorn Hall Extension, New York, New York 10027 USA [jsh2207@columbia.edu];*
[2]*Center for Biodiversity and Conservation, American Museum of Natural History, 200 Central Park West, New York, New York 10024 USA [smacey@amnh.org];*
[3]*Ecology, Evolution, and Environmental Biology Department, Columbia University, 1200 Amsterdam Avenue, New York, New York 10027 USA;*
[4]*Great Hollow Nature Preserve and Ecological Research Center, 225 CT-37, New Fairfield, Connecticut 06812 USA [jfoley@greathollow.org; cseewagen@greathollow.org];*
[5]*Department of Natural Resources and the Environment, University of Connecticut, 1376 Storrs Road, Storrs, Connecticut 06269 USA;*
[6]*Wildlife and Fisheries Conservation Center, University of Connecticut, 1376 Storrs Road, Storrs, Connecticut 06269 USA*
[7]*Both authors contributed equally to this work*
**Corresponding author*

Abstract. – Knowledge of the spatial ecology of many turtle species is lacking or limited by small sample sizes of study animals, short study periods, or incomplete representation of the species' geographic range, all of which can present barriers to science-based management and conservation. The wood turtle (*Glyptemys insculpta*) is a declining North American freshwater turtle that is now listed as threatened or endangered in several US states and Canadian provinces. Local-scale knowledge of wood turtle movement patterns and home range sizes is needed for more effective management and regulatory protection, yet the spatial ecology of this species remains undescribed in large portions of its range. We radiotracked 31 wood turtles for 1–5 yrs each in a stream system along the border of New York and Connecticut to describe their movement behavior and inform management efforts in this previously unstudied region. Annual and multiyear 95% minimum convex polygon home range sizes averaged 2.8 (± 3.79 SD) ha and 5.2 (± 7.36 SD) ha, respectively. Males had significantly larger annual and multiyear home ranges than did females, often by severalfold. Overlap of home ranges from one year to the next ranged from 10.5% to 99.7% and averaged 62.6% (± 22.86% SD). Home range centroids shifted 3.8–328.1 m ($\bar{x}$ = 70.3 ± 80.31 m SD) from year to year and averaged 41.2 m (± 40.56 m SD) from the stream and 138.4 m (± 70.66 m SD) from the nearest road across all individuals. Most turtles' home ranges spanned one or both of the major roads in our study area, illuminating the threat of vehicle collision mortality to the viability of this population. Hibernaculum fidelity was low, with only 15% of turtles hibernating in the same location as in the previous year. Our results suggest that management efforts for wood turtles in western Connecticut and the adjacent region of New York should consider that males (the wider-ranging sex) use an average of 5.3 ha to meet their resource requirements over the course of one annual cycle, buffers of at least 116 m surrounding streams should be protected, habitats that are distant from roads should be prioritized for conservation, and measures that facilitate safe passage beneath roads should be implemented whenever roads are present near occupied wood turtle habitat.

Key Words. – Connecticut; conservation; habitat fidelity; hibernaculum; home range; New York; spatial behavior

North America is a hotspot of turtle endemism, supporting 58 native species that represent close to 20% of the global total (Lovich and Ennen 2013). Many are threatened with extinction due to habitat loss and degradation, vehicle collisions, collection for the pet trade, climate change, and disease (Ernst and Lovich 2009). More than half have declined to the extent that they require federal or international protection under the US Endangered Species Act (United States 1983), Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES 2013), or the International Union for Conservation of Nature (IUCN 2011) Red List (Ernst and Lovich 2009; Lovich and Ennen 2013), and still others are listed as threatened or endangered at the state or provincial level. As with most wildlife, effective management and regulatory protection of turtles requires a sound understanding of their spatial ecology so their habitat requirements can be met. Such information is often lacking entirely or is limited by small sample sizes of study animals, short study periods, or incomplete representation of the species' geographic range, all of which can impede science-based management and conservation (Börger et al. 2006; Allen and Singh 2016; Averill-Murray et al. 2020).

One of many imperiled species of North American turtles is the wood turtle (*Glyptemys insculpta*), a freshwater turtle that ranges from eastern Canada to northern Virginia and west to Minnesota. The wood turtle's status was elevated in 2010 from Vulnerable to Endangered by the IUCN due to an estimated 50% decline over the past half century (IUCN 2011). The species is federally listed as Threatened in Canada, under consideration for federal listing as Threatened in the United States, and listed as Endangered, Threatened, or of Special Concern by 14 of its 21 range states and provinces. Like many declining turtle species in North America, wood turtles have been impacted primarily by habitat loss and degradation, vehicle collisions, and illegal collection as well as predation by synanthropic species (reviewed by Jones et al. 2018). Road mortality has a particularly significant impact, as it disproportionately affects females moving in search of nesting sites (Steen et al. 2006; Curtis and Vila 2015). This mortality results in losses to the overall effective population that are difficult to overcome due to slow sexual maturation rates and low recruitment levels (Harding and Bloomer 1979; Steen and Gibbs 2004).

A multistate working group of wood turtle biologists and managers recently determined that more local-scale information about wood turtle movement patterns and home range sizes was needed to better mitigate existing threats and develop effective conservation plans, management strategies, and regulatory protections (Jones et al. 2018). To date, wood turtle home range sizes and movement patterns have been described in multiple states and provinces, with average home ranges spanning anywhere from 0.3 to 32.2 ha, tending to be larger among males than females, and generally increasing with habitat availability and latitude (Arvisais et al. 2002; Curtis and Vila 2015; Jones et al. 2018; Thompson et al. 2018). However, published studies are still sparse or lacking in many parts of the species' geographic range, hindering efforts of managers in those areas to buffer populations from encroaching development and ensure that the area requirements of wood turtles are maintained. Even in areas where wood turtle movement ecology has been relatively well studied in the past, research will continue to be needed to monitor changes in space use that will occur in response to a changing climate and other anthropogenic activities that affect the relationship of animals with their environment and their ability to move across the landscape (Fraser et al. 2018).

We radiotracked 31 wood turtles for as many as five consecutive years in a stream system along the border of New York and Connecticut to examine home range sizes and other aspects of the spatial ecology of the species in this previously unstudied, central portion of its range. We calculated the distances at which male and female wood turtles moved away from their stream and came within major roads, and their annual fidelity to hibernacula, all to further inform management practices for wood turtle populations in the eastern New York and western Connecticut area.

METHODS

Study Area. — We studied wood turtles along an approximately 3.3-km section of freshwater stream that spans the border of New York and Connecticut in the lower Hudson River watershed. The stream is relatively undisturbed, has high water quality relative to other streams in the watershed, and supports wild brook trout (*Salvelinus fontinalis*), a general indicator of stream health (Bellucci et al. 2011). Most of the stream in the study area is within 100 m of a major road. One of these roads crosses a concrete-beam bridge over the stream and runs both perpendicular to and parallel with the stream at different points, while the other road runs only parallel with the stream. Overall, however, development in the surrounding landscape is minimal and best described as exurban residential land use. Habitats bordering the stream segment include second-growth deciduous forest, old field, and shrubland as well as an area of open wetland and riparian shrubland that is maintained by American beaver (*Castor canadensis*) activity. The wood turtles in our study ranged up- and downstream from and through the beaver impoundment.

Radio Telemetry. — We deployed radio transmitters on adult wood turtles that were found by opportunistically searching the stream's channel, banks, and adjacent uplands (up to approximately 50 m away from the stream) between late March and late June of the years 2010–2016. Prior to tagging, we determined the sex of each wood turtle based on plastron concavity. We classified turtles as adults when maximum straight-line carapace length was greater than 160 mm and body mass exceeded 600 g (Lovich et al. 1990; Curtis and Vila 2015; Cross et al. 2018). The 25-g transmitters (Advanced Telemetry Solutions, model R2030) were attached with epoxy to the posterior of the carapace and represented less than 5% of the turtles' body mass to avoid interference with their movement (Parren 2013). The turtles were then released in the same locations in which they had been found.

We radiotracked turtles during their active season in our study area (late March to early November) by homing (White and Garrott 1990) with a handheld receiver (Communications Specialist R1000) and Yagi antenna (Telonics RA-23K) and recorded the Global Positioning System (GPS) coordinates of their locations. From 2010 to 2015, we attempted to locate turtles every 1–2 wks during the emergence (March–April), nesting (May–June), and prehibernation (September–November) periods, when they are most active, and every 2–3 wks during the relatively sedentary aestivation period (July–August). This sampling interval of at least 1 wk allowed turtles ample time to move throughout their home ranges between tracking events such that successive observations were independent of one another (White and Garrott 1990). In 2016, we were able to track turtles only opportunistically and irregularly (less often than biweekly) during their active period. We also tracked some turtles opportunistically during the overwintering period, in December, January, and/or February 2010–2016, to locate hibernacula. We considered a location to be a turtle's hibernaculum if the turtle was found there two or more times at least 1 wk apart.

Spatial Analyses. — Of 31 turtles tracked, we estimated the annual home range sizes of the 24 wood turtles for which we had 15 or more locations in each of two or more years ($n = 9$ males, 15 females). We then measured the multiyear home ranges of each of these 24 turtles using all locations pooled across multiple years. We also measured the multiyear home ranges of an additional 7 wood turtles (1 male, 6 females) that did not meet our location criteria for any single year, but for which we had a total of 20 or more locations across two or more years. The location sample size criteria that we used for these analyses were intended to maximize the number of turtles that could be included while remaining comparable to the number of locations used in similar wood turtle studies (e.g., Arvisais et al. 2002; Sweeten 2008; McCoard et al. 2016; Thompson et al. 2018).

We estimated annual and multiyear home range sizes using minimum convex polygons (MCP; adehabitatHR package in R version 1.2.5033; Calenge 2006). We used isopleths of 95%, representing the "total" home range, and 50%, representing the "core" home range. We measured annual home range fidelity in Quantum GIS (QGIS; QGIS Development Team 2019) as the proportion of an individual's 95% MCP home range in 1 yr that was utilized the subsequent year (Arvisais et al. 2002). We also used the centroids tool in QGIS to measure 1) the distances at which the centroid of a turtle's 95% annual home range shifted between successive years, and 2) the distances of 95% multiyear home range centroids from the center of the stream and the edge of the nearest road, as represented in TIGER line shapefiles for New York and Connecticut (US Census Bureau 2019). To further characterize the turtles' relationships with these landscape features, we measured the distance of each location point for each turtle to the closest road and the stream to calculate mean, minimum, and maximum distances.

Thirteen turtles (7 males, 6 females) were tracked to their winter hibernaculum in two or three consecutive years, allowing us to assess hibernaculum fidelity. Notes describing the features and location of each hibernaculum, made by the same observer (J.D.F.) each year, were used in the field along with GPS coordinates to determine whether turtles were hibernating in the same location as the prior year. We considered visually estimated distances of < 10 m between successive hibernacula as indicative of fidelity (modified from Henriquez et al. 2017). When turtles were found hibernating more than an estimated 10 m from the prior year's hibernaculum, we used the GPS coordinates of those two locations to measure the distance between them in QGIS.

Statistical Analyses. — All statistical analyses were performed in R version 1.2.5033. We first log-transformed home range sizes to normalize distributions and used a Cook's-Distance test to identify outliers to omit from subsequent analyses. We used generalized linear mixed models (lme4 package; Bates et al. 2015) to model the relationship of sex with 1) multiyear 50% and 95% MCP home range size, 2) annual 50% and 95% home range size, 3) annual 95% MCP home range overlap, 4) maximum distance found from the stream, 5) mean distance of all locations from the stream, 6) minimum distance from the nearest road, 7) mean distance of all locations from the nearest road, 8) multiyear 95% MCP home range centroid distance from the stream, and 9) multiyear 95% MCP home range centroid distance from the nearest road. We included number of locations as a fixed effect and year and turtle ID as random effects (turtle ID was only included for modeling annual 95% and 50% home range sizes). We then used likelihood ratio tests (lmtest; Zeileis and Hothorn 2002) to compare full models to nested models from which sex was removed to test for sex differences in each of these movement parameters ($\alpha = 0.05$).

RESULTS

We collected 1910 total locations from 31 wood turtles (10 males, 21 females) between 2010 and 2016. The mean tracking duration for all wood turtles was 3.4 yrs ($\pm$ 0.98 yrs standard deviation [SD]); males were tracked an average of 3.6 yrs ($\pm$ 0.68 yrs SD) and females were tracked an average of 3.3 yrs ($\pm$ 1.07 yrs SD). Turtles were located an average of every 13.9 d ($\pm$ 14.51 d SD) during the March–November active season. After omitting one (male) outlier whose movements were more indicative of dispersal than true home range use (see below), there were 8 male and 15 female wood turtles with a sufficient number of locations within individual years (≥ 15) to allow us to measure annual home range size. The number of locations used to measure annual home range size ranged from 15 to 35 and averaged 21 ($\pm$ 5 SD; $n = 23$) per year; the number of total locations used to measure multiyear home range size ranged from 20 to 115 and averaged 61 ($\pm$ 27 SD; $n = 30$). There was no significant correlation between location sample size and annual or multiyear home range size (at 95% or 50%; Pearson correlation tests: all $r < 0.23$, $p > 0.22$).

Annual home range sizes ranged from 0.1 to 24.8 ha and from < 0.1 to 3.1 ha at 95% and 50%, respectively. Males had significantly larger annual 95% and 50% home range sizes than did females (Table 1). Multiyear 95% home range sizes ranged from 0.4 to 36.5 ha; multiyear 50% home range sizes ranged from 0.1 to 6.5 ha. Males

Table 1. Sex differences in wood turtle (*Glyptemys insculpta*) annual and multiyear 95% and 50% home range sizes (ha) and centroid shifts (m), home range overlap, maximum and mean distances of locations from the stream (m), home range centroid distance from the stream (m), and minimum, mean, and home range centroid distances from the nearest road (m) in a study area along the New York–Connecticut, USA, border. All values are means ± SD (with ranges in parentheses below) and exclude one outlier (see text).

Parameter	All turtles	Males	Females	χ^2	*p*-value
Annual 95% MCP	2.8 ± 3.79 (0.1–24.8)	5.3 ± 5.09 (0.4–24.8)	1.3 ± 1.25 (0.1–5.4)	14.68	< 0.001
Annual 50% MCP	0.5 ± 0.60 (< 0.1–3.1)	0.9 ± 0.77 (< 0.1–3.1)	0.2 ± 0.23 (< 0.1–0.8)	19.44	< 0.001
Multiyear 95% MCP	5.2 ± 7.36 (0.4–36.5)	11.8 ± 10.49 (1.5–36.5)	2.3 ± 1.80 (0.4–6.7)	15.80	< 0.001
Multiyear 50% MCP	1.3 ± 1.66 (0.1–6.5)	2.6 ± 2.07 (0.3–6.5)	0.8 ± 1.05 (0.1–5.1)	10.63	0.001
Mean annual home range overlap	62.6% ± 22.86% (10.5%–99.7%)	65.4% ± 23.70% (25.4%–99.7%)	60.9% ± 22.19% (10.5%–99.6%)	0.26	0.607
Annual centroid shift	70.3 ± 80.31 (3.8–328.1)	121.7 ± 95.48 (10.4–328.1)	40.7 ± 50.19 (3.8–238.7)	8.44	0.004
Max. distance to stream	115.7 ± 86.82 (28.9–487.7)	122.0 ± 67.15 (59.0–249.8)	113.0 ± 93.87 (28.9–487.7)	0.58	0.445
Mean distance to stream	28.4 ± 21.80 (10.3–133.5)	21.8 ± 5.98 (11.0–29.8)	31.3 ± 25.23 (10.3–133.5)	0.72	0.396
Centroid distance to stream	41.2 ± 40.56 (0.6–217.3)	42.5 ± 22.98 (9.7–85.7)	40.7 ± 46.07 (0.6–217.3)	0.73	0.393
Min. distance to road	46.5 ± 39.01 (0.3–158.5)	26.9 ± 25.09 (0.3–81.0)	54.8 ± 40.87 (1.3–158.5)	3.67	0.055
Mean distance to road	199.5 ± 117.30 (61.7–447.3)	161.9 ± 93.41 (80.5–335.3)	215.7 ± 122.68 (61.7–447.3)	0.85	0.357
Centroid distance to road	138.4 ± 70.66 (34.9–282.7)	122.3 ± 79.29 (34.9–261.5)	145.3 ± 65.41 (58.9–282.7)	1.08	0.300

had significantly larger multiyear 95% and 50% home ranges than females (Table 1).

After excluding the outlier, overlap in the area used from one year to the next varied widely from 10.5% to 99.7% and averaged 62.6% (± 22.86 SD) among the 23 wood turtles for which we measured annual home range size in multiple individual years (Table 1). Males and females did not differ in the amount of overlap from year to year ($\chi^2 = 0.26$, $p = 0.607$; Table 1). Annual home range centroid shifts ranged from 3.8 to 328.1 m and averaged 70.3 m (± 80.31 SD). The outlier's home range centroid shifted 639.8 m from 2014 to 2015 and its average annual centroid shift (587.5 m, from 2012 to 2015) was twice that of any other turtle.

The farthest a wood turtle was located from the stream was 249.8 m for the males (excluding outlier) and 487.7 m for the females. Males and females did not differ significantly in maximum or mean distances from the stream or home range centroid distance from the stream (Table 1). There was also no sex difference in minimum or mean distance to the nearest road or multiyear 95% home range centroid distance to the nearest road (Table 1). Ten turtles (7 males, 3 females) had two or more successive locations on opposite sides of a road, indicating that they may have crossed the road between observations.

Two of the 13 wood turtles (15%) tracked to their hibernacula returned to within 10 m of the previous year's location. Distances between successive hibernacula otherwise ranged from 12.3 to 876.4 m, with half of all turtles hibernating at least 50 m from their prior hibernaculum. Overall, wood turtles hibernated an average of 126.7 m (± 181.33 SD) from where they had hibernated in previous years.

DISCUSSION

The wood turtle is an imperiled species in immediate need of more effective management to increase or at least stabilize populations. This need requires a local- or population-scale understanding of movement behavior and home range sizes (Jones et al. 2018), yet the spatial ecology of the wood turtle remains undescribed in large parts of its geographic range. We used multiple years of radio telemetry data from 31 wood turtles in a stream system along the New York–Connecticut border to provide some of the first information on the species' total and core home range sizes, home range and hibernaculum fidelity, and association with roads in this area. Our results indicate that the area requirements of wood turtles in this central portion of their range are less than those reported for wood turtles to the north but greater than those to the south, possibly as a result of a climatically driven latitudinal gradient in resource availability and energy requirements (Arvisais et al. 2002; Cross et al. 2018). Males had larger home range sizes than females, as has been observed elsewhere (Curtis and Vila 2015; Jones et al. 2018; Thompson et al. 2018), but the sex difference was greater than in previous studies. We also found a high degree of individual variation in home range overlap from year to year and little hibernaculum fidelity. Most turtles' home ranges spanned one or both of the major roads in our study area, and many individuals were located in close proximity to roads, underscoring the already well-

Table 2. Average home range sizes of wood turtle (*Glyptemys insculpta*) populations across various movement studies. Studies are arranged top to bottom from north to south, based on latitude. Home range sizes were averaged over a single year of tracking (Annual) or over multiple years (Multiyear). Home range sizes reported were all calculated using the 95% Minimum Convex Polygon (MCP) method.

Study	Location	Latitude	Mean home range size of all turtles (ha)	Annual or multiyear
Thompson et al. 2018	Ontario	47.9	21.5	Multiyear
Arvisais et al. 2002	Quebec	46.7	28.3	Multiyear
Remsberg et al. 2006	Northern Michigan	44.2	30.2	Annual
Tuttle and Carroll 2003	New Hampshire	43.3	15.5	Annual
Jones 2009	Massachusetts	42.4	5.2 (Median)	Multiyear
This study	Connecticut	41.5	5.2	Multiyear
This study	Connecticut	41.5	2.8	Annual
Kaufmann 1995	Central Pennsylvania	40.4	3.3	Multiyear
McCoard et al. 2016	West Virginia	39.4	5.8	Multiyear
Curtis and Vila 2015	West Virginia	39.4	2.7	Multiyear
Sweeten 2008	Virginia	38.5	15.6	Multiyear

recognized threat of vehicle collision mortality to the viability of wood turtle populations (Steen et al. 2006; Jones et al. 2018).

The home range sizes of the wood turtles that we studied were small, on average, relative to those reported by other studies (e.g., Arvisais et al. 2002; Tuttle and Carroll 2003; Remsberg et al. 2006; Thompson et al. 2018). Wood turtle home range size is expected to be heavily influenced by habitat quality, with less disturbed, high-quality habitats allowing wood turtles to use less space than they do in degraded habitats to acquire the resources they need (Remsberg et al. 2006; Cross et al. 2018). The small home ranges we observed compared with those reported in many other locations may therefore indicate that the stream and its adjacent uplands in which we conducted our study provide high-quality habitat for wood turtles. This possibility is consistent with other health assessments of this stream based on water quality, fish and macroinvertebrate community composition (Bode et al. 2004; Beauchene et al. 2014), and the protection of the surrounding uplands as conservation land for more than 50 yrs. However, home range size may also be largely influenced by latitude, as resource availability for wood turtles decreases spatially and temporally from south to north (Brooks et al. 1992; Arvisais et al. 2002; Cross et al. 2018). This pattern can be seen in the large home ranges of wood turtles at the northern limit of their range in Quebec (Arvisais et al. 2002) and Ontario (Thompson et al. 2018) compared with those of wood turtles at the southern end of their range in Pennsylvania (Kaufmann 1995) and West Virginia (Curtis and Vila 2015; McCoard et al. 2016; Table 2). The home ranges of the wood turtles we studied along the New York–Connecticut border are consistent with this trend, averaging smaller than those found with the same estimation methods to our north in Quebec (Arvisais et al. 2002), Ontario (Thompson et al. 2018), Michigan (Remsberg et al. 2006), and Massachusetts (Jones et al. 2018) and larger than those found to our south in Pennsylvania (Kaufmann 1995) and West Virginia (Curtis and Vila 2015; but see McCoard et al. 2016). One notable exception, however, is Sweeten (2008), who found multiyear home range sizes of wood turtles in Virginia to average considerably greater than those elsewhere in the southern portion of the species' geographic range and in our study (Table 2).

Many tracking studies, including ours, find wood turtle activity to be limited to well-defined core areas except for occasional, long-distance movements into surrounding uplands (e.g., Kaufmann 1992; Arvisais et al. 2002; McCoard et al. 2016). In addition to finding wood turtles occasionally in far-removed locations before they eventually returned to their primary activity areas, we observed one wood turtle that moved longer distances to habitat elsewhere in the stream system without ever returning to previous areas of concentrated activity. This male made several extreme, unidirectional movements in multiple years that resulted in a home range estimate greater than 10 times the average of all other turtles in our study. We do not consider such long-distance movements to represent use of a true home range but rather relocation or dispersal events (Jones and Willey 2020). As such, we chose to exclude this individual from our home range analyses, but we suggest that such behavior should not be entirely overlooked in the conservation planning process. Basing habitat protection efforts solely on the home range sizes of wood turtles could fail to maintain connectivity to other habitats that wood turtles appear to need for such relocations and that likely play a vital role in gene flow and the persistence of metapopulations across a landscape.

We observed a sex difference in home range size consistent with, although greater than, what has been found in many other wood turtle populations. Males in our population used on average more than four times the area of females. In Iowa, 95% MCP home ranges of male wood turtles averaged three times larger than for females (Otten 2017). Male 95% MCP home range sizes averaged nearly double those of females in a meta-analysis of 13 different wood turtle studies in multiple states and provinces (Jones et al. 2018). Thompson et al. (2018) also recently reported annual 95% MCP home range sizes measured with radio

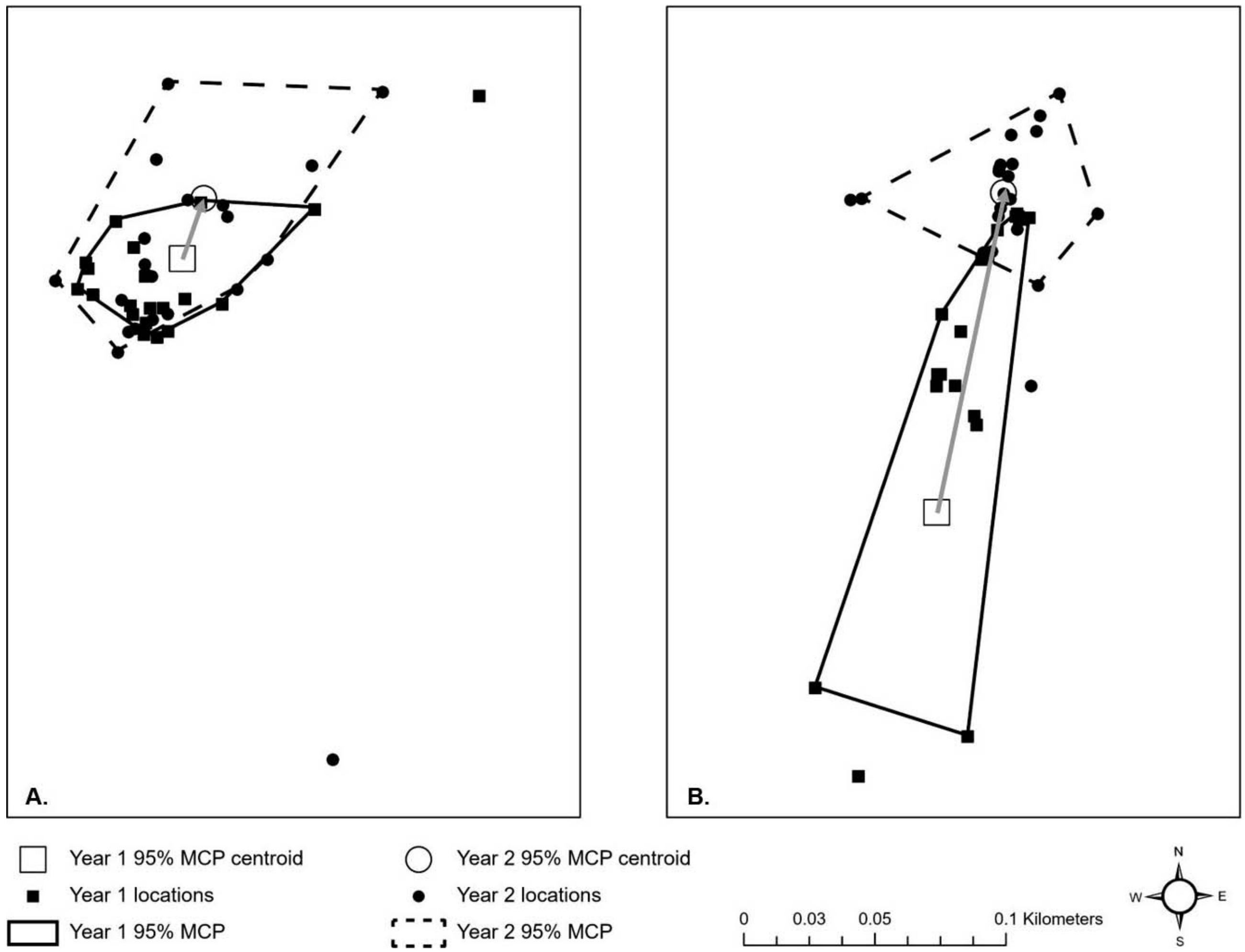

Figure 1. Example of wood turtles (*Glyptemys insculpta*) with high (A) and low (B) home range fidelity. Home range fidelity from year 1 to year 2 was 92.1% for turtle A (female) and 10.5% for turtle B (female). Centroid shift from year 1 to year 2 (42 m for turtle A, 239 m for turtle B) is marked by a light gray arrow. Streams, roads, and other landmarks not shown to protect the location of the turtles.

telemetry and finer temporal resolution GPS tracking data to be larger among males than females in Ontario, albeit only significantly in the radio telemetry data. Male wood turtles likely maintain larger home ranges than females to increase mating opportunities because having multiple mates conveys greater fitness benefits to male than to female turtles (Pearse and Avise 2001). The larger home ranges of male wood turtles may also help maintain dominance hierarchies, which affect access to mates and the number of offspring sired (Galbraith 1991; Kaufmann 1992).

Other studies have reported that wood turtles exhibit a strong degree of interannual home range fidelity (Harding and Bloomer 1979; Quinn and Tate 1991; Kaufmann 1992; Arvisais et al. 2002; Thompson et al. 2018) despite being non-territorial and commonly overlapping with conspecifics of the same or opposite sex (Kaufmann 1992; Parren 2013). The annual home range fidelity exhibited by our wood turtles is consistent with these observations (Fig. 1). Wood turtles at the northern limit of their range in Quebec, which had considerably larger home range sizes than the turtles in our study, also had a nearly identical degree of interannual overlap (60.7%; Arvisais et al. 2002). The affinity of wood turtles for particular areas and their repeated use from year to year is likely due to the irregular distribution and possibly limited availability of preferred macrohabitat features such as sand and gravel bars, upland basking and nesting areas, and scoured riverbanks (Thompson et al. 2018). This preference was clear among many of the turtles in our study, which we repeatedly found basking, foraging, nesting, and hibernating in the same general areas year after year. Repeated use of the same areas, as we observed, could be a further indication that the habitat in our study site is sufficiently meeting the resource requirements of wood turtles.

In contrast to the large degree of home range fidelity we observed, we found wood turtles rarely returning to the same hibernaculum that they used in the previous year. Only 2 (1 male, 1 female) of the 13 individuals we were able to track to their hibernaculum in more than 1 yr hibernated within 10 m of their prior hibernacula. This pattern is similar to what has been observed in wood turtles elsewhere. For example, in a 2-yr study in western Virginia, Sweeten (2008) found that only half of the females (4 of 8) and none of the males (0 of 10) used the same hibernaculum in both winters. Greaves and Litzgus (2007, 2008) observed no hibernaculum fidelity among 6 males and 7 females in Ontario. Parren (2013) interestingly observed repeated use of hibernacula by wood turtles in non-consecutive years in Vermont. There, 6 of 8 adult females used the same hibernaculum more than once, but only 2 of those did so in two or more consecutive winters while the others went as long as 7 yrs before returning. Movements to different hibernacula from one year to the next are thought to be largely driven by the dynamics of riverine systems, with important structural features of the hibernacula lost to or altered by floods, ice scouring, or other such events over time (Greaves and Litzgus 2007; Parren 2013). We observed one clear instance of this when a snag laying across the stream that was used as a hibernaculum by multiple wood turtles in our study was dislodged and carried downstream, forcing those turtles to hibernate in another location the following winter. We also suspect that beaver activity in our study system has a large influence on the distribution and availability of suitable hibernacula from year to year by altering hydrology and potentially accounting for some of the large movements of wood turtles between hibernacula.

Many of the turtles in our study commonly occurred in close proximity to one or both of the major roads that occur parallel with and perpendicular to the stream. Some individuals may have directly crossed from one side of a road to the other at least once. Because a bridge over the stream allows turtles to pass underneath a section of one of the roads and access habitat on both sides, we cannot be certain to what extent, if at all, the telemetered wood turtles crossed over either road. However, we observed numerous non-telemetered wood turtles on these roads during our 7-yr study period, including one injured and 14 dead individuals, and have observed others in the years since, confirming that vehicle collisions are a persistent threat to this population. Road mortality is one of the greatest contributors to population declines of North American freshwater turtles (Gibbs and Shriver 2002; Steen et al. 2006), including the wood turtle (Jones et al. 2018). Wood turtles are considered highly vulnerable to vehicle collisions wherever the two occur in close proximity (Steen et al. 2006; Jones et al. 2018), raising concerns about the long-term viability of our study population even if all other habitat requirements are met. Dry passage culverts, roadside fencing, and seasonal signage to motorists can be effective measures for reducing vehicle mortality of wood turtles (Jones et al. 2018) and should be considered by the transportation agencies that manage the roads in our study area.

Successful conservation of the wood turtle will depend on meeting the species' full habitat needs in the face of increasing development pressure while also minimizing road mortality and other direct anthropogenic impacts. This pursuit requires a sound understanding of the wood turtle's movement patterns and area requirements throughout its broad geographic range. Here, in the central portion of its range, we have shown that wood turtles have smaller area requirements than what has been found in studies to the north and greater area requirements than to the south, they exhibit strong home range but weak hibernaculum fidelity from year to year, and they commonly come in close proximity to the roads intersecting and bordering a stream corridor. The movements of the turtles we studied suggest that habitat acquisition and conservation efforts for wood turtles in this part of their range should consider that males (the wider-ranging sex) utilize an average area of 5.3 ha annually to meet their resource requirements (although much smaller and larger annual home ranges are also common); that buffers of at least 116 m surrounding their home stream/river should be protected from development and other impactful human activities; that habitats that are distant from roads should be prioritized; and measures that facilitate safe passage beneath roads should be implemented whenever roads are present near occupied wood turtle habitat. The states of New York and Connecticut, where we conducted our study, currently do not afford wood turtle habitat any standalone regulatory protection and impose buffers of only 100 ft (30.5 m) around streams to protect water quality. Our results indicate that these stream buffers are inadequate to maintain sufficient upland habitat for wood turtles and that regulatory protection of wood turtle habitat should be considered by these states to help sustain their wood turtle populations.

Acknowledgments

M. Musnick contributed invaluable assistance in the field and P. Galante assisted with statistical analyses and R code. Field methods were authorized by the New York State Department of Environmental Conservation (License to Collect and Possess no. 1374) and Connecticut Department of Energy and Environmental Protection (Scientific Collecting Permit no. 1217001) and were concordant with the American Society of Ichthyologists and Herpetologists' Guidelines for Use of Live Amphibians and Reptiles in Field and Laboratory Research. Funding for this research was provided by Friends of the Great Swamp, the Goldring Family Foundation, and Great Hollow Nature Preserve & Ecological Research Center. We also thank two anonymous reviewers for their valuable comments and suggestions, which improved the quality of this manuscript.

LITERATURE CITED

Allen, A.M. and Singh, N.J. 2016. Linking movement ecology with wildlife management and conservation. Frontiers in Ecology and Evolution 3:155.

Arvisais, M., Bourgeois, J.C., Levesque, E., Daigle, C., Masse, D., and Jutras, J. 2002. Home range and movements of a wood turtle (*Clemmys insculpta*) population at the northern limit of its range. Canadian Journal of Zoology 80:402–408.

AVERILL-MURRAY, R.C., FLEMING, C.H., AND RIEDLE, J.D. 2020. Reptile home ranges revisited: a case study of space use of Sonoran Desert tortoises (*Gopherus morafkai*). Herpetological Conservation and Biology 15:253–271.

BATES, D., MAECHLER, M., BOLKER, B., AND WALKER, S. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

BEAUCHENE, M., BECKER, M., BELLUCCI, C.J., HAGSTROM, N., AND KANNO, Y. 2014. Summer thermal thresholds of fish community transitions in Connecticut streams. North American Journal of Fisheries Management 34:119–131.

BELLUCCI, C.J., BECKER, M., AND BEAUCHENE, M. 2011. Characteristics of macroinvertebrate and fish communities from 30 least disturbed small streams in Connecticut. Northeastern Naturalist 18:411–444.

BODE, R.W., NOVAK, M.A., ABELE, L.E., HEITZMAN, D.L., AND SMITH, A.J. 2004. 30-year trends in water quality of rivers and streams in New York State based on macroinvertebrate data, 1972–2002. Division of Water, New York State Department of Environmental Conservation, Albany, New York. https://www.dec.ny.gov/docs/water_pdf/sbu30yrtrends.pdf (1 October 2020).

BÖRGER, L., FRANCONI, N., DE MICHELE, G., GANTZ, A., MESCHI, F., MANICA, A., LOVARI, S., AND COULSON, T.I.M. 2006. Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology 75:1393–1405.

BROOKS, R.J., SHILTON, C.M., BROWN, G.P., AND QUINN, N.W.S. 1992. Body size, age distribution, and reproduction in a northern population of wood turtles (*Clemmys insculpta*). Canadian Journal of Zoology 70:462–469.

CALENGE, C. 2006. The package 'adehabitat' for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modeling 197:516–519.

CONVENTION ON INTERNATIONAL TRADE IN ENDANGERED SPECIES OF WILD FLORA AND FAUNA (CITES). 2013. Checklist of CITES Species. https://checklist.cites.org/#/en (29 September 2020).

CROSS, J., CROSS, R., CHARTRAND, D., AND THOMPSON, D.G. 2018. Characterizing wood turtle (*Glyptemys insculpta*) populations at the northwestern periphery of the species' range in Canada. Northeastern Naturalist 25:571–586.

CURTIS, J. AND VILA, P. 2015. The ecology of the wood turtle (*Glyptemys insculpta*) in the eastern panhandle of West Virginia. Northeastern Naturalist 22:387–402.

ERNST, C.H. AND LOVICH, J.E. 2009. Turtles of the United States and Canada. Baltimore: Johns Hopkins University Press, 840 pp.

FRASER, K.C., DAVIES, K.T., DAVY, C.M., FORD, A.T., FLOCKHART, D.T., AND MARTINS, E.G. 2018. Tracking the conservation promise of movement ecology. Frontiers in Ecology and Evolution 6:150.

GALBRAITH, D.A. 1991. Studies of mating systems in wood turtles (*Clemmys insculpta*) and snapping turtles (*Chelydra serpentina*) using DNA fingerprinting. PhD Thesis, Queen's University, Ontario, Canada.

GIBBS, J.P. AND SHRIVER, W.G. 2002. Estimating the effects of road mortality on turtle populations. Conservation Biology 16: 1647–1652.

GREAVES, W.F. AND LITZGUS, J.D. 2007. Overwintering ecology of wood turtles (*Glyptemys insculpta*) at the species' northern range limit. Journal of Herpetology 41:32–41.

GREAVES, W.F. AND LITZGUS, J.D. 2008. Chemical, thermal, and physical properties of sites selected for overwintering by northern wood turtles (*Glyptemys insculpta*). Canadian Journal of Zoology 86:659–667.

HARDING, J.H. AND BLOOMER, T.J. 1979. The wood turtle, *Clemmys insculpta*: a natural history. Bulletin of the New York Herpetological Society 15:9–26.

HENRIQUEZ, M.C., MACEY, S.K., BAKER, E.E., KELLY, L.B., BETTS, R.L., RUBBO, M.J., AND CLARK, J.A. 2017. Translocated and resident eastern box turtles (*Terrapene c. carolina*) in New York: movement patterns and habitat use. Northeastern Naturalist 24:249–267.

INTERNATIONAL UNION FOR CONSERVATION OF NATURE (IUCN). 2011. IUCN Red List of Threatened Species. Wood turtle (*Glyptemys insculpta*). https://www.iucnredlist.org/fr/species/4965/97416259 (29 September 2020).

JONES, M.T., ROBERTS, H.P., AND WILLEY, L.L. 2018. Conservation plan for the wood turtle in the northeastern United States, Appendix VII. Report to the Massachusetts Division of Fisheries and Wildlife and the US Fish and Wildlife Service, 242 pp.

JONES, M.T. AND WILLEY, L.L. 2020. Cross-watershed dispersal and annual movement in adult wood turtles (*Glyptemys insculpta*). Herpetological Review 51:208–211.

KAUFMANN, J.H. 1992. The social behavior of wood turtles, *Clemmys insculpta*, in central Pennsylvania. Herpetological Monographs 6:1–25.

KAUFMANN, J.H. 1995. Home ranges and movements of wood turtles, *Clemmys insculpta*, in central Pennsylvania. Copeia 1995:22–27.

LOVICH, J.E. AND ENNEN, J.R. 2013. A quantitative analysis of the state of knowledge of turtles of the United States and Canada. Amphibia-Reptilia 34:11–23.

LOVICH, J.E., ERNST, C.H., AND MCBREEN, J.F. 1990. Growth, maturity, and sexual dimorphism in the wood turtle, *Clemmys insculpta*. Canadian Journal of Zoology 68:672–677.

MCCOARD, K.R.P., BILLINGS, A.A., AND ANDERSON, J.T. 2016. Wood turtle home range and habitat use in the central Appalachians. Chelonian Conservation and Biology 15:173–180.

OTTEN, J.G. 2017. Factors influencing wood turtle (*Glyptemys insculpta*) home range size in Iowa: a comparison between suburban and rural populations. MS Thesis, University of Northern Iowa, Cedar Falls.

PARREN, S.G. 2013. A twenty-five-year study of the wood turtle (*Glyptemys insculpta*) in Vermont: movements, behavior, injuries, and death. Herpetological Conservation and Biology 8:176–190.

PEARCE, D.E. AND AVISE, J.C. 2001. Turtle mating systems: behavior, sperm storage, and genetic paternity. Journal of Heredity 92:206–211.

QGIS DEVELOPMENT TEAM. 2019. QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org (29 September 2020).

QUINN, N.W. AND TATE, D.P. 1991. Seasonal movements and habitat of wood turtles (*Clemmys insculpta*) in Algonquin Park. Canadian Journal of Herpetology 5:217–220.

REMSBERG, A.J., LEWIS, T.L., HUBER, P.W., AND ASMUS, K.A. 2006. Home ranges of wood turtles (*Glyptemys insculpta*) in northern Michigan. Chelonian Conservation and Biology 5: 42–47.

STEEN, D.A., ARESCO, M.J., BEILKE, S.G., COMPTON, B.W., CONDON, E.P., DODD, C.K., JR., FORRESTER, H., GIBBONS, J.W., GREENE, J.L., JOHNSON, G., LANGEN, A., AND OLDHAM, M.J. 2006. Relative vulnerability of female turtles to road mortality. Animal Conservation 9:269–273.

STEEN, D.A. AND GIBBS, J.P. 2004. Effects of roads on the structure of freshwater turtle populations. Conservation Biology 18:1143–1148.

SWEETEN, S.E. 2008. Home range, hibernacula fidelity, and best management practices for wood turtles (*Glyptemys insculpta*) in Virginia. MS Thesis, James Madison University, Harrisonburg, VA.

THOMPSON, D.G., SWYSTUN, T., CROSS, J., CROSS, R., CHARTRAND, D., AND EDGE, C.B. 2018. Fine-and coarse-scale movements and habitat use by wood turtles (*Glyptemys insculpta*) based on probabilistic modeling of radiotelemetry and GPS-telemetry data. Canadian Journal of Zoology 96:1153–1164.

TUTTLE, S.E. AND CARROLL, D.M. 2003. Home range and seasonal movements of the wood turtle (*Glyptemys insculpta*) in southern New Hampshire. Chelonian Conservation and Biology 4(3):656–663.

UNITED STATES. 1983. The Endangered Species Act as amended by Public Law 97-304 (the Endangered Species Act amendments of 1982). Washington, DC: US Government Printing Office.

US CENSUS BUREAU. 2019. TIGER/Line Shapefiles (machinereadable data files). https://www.census.gov/cgi-bin/geo/shapefiles/index.php (29 September 2020).

WHITE, G.C. AND GARROTT, R.A. 1990. Analysis of wildlife radiotracking data. San Diego: Academic Press, 383 pp.

ZEILEIS, A. AND HOTHORN, T. 2002. Diagnostic checking in regression relationships. R News 2:7–10. https://CRAN.R-project.org/doc/Rnews/.

Received: 26 January 2021
Revised and Accepted: 20 August 2021
Published Online: 2 December 2021
Handling Editor: Peter V. Lindeman