Journal of Herpetology, Vol. 50, No. 3, 347–356, 2016

Spatial and Temporal Habitat-Use Patterns of Wood Turtles at the Western Edge of Their Distribution

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Abstract.—**Wood Turtles (*Glyptemys insculpta*) are a state threatened species at the western edge of their geographic distribution in Minnesota, United States. There is currently little published information regarding habitat use of western populations to assist with conservation initiatives. The primary purpose of this study was to investigate habitat use of a population of Wood Turtles in northeastern Minnesota to determine if habitat-use patterns were similar to other regions. In addition, we assessed the efficacy of two land-cover data sets (National Land Cover Dataset and LANDFIRE Existing Vegetation Type), relative to an aerial-photo–based habitat layer, for assessing habitat use and delineating preferred or avoided habitat classes. We performed this analysis to gauge the value of widely used habitat layers for Wood Turtle management and research. We used radio telemetry data collected on 8 males and 14 females between May and November 1990 to assess habitat associations and space-use patterns. We found that Wood Turtles heavily used and generally remained within 100 m of flowing water. Individuals also appeared to prefer other aquatic and semiaquatic habitats when not in or adjacent to flowing water. Despite this population inhabiting a primarily forested landscape, we found little evidence that forest habitat classes were preferred by this species; however, forest age could be an important variable, with younger, more open forest types being used more frequently. We found that neither NLCD nor LANDFIRE were adequate for assessing habitat associations or delineating habitat classes at the scale at which Wood Turtles use the landscape.**

Wood Turtles [*Glyptemys insculpta* (= *Clemmys insculpta*) LeConte, 1830] are semiaquatic freshwater turtles endemic to northeastern North America. Their northern distribution spans from Nova Scotia to eastern Minnesota, and the species occurs as far south as northern Virginia in the eastern United States (Amato et al., 2008). Wood Turtle population declines have been observed across the species' range (Garber and Burger, 1995; Daigle and Jutras, 2005; Willoughby et al., 2013), with current evidence indicating that declines are caused primarily by direct (e.g., injury and death from agricultural equipment, road mortality, habitat loss) and indirect (e.g., changes in river hydrology) anthropogenic impacts (Saumure and Bider, 1998; Saumure et al., 2007; Spradling et al., 2010; Parren, 2013). Notably, the species was historically valued for the pet trade, biological supply houses, and as a food resource (Harding and Bloomer, 1979); even with increased legal protection, Wood Turtles remain a valued species in the live animal trade (Levell, 2000; Kiester and Olson, 2011). Because of perceived broad-scale declines, the species is considered endangered by the International Union for Conservation of Nature and Natural Resources (IUCN; van Dijk and Harding, 2011), threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2007), and has been proposed for listing under the Endangered Species Act in the United States (U.S. Fish and Wildlife Service, 2013).

Human-dominated systems clearly have negative impacts on Wood Turtle populations. Therefore, many conservation programs seek to minimize human interactions with the species, such as placing restrictions on forestry practices near occupied river stretches (Wisconsin Department of Natural Resources, 2013). Although studies have concluded Wood Turtles depend heavily on suitable riverine waterways, individuals are largely terrestrial during summer months (Kaufmann, 1992a; Castellano et al., 2008). Therefore, creating effective conservation plans requires knowledge of both aquatic and terrestrial habitat requirements, seasonal preferences, and habitat-use patterns. Further, understanding landscape-use patterns is important to consider explicitly how a major landscape feature (i.e., flowing water) influences nonriverine spatial patterns; otherwise, estimates of habitat availability are likely to be severely biased. Availability implies a measure of "...accessibility and procurability of physical and biological components of a habitat by animals" (Hall et al., 1997); abundance refers to the broader quantity of land-cover classes and features, regardless of their availability to an individual. In this study we explicitly addressed habitat availability by considering turtle movement characteristics.

Across the species' geographic range, about 35 published studies to date have provided quantitative information on Wood Turtle habitat association or movement metrics, with the majority of studies conducted in U.S. east coast states. To our knowledge, only two published studies have been conducted in Wisconsin (Brewster and Brewster, 1991; Ross et al., 1991), and one in Minnesota (published herein), despite the species being listed as threatened in both states. Two publications resulting from the Minnesota study focused exclusively on nest site characteristics (Buech et al., 1997; Buech and Nelson, 1997). Therefore, little information exists regarding nonnesting habitat use at the western edge of the Wood Turtle's distribution to guide management and conservation efforts. Importantly, habitat-use patterns and population dynamics of semiaquatic turtles can vary across habitat types and climates (Hecnar, 1999; Baldwin et al., 2004; Marchand and Litvaitis, 2004; Currylow et al., 2012), making an understanding of Wood Turtle habitat-use patterns at the western edge of its geographic distribution

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DOI: 10.1670/15-139

imperative to ensure that conservation and recovery efforts are implemented appropriately.

The primary purpose of this study was to investigate habitat-use and movement patterns for a population of Wood Turtles in northeastern Minnesota. We focused on habitat association and movement analyses useful for conservation planning. Specifically, we investigated habitat class associations with the use of local (fine-scale) and landscape-scale availability approaches, based on an aerial-photo interpreted habitat map. We also assessed the value of two widely available land-cover data sets for Wood Turtle habitat classification and delineation (i.e., we gauged their application value for Wood Turtle research and management in other landscapes beyond the study area). Finally, we investigated space-use patterns, with the goal of quantifying temporal and spatial use of occupied habitat to assist with management regulations. Based on previous research conducted on eastern and northern populations, we hypothesized that Wood Turtles in Minnesota would become largely terrestrial during the summer months, but would stay close to flowing water bodies, used for thermoregulation and as travel corridors (Arvisais et al., 2002; Dubois et al., 2009; Parren, 2013).

Materials and Methods

We used radio telemetry data collected from a population of Wood Turtles occupying about a 15-km stretch of a river in northeastern Minnesota in 1990 (specific locations withheld in compliance with state of Minnesota data practices law). More than 90% of the surrounding land was forested, with the remainder in nonforest and aquatic habitat classes; ca. 75% of the area was in public ownership. Mesic forest types, which comprised 80% of the area, were dominated by aspen (*Populus* spp.), balsam fir (*Abies balsamea*), and paper birch (*Betula papyrifera*). Although pine forest types were less common in the surrounding landscape, they were notable within sandy soils adjacent to some nest sites at river cutbanks. Black spruce (*Picea mariana*), balsam fir, northern white cedar (*Thuja occidentalis*), and tamarack (*Larix laricina*) comprised over 90% of hydric forest types in the surrounding area. Nonforest vegetation consisting of lowland alder (*Alnus* spp.), grass/forb openings, oxbow lakes, and other nonflowing water features, also occurred in the study area.

We captured 225 unique individuals in 1990. We recorded standard measurements on all captured individuals and mounted radio transmitters on the carapace of 30 turtles (11 males and 19 females), secured and protected with an epoxy adhesive and a silicone sealant, respectively. In addition, we ensured transmitters remained attached by drilling two holes through marginal carapace scutes and securing the transmitters with brass bolts and nuts. For this article, we used telemetry data from 22 of the turtles (8 males and 14 females), that were radio-tracked from 8 May to 20 November 1990. We excluded the remaining eight turtles from our analyses, primarily because their locations were not proximal to the main group of radio-tracked individuals (individuals were located ca. 8 to 18 km straight-line distance from the nearest turtle included in this study). One of the excluded individuals was relocated only three times, and four of the excluded individuals were juveniles. We attempted to locate individuals twice weekly, obtaining between 28 and 43 locations per individual (median = 36.5). Each time we found an individual, we marked its location via pinprick and handwritten notation on aerial photographs of the study area (1:15,800 scale), using natural landmarks visible on each photograph to determine precise locations.

Habitat Associations.—Wildlife habitat selection occurs hierarchically at four scales: 1) geographic distribution of the species, 2) individual animal home range or general activity area, 3) selected locations or components within home ranges or general activity areas, and 4) resources procured within selected locations (Johnson, 1980; Hutto, 1985; Nelson et al., 2009). Most habitat selection studies address scale 2 or 3, and importantly, the scale chosen influences how habitat availability is defined and, subsequently, habitat selection inferences (Boyce, 2006; Beyer et al., 2010; Manly et al., 2010). For this study we did not investigate Wood Turtle habitat associations at the broadest scale (see Buech and Nelson, 1997, for a discussion of this topic), or at the finest scale. Rather, we investigated associations across the landscape to delineate general activity areas (scale 2; landscape availability approach) and habitat associations within those activity areas (scale 3; local availability approach). The term *landscape* in this study refers to the available habitat based solely on the distance from flowing water distribution observed for the population we studied; potential habitat beyond this distance was not treated as accessible habitat. Using a local-availability approach was appropriate, because it addressed limitations to habitat class choices due to inherent Wood Turtle movement and behavioral patterns. Using a landscape-availability approach was appropriate, because it allowed us to investigate broader habitat associations that could be missed when habitat availability was constrained to only those habitat classes near where the tracked individuals were observed.

To investigate habitat associations, we obtained aerial images of the study area taken in 1981 (1:15,800 scale black and white photographs). We scanned the aerial images at 300 dots-per-inch resolution and then combined and georeferenced images with the use of a geographic information system (GIS). We then "heads-up" digitized (i.e., manually drew features) the radio-tracked turtle locations and delineated flowing water and 26 adjacent habitat types based on 20 habitat categories from the U.S. Forest Service's NORTHWOODS wildlife habitat database (Benyus et al., 1992; Nelson et al., 1992), augmented with six additional local classes (e.g., gravel and sand pit, oxbow lake). Resulting map accuracy was not explicitly assessed, but accuracy and resolution were maximized by using features in the aerial imagery coupled with habitat observations while collecting field data. The habitat appeared similar in 1990 as it did in 1981, when the photographs were taken.

For habitat association based on local availability, we used two additional widely available land-cover geospatial data sets to determine if their accuracy and resolution was sufficient for Wood Turtle management and research in our study area, under the assumption that the NORTHWOODS layer represented a high-accuracy representation of the habitat. The additional layers were the National Land Cover Dataset (NLCD) layer from 1992 (available at http://landcover.usgs.gov/natllandcover.php) and the LANDFIRE existing vegetation type (EVT) land-cover layer from 2010 (available at http://www.landfire.gov/data_overviews.php). Our study area had 11 of 21 potential NLCD classes and 21 of 35 potential LANDFIRE System Groups within the Great Lakes Super Zone. At the landscape scale, Wickham et al. (2004) reported that NLCD 1992 classification accuracy in the Midwestern United States was 56% when agricultural categories were combined. Classification accuracy for LANDFIRE EVT is 52% agreement between 35 vegetation types and vegetation plot data in the Great Lakes

TABLE 1. Habitat classes used in this study assessing Wood Turtle (*Glyptemys insculpta*) habitat associations in northern Minnesota and original habitat types for the three land-cover data sets used in our investigation. The data sets included a supervised NORTHWOODS habitat type classification based on aerial imagery from 1981, National Land Cover Data (NLCD) from 1992, and LANDFIRE Existing Vegetation Type (EVT) System Group data from 2010.

Habitat class	NORTHWOODS	NLCD92	LANDFIRE EVT
Flowing water	River and stream	N/A	N/A
Still water	Lake; oxbow lake; pond	Open water	Open water
Coniferous forest	Closed-canopy lowland coniferous; mature upland coniferous; semi-open lowland coniferous; young upland coniferous	Evergreen forest	Peatland forest; red pine-white pine
Deciduous forest	Mature lowland deciduous; mature upland deciduous; young lowland deciduous; young upland deciduous	Deciduous forest	Aspen-birch; yellow birch-sugar maple
Mixed forest	Mature upland mixed; young upland mixed	Mixed forest	Atlantic swamp forest; eastern floodplain forest; spruce-fir-hardwood; upland mixed forest
Marshy	Marsh; sedge meadow; shrub swamp	Emergent herbaceous wetlands; woody wetlands	Herbaceous wetlands; inland marshes and prairies
Open terrestrial	Gravel ridge; gravel and sand pit; large field; shrub-sapling opening; small grass opening	Barren; cultivated crops; grassland/herbaceous; pasture/hay	Crops; herbaceous semi-dry; pasture and hayland; transitional herbaceous vegetation; upland shrubland

Super Zone (LANDFIRE data quality assessments available at http://www.landfire.gov/dp_quality_assessment.php), excluding other land-cover classes (e.g., water, urban, agriculture). Both NLCD and LANDFIRE classify habitat at a spatial resolution of 30 m.

That Wood Turtles heavily use flowing water bodies and adjacent habitat is well documented (e.g., Compton et al., 2002; Arvisais et al., 2004; Jones and Sievert, 2009). For each of the three habitat layers we superimposed all flowing water (i.e., the main river channel and associated tributaries) as an additional habitat class, and assessed flowing water vs. non–flowing water use as an independent analysis. To investigate non–flowing water habitat selection, we added a 20-m buffer on either side of the flowing water polygons. This minimized the influence of the flowing water habitat class on habitat association modeling for the other classes. The buffer also eliminated potential habitat misclassifications for turtle points at flowing water–terrestrial-habitat interfaces, where small spatial location errors for either turtle points or flowing water boundaries could result in misclassifications and therefore introduce substantial noise to the data set. We grouped each habitat type into one of seven broader habitat classes to maximize comparability of results among land-cover data sets (Table 1), and because the number of observations was low with respect to the number of potential habitat types to be selected in the NORTHWOODS and LANDFIRE data sets. We removed one LANDFIRE habitat type from the data set (roads; 0.5% of available habitat observations), because it did not fit well with our layer comparison design and only one turtle observation occurred in the "roads" habitat type.

To estimate available local habitat within activity areas, we used the step selection method (Fortin et al., 2005; Forester et al., 2009), where real turtle steps (i.e., the distance and angle moved between consecutive observations) were matched with potential steps (i.e., distances and angles the turtles could have taken if movement was random within defined movement distributions). Because days between observations varied both within and among individuals, we initially plotted distance moved versus days since last observation to determine if this issue would bias our potential step distributions. Surprisingly, there was no evidence that distance moved increased with days since last observation (i.e., a simple linear regression did not indicate a strong positive relationship), and therefore we proceeded with defining distance distributions based on the full data sets. The lack of a detectable relationship between distance moved and days since last observation probably was because of the long temporal scale of relocation data (i.e., days to weeks), which reduced autocorrelation between relocation points. We created separate distance distributions for males and females with the use of the empirical movement observations by considering the lower 90% of distances moved as representative of local movement patterns. This method allowed males to move up to 270 m per step and females to move up to 210 m per step. To create the random potential steps, we used a random angle distribution and simulated 100 potential real step (i.e., movement) events. Further, each turtle in the data set was divided into "subturtles" to ensure all real turtle points also represented local movement events. If a real male or female moved more than 270 or 210 m, respectively, that event was not included in the data set. Rather, the local movements prior to, and after, the long-distance movement event belonged to different subturtles. This was necessary because individuals occasionally moved several hundred to thousands of meters between consecutive observations. Based on field observations, we assumed such movements represented dispersal or migration events rather than local habitat selection events. In addition, this decision ensured the real and random turtle data sets were directly comparable and kept simulated turtle movements within realistic distances from flowing water. We simulated turtle movements with the use of the program Geospatial Modeling Environment (Version 0.7.2.1, www.spatialecology.com), in conjunction with the programs R (Version 3.0.2, www.r-project.org), and ArcMap v. 10.1 (ESRI, Inc., Relands, California, USA). At the end of each movement step, we determined each point's habitat class in each habitat layer with the use of ArcMap.

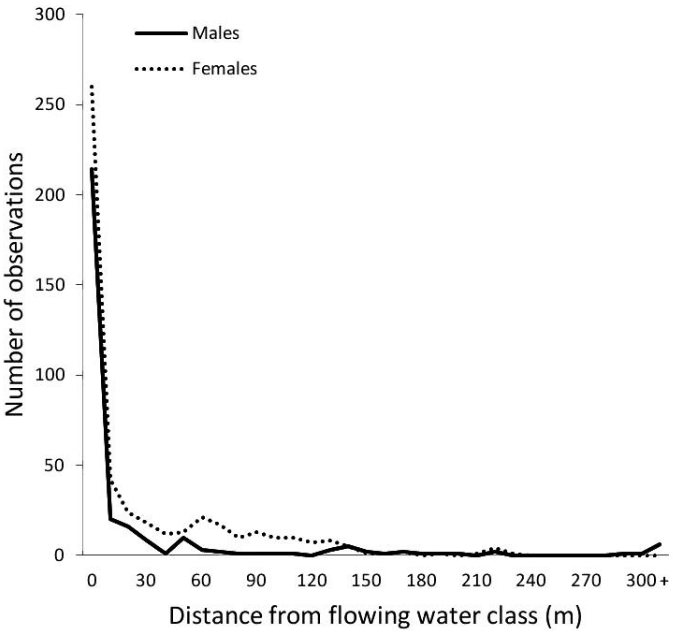

FIG. 1. Number of male and female Wood Turtle (*Glyptemys insculpta*) observations relative to distance from the flowing water habitat class. The habitat class included the main river channel and associated tributaries for the study area in northeastern Minnesota, USA, and a 20-m buffer on either side of the flowing water bodies. The figure indicates the majority of individuals were located in or adjacent to flowing water.

To estimate available habitat at the landscape scale, we calculated the amount of area for each habitat class at 10-m intervals from the flowing water class. We then weighted each habitat class based on the empirical relationship between the number of turtle observations relative to distance from the flowing water class, separately for males and females. The purpose of weighting habitat classes was to reflect habitat availability on the landscape more accurately, given that spatial distribution of Wood Turtles at the landscape scale was clearly influenced by distance from flowing water (Fig. 1).

Space Use.—We investigated temporal space-use dynamics to improve our understanding of seasonal space-use patterns for western populations. We focused on quantifying when Wood Turtles were likely to be on land and the potential relationship between season and distance from flowing water. We hypothesized that with higher temperatures in summer, Wood Turtles would become not only more terrestrial, but also would venture farther from flowing water, as the thermal advantage of returning to water at night decreased (Dubois et al., 2009). Both of these investigations are useful for management purposes, such as defining time frames for vulnerability to terrestrial habitat management actions, and designating buffer zone distances for disturbance activities (e.g., logging) during vulnerable periods.

Statistical Analyses.—We assessed habitat associations based on local availability with the use of conditional logistic regression (CLR), a type of generalized linear model (Faraway, 2006). In CLR, cases (i.e., real turtle steps) are paired with controls (i.e., random turtle steps) at each sampling point, forming matched sets to determine if turtles were found in a habitat class more or less often than expected, based on the prevalence of the habitat classes in the control data set. We did not have enough individual-level observations to assess habitat association differences among individuals, and therefore we tested for population-level habitat associations, analyzing males and females separately. We stratified the data by turtle step (i.e., the real turtle habitat class at each step was paired with the potential habitat classes at that step based on the step-selection simulations). Therefore, although we aggregated the data by sex for statistical analyses, the individual step case-control matches were preserved.

For each habitat layer, we initially included the flowing water habitat class to ensure that our assumption of high preference for that class was supported. We then removed flowing water observations from the data sets and assessed habitat associations among the remaining six classes. This approach was necessary because, through preliminary analyses, we found the strength of association with flowing water was so great that coefficients for all other habitat classes were strongly negative, negating our ability to detect potential positive habitat associations within terrestrial and nonflowing aquatic habitat use away from flowing water.

We tested each habitat class separately; real and random observations for a given habitat class were tested against all other classes combined in each analysis, with only those strata included for which the habitat class of interest had at least one real or available observation. The alternate approach, where all predictors would be included in one analysis, was unattractive for our interests because if all coefficients are included, one is used as the control against which all others are tested (i.e., there is no intercept in CLR). Therefore, coefficient signs and P values for each habitat class will change depending on the habitat class chosen as the control. We gauged significance of habitat class predictors with the use of model coefficient z scores. Because P values in CLR are conservative (Agresti, 2007), we considered $\alpha = 0.1$ to indicate a significant association. We performed CLR analyses with the use of the package Epi (Version 1.1.49) in the program R.

For habitat associations based on landscape availability, we focused on three questions. First, did males and females exhibit homogenous use of non–flowing water habitat types? Second, was non–flowing water habitat use consistent with random use of the landscape, or were habitat associations apparent? Finally, were habitat associations consistent between habitat types and the habitat classes defined in Table 1? Broad habitat associations are attractive for extrapolating inference to other regions, but finer-scale inferences are lost because of aggregation of habitat types. Therefore, our aim here was to identify any finer-scale habitat associations based on landscape availability.

Statistical analyses for the first two questions included NORTHWOODS habitat types that were used by at least two turtles (thereby reducing the potential for a single turtle to over weight inferences). For the third question, we included all of the observations because habitat types were grouped into classes. Preliminary analyses indicated habitat associations were heterogeneous across individuals within each sex ($P < 0.001$), so we accounted for interindividual variability in each analysis. To assess if non–flowing water habitat associations differed by sex, and which habitat types and classes had statistically positive, negative, and neutral associations, we constructed two-way tables and performed randomization tests with the method of Koehler and Wilson (1986) in the program TableSim (Rugg, 2003). For randomization tests, we considered $\alpha = 0.05$ to indicate a significant association.

To assess potential seasonal and sex differences in use of flowing water, we calculated the proportion of observations not in flowing water by month for each individual and summarized

TABLE 2. Results from conditional logistic regressions (CLR) used to investigate habitat class associations for 8 male (M) and 14 female (F) Wood Turtles (*Glyptemys insculpta*) in northern Minnesota, USA, based on a local class availability approach. The NORTHWOODS layer represented a high-resolution supervised classification of habitat types. We included two additional general land-cover data sets (NLCD 1992 and LANDFIRE Existing Vegetation Type [EVT] 2010) to gauge their value for investigating Wood Turtle habitat associations and their habitat classification accuracy. The flowing water habitat class was transposed onto the general land-cover layers, because no complimentary habitat class existed. Positive coefficients indicate the real turtles were observed in a habitat class more often than simulated turtles, and P values indicate the strength of statistical support for perceived associations (statistical significance at $\alpha = 0.1$ denoted by asterisks).

		NORTHWOODS			NLCD			LANDFIRE		
Sex	Habitat class	Coefficient	Z	P	Coefficient	Z	P	Coefficient	Z	P
M	Flowing water	1.540	9.18	<0.01*	1.560	9.37	<0.01	1.550	4.70	<0.01*
F	Flowing water	0.996	8.12	<0.01*	1.040	8.60	<0.01	1.040	8.57	<0.01*
M	Still water	1.980	4.64	<0.01*	−9.240	−0.08	0.93	−6.030	−0.05	0.96
F	Still water	−0.233	−0.31	0.76	0.113	0.11	0.92	2.820	2.41	0.02*
M	Coniferous forest	−0.840	−0.79	0.43	−0.471	−0.88	0.38	0.258	0.93	0.35
F	Coniferous forest	−0.369	−1.38	0.17	0.301	1.31	0.19	0.167	0.92	0.36
M	Deciduous forest	0.034	0.10	0.92	0.244	0.78	0.43	−0.662	−1.07	0.28
F	Deciduous forest	−0.435	−1.62	0.11	0.045	0.22	0.83	0.156	0.58	0.56
M	Mixed forest	−1.060	−2.84	<0.01*	−0.102	−0.27	0.79	0.002	0.01	1.00
F	Mixed forest	0.235	1.16	0.25	0.001	0.01	1.00	−0.182	−1.08	0.28
M	Marshy	0.269	0.66	0.51	0.203	0.62	0.54	−9.150	−0.09	0.93
F	Marshy	0.477	1.68	0.09*	−0.241	−1.07	0.29	−0.863	−0.82	0.41
M	Open terrestrial	−0.005	−0.01	0.99	−9.160	−0.10	0.92	−7.070	−0.08	0.94
F	Open terrestrial	0.205	0.49	0.62	−9.190	−0.14	0.89	−0.432	−0.47	0.64

those proportions graphically for each sex. These observations were recorded in the field for each relocated turtle, so categorization was not influenced by spatial mapping accuracy. The plots qualitatively indicated potential sex differences during the summer months (June to August), and we tested this potential difference with the use of a randomization test with 10,000 iterations (Sokal and Rohlf, 1995). For this test we used the proportion of observations not in flowing water for each individual and each of the summer months ($n = 42$ female and 24 male proportions from the 14 and 8 telemetered individuals, respectively), and determined if the difference between the observed means was as great or greater than expected, based on the randomized data set.

To assess the potential relationship between season and distance from flowing water, we first calculated the Euclidean distance from flowing water (ignoring topographic effects) for each turtle observation point. We then used a generalized additive model (GAM) to model the relationship between distance from flowing water and Julian day (Hastie and Tibshirani, 1999), for males and females separately. Graphical diagnostic plots indicated a Gaussian distribution was appropriate for our data sets. We initially included individuals as a factor predictor in the analyses to determine if there was heterogeneity among individuals that should be accounted for in the model (Zuur et al., 2009). The analyses indicated there was individual heterogeneity, so we included individuals as a random effect in the final models. We fit the smoothing curve using penalized regression splines with the optimal amount of smoothing determined with the use of a cross-validation algorithm (Wood, 2011). These analyses were conducted with the use of the package 'mgcv' (v. 1.7-27) in the program R.

RESULTS

Turtles were observed in 18 of the 26 possible NORTHWOODS habitat types in our study area. Of the 18 habitat types containing observations, 13 were used by at least two turtles: forest—mature lowland deciduous, forest—mature upland coniferous, forest—mature upland deciduous, forest—mature upland mixed, forest—semiopen lowland coniferous, forest—young lowland deciduous, gravel and sand pit, gravel ridge, marsh, pond, river and stream, sedge meadow, and shrub swamp.

For habitat associations based on local-scale availability, the flowing water class was a strong positive predictor regardless of habitat layer used (Table 2). When the flowing water class was removed, the NORTHWOODS layer indicated males were negatively associated with the mixed forest class (coefficient = −1.06, $Z = -2.84$, $P = 0.005$) and positively associated with the still-water class (coefficient = 1.98, $Z = 4.64$, $P < 0.001$), whereas females were positively associated with the marshy class (coefficient = 0.48, $Z = 1.68$, $P = 0.093$). The NLCD layer did not indicate any significant habitat associations, and the LANDFIRE layer indicated females were positively associated with the still-water class (coefficient = 2.82, $Z = 2.41$, $P = 0.016$). Based on NORTHWOODS layer coefficient signs, there was some, albeit weak, evidence that both males and females appeared to avoid forested habitat in general.

General habitat association agreement between the NORTHWOODS layer and the NLCD and LANDFIRE layers was low, with habitat class coefficient signs differing in 6 of 12 cases for NLCD, and 11 of 12 cases for LANDFIRE. Percentages of available habitat classes were consistent for the two least available classes (open terrestrial and still water), but differed otherwise. For example, the second highest percentage class in LANDFIRE was coniferous forest, containing 28.6% of points. In contrast, only 15.7% and 10.7% of points were classified as coniferous in the NLCD and NORTHWOODS layers, respectively. The NLCD layer overclassified, and the LANDFIRE layer underclassified, marshy habitat (39.5% and 1.0% of points, respectively), relative to the NORTHWOODS layer (16.7% of points).

For habitat associations based on landscape availability, we found that male and female associations differed for several non–flowing water habitat types ($P < 0.001$). For males, the

TABLE 3. Male (M) and female (F) Wood Turtle (*Glyptemys insculpta*) habitat associations based on landscape availability in northern Minnesota, USA, under the NORTHWOODS habitat type classification system. The table contains availability and use of the 12 habitat types that were used by at least 2 turtles, as well as availability and use of habitat classes as defined in Table 1. We found males and females to be nonrandomly associated with 8 and 6 of the 12 habitat types, respectively, and 4 and 1 of the 6 habitat classes, respectively (statistical significance at $\alpha = 0.05$ denoted by asterisks).

Sex		Availability (%)	Use (%)	Association (+/−)
	Habitat Type			
M	Forest—Mature upland coniferous	12.99	2.47	−*
F	Forest—Mature upland coniferous	12.97	4.98	−*
M	Forest—Mature upland deciduous	4.14	0.00	−
F	Forest—Mature upland deciduous	18.42	17.65	−
M	Forest—Mature upland mixed	25.23	20.99	−
F	Forest—Mature upland mixed	25.29	41.63	+*
M	Forest—Semi-open lowland coniferous	1.49	0.00	−
F	Forest—Semi-open lowland coniferous	1.45	4.98	+*
M	Forest—Young lowland deciduous	3.30	0.00	−
F	Forest—Young lowland deciduous	3.30	0.45	+*
M	Forest—Young upland deciduous	0.32	2.47	+*
F	Forest—Young upland deciduous	0.27	0.00	−
M	Gravel and sand pit	0.56	12.35	+*
F	Gravel and sand pit	0.44	2.26	+*
M	Gravel ridge	0.44	3.70	+*
F	Gravel ridge	0.58	1.36	+
M	Marsh	0.91	0.00	−
F	Marsh	1.05	2.26	+
M	Pond	0.47	2.47	+*
F	Pond	0.24	0.90	+*
M	Sedge meadow	2.66	0.00	−
F	Sedge meadow	3.16	8.60	+*
M	Shrub swamp	17.74	29.63	+*
F	Shrub swamp	18.07	7.24	−*
	Habitat Class			
M	Still water	2.24	12.22	+*
F	Still water	2.07	0.90	−
M	Coniferous forest	16.82	2.22	−*
F	Coniferous forest	15.77	10.41	−
M	Deciduous forest	26.28	25.55	−
F	Deciduous forest	26.56	21.27	−
M	Mixed forest	28.38	18.89	−*
F	Mixed forest	28.38	43.89	+*
M	Marshy	21.24	26.67	+
F	Marshy	22.28	18.10	−
M	Open terrestrial	4.85	14.44	+*
F	Open terrestrial	4.78	5.43	+

randomization tests indicated habitat use was greater than expected, based on availability for young upland deciduous forest, gravel and sand pit, gravel ridge, pond, and shrub swamp, and less than expected for mature upland coniferous forest (Table 3). For females, the randomization tests indicated habitat use was greater than expected based on availability for mature upland mixed forest, semiopen lowland coniferous forest, gravel and sand pit, pond, and sedge meadow, and less than expected for mature upland coniferous forest, young lowland deciduous forest, and shrub swamp. For habitat classes, the randomization tests indicated males used still-water and open terrestrial habitat more than expected, and coniferous forest and mixed forest less than expected, and females used mixed forest less than expected.

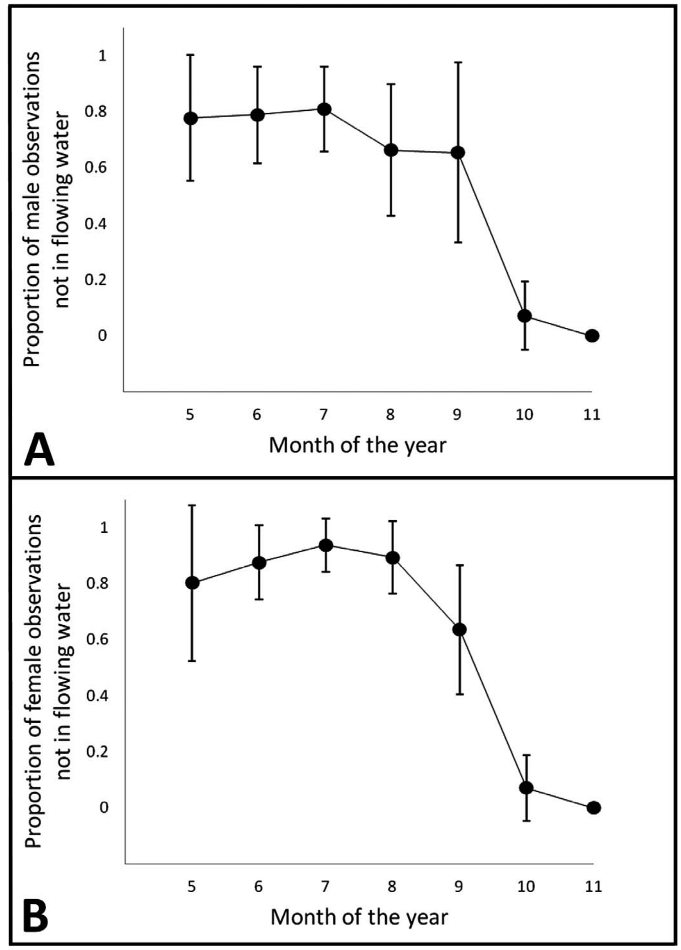

FIG. 2. Proportion of male (A) and female (B) Wood Turtle (*Glyptemys insculpta*) observations not in flowing water for each month of this study conducted along a river in northeastern Minnesota, USA. Black circles represent the mean (± 1 SD) proportion among individuals with the use of 8 and 14 radio-tracked males and females, respectively.

We found that our Wood Turtle population used flowing water during all study months. The proportion of observations in surrounding habitat was greater than in flowing water between May and September, with use of surrounding habitat highest in July for both males and females (Fig. 2). Further, the randomization test indicated that males used flowing water more than females in the summer months (June to August; $P < 0.001$). Individuals became primarily aquatic in October, with 92.8% of observations located in flowing water; in November all observations were in flowing water.

The mean distance from flowing water was 28.4 and 37.3 m for males and females, respectively (Fig. 3). The GAM models indicated the Julian day smooth term was a significant predictor of distance from flowing water for both males ($F_{6.2,7.3} = 4.93$, approximate $P < 0.001$, deviance explained = 29%) and females ($F_{7.1,8.2} = 26.69$, approximate $P < 0.001$, deviance explained = 37%). Further, the models indicated a quadratic relationship

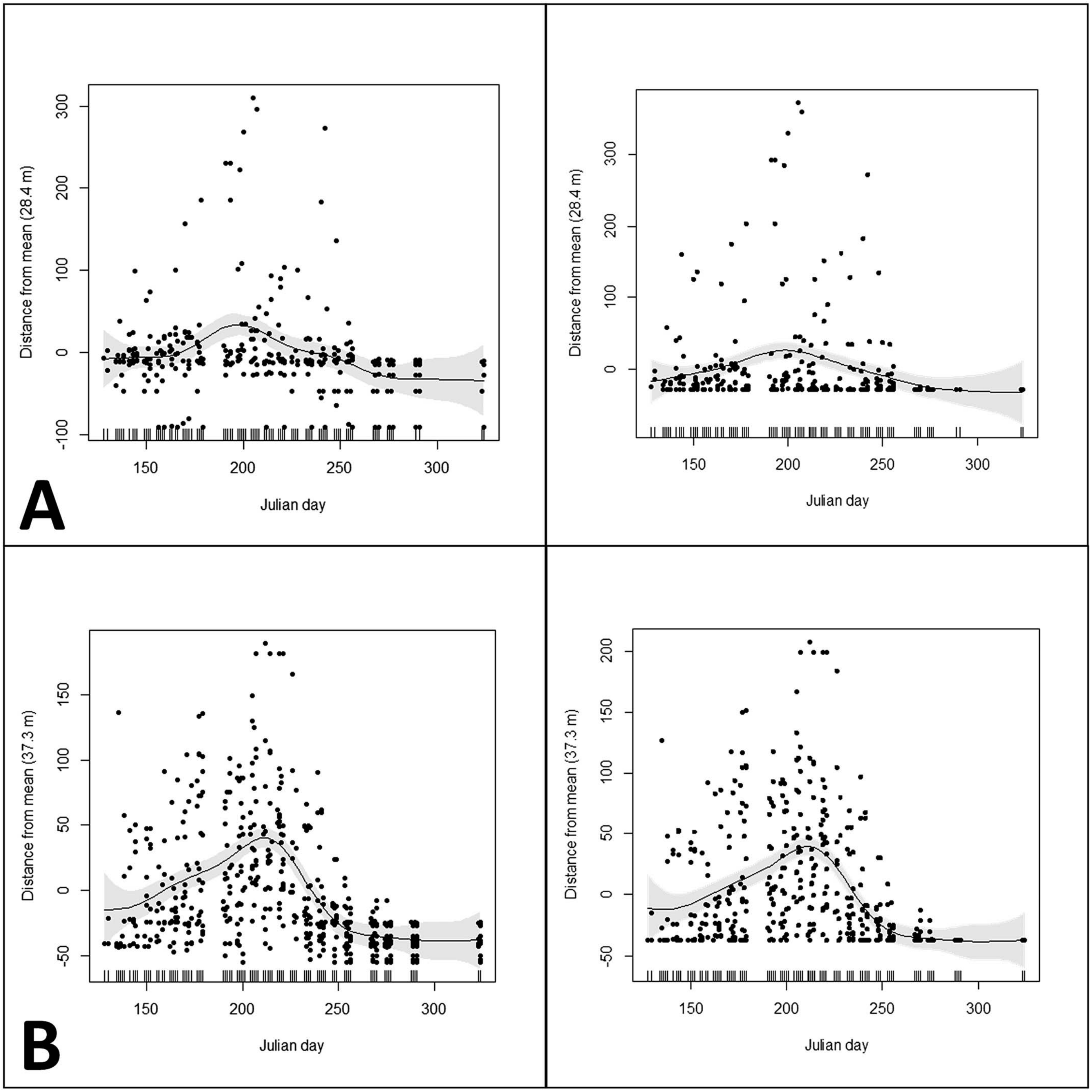

FIG. 3. Relationship between distance from the flowing water and Julian day for male (A) and female (B) Wood Turtles (*Glyptemys insculpta*) along a river in northeastern Minnesota, USA, based on generalized additive models (GAM). The mean male and female distance from flowing water was 28.4 m and 37.3 m, respectively. The modeled distance increased by ca. 50 m during peak non–flowing water habitat use (mid- and late-July for males and females, respectively). The gray bands represent the approximate 95% confidence intervals for the smoothing curves, and the black circles represent the observed turtle distances with (left panel) and without (right panel) individuals treated as a random effects factor variable. The left panels were used for statistical analyses because of detected heterogeneity among individuals. The right panels are useful as a visual reference because they only include the actual observation points.

between distance from flowing water and Julian day for both males and females, with male and female distance peaking in mid- and late July, respectively. The observed maximum distance from flowing water was 401 m and 245 m for males and females, respectively; however, 90% of male and female observations were within 70 m and 100 m of flowing water, respectively, and 95% of observations were within 160 and 120 m, respectively.

DISCUSSION

We found that Wood Turtles in northeastern Minnesota used flowing water heavily, a result consistent with studies across their geographic distribution (e.g., Arvisais et al., 2002; Compton et al., 2002; Jones and Sievert, 2009). We found, however, that although terrestrial use increased, both males and females continued to use flowing water during the summer (i.e., 25.1 and 10.4% of total male and female observations from June to August were in flowing water). In contrast, eastern and southeastern U.S. populations appear to become almost exclusively terrestrial in the summer months (Harding and Bloomer, 1979; Niederberger and Seidel, 1999). Note that all observation locations were recorded during daylight hours ($x \approx 1400$, range = 0745 to 2140), when air temperatures are presumed to be warmer on average than at night. Therefore, if cold night air temperatures resulted in substantial nocturnal use of flowing water, our results represent biased estimates of seasonal flowing water vs. non–flowing water use. In addition, Wood Turtles in Iowa appear to be more aquatic during warm and dry years than cool and wet years (J. Tamplin, pers. comm.; also see Berg, 2014, for within-year temperature–habitat-use correlations in Iowa), and this could also occur in Minnesota. Based on National Climatic Data Center weather data collected from a station adjacent to our sampling area, the mean total precipitation during the months of June, July, and August, between 1960 and 2013, was 9.4, 9.7, and 8.8 cm, respectively; the mean daily temperature during this time frame was 15.0, 17.5, and 16.4°C, respectively (note months with no reported data were ignored in this summary). In 1990, the reported total precipitation in June, July, and August was 9.3, 5.0, and 5.4 cm, respectively, and the mean daily temperature was 16.4, 17.0, and 17.8°C, respectively. Therefore, July and August were dryer than average months, and June and August were warmer than average months, which potentially resulted in more aquatic habitat use than would occur in wetter, cooler years.

Our results agreed with studies indicating that males were more aquatic than females (Kaufmann, 1992a; Tuttle and Carroll, 1997; Compton et al., 2002; Parren, 2013). We did not test for causes of this difference, but we hypothesize it could relate to a male strategy for intercepting females within river corridors for breeding or to establish and maintain male dominance hierarchies (Kaufmann, 1992a,b; Niederberger and Seidel, 1999; Parren, 2013), and/or a female requirement to raise body temperature for egg development (Brenner, 1970; Dubois et al., 2009).

The results of this study agreed with our hypothesis that individuals would typically remain near flowing water, even in the summer months when we expected primarily terrestrial habitat use. We found that males and females generally stayed within 70 and 100 m of flowing water (i.e., 90% of observations), respectively. The apparent strong effect of flowing water on space use is consistent with studies conducted on northern, eastern, and southern (i.e., Iowa) populations. Sweeten (2008) reported that in Virginia, 93% of Wood Turtle observations in the summer were within 90 m of flowing water. In New Hampshire, 95% of male and female locations were within 61 and 188 m of flowing water, respectively (Tuttle and Carroll, 2003). Arvisais et al. (2002) found that 90% of observations were within 150 m of flowing water in Québec. Williams (2013) reported the maximum observed distance from water was 155 m and mean distances were within 50 m for all activity periods in Iowa. Therefore, both our study and the broader literature across the species' distribution indicate land management and human use impacts are most influential on Wood Turtles within ca. 100 m of flowing water. During summer months, however, individuals commonly moved well beyond 100 m of flowing water. Therefore, managers might consider restricting disturbance activities within 200 m or more of known occupied river stretches during the summer months. Current regulations in Wisconsin (300 m buffer zones during the summer months; Wisconsin Department of Natural Resources, 2013) and Ontario (500-m buffer zones in forested areas and 200-m buffer zones in agricultural areas; Ontario Wood Turtle Recovery Team, 2010) appear sufficient to minimize mortality by habitat disturbance activities (e.g., logging), but state regulations currently are lacking in Minnesota.

Although the Wood Turtle population we studied inhabited a primarily forested landscape, there was little indication that forested habitat patches were preferred by the species. Rather, individuals seemed to prefer to be in or near other aquatic and semiaquatic habitat types when not in flowing water. Arvisais et al. (2004) found similar results for Wood Turtles in Québec. In general, Wood Turtles appear to prefer open-canopy habitats to closed-canopy habitats (Compton et al., 2002; Dubois et al., 2009; Tingley et al., 2010), but are fairly generalistic with respect to terrestrial habitat selection (Quinn and Tate, 1991). Although located within a larger context of forested and riparian landscapes, Wood Turtles might avoid individual forest patches because of their lower value for thermoregulatory needs, foraging resources, or proximity to flowing water. Kaufmann (1992a) described the Wood Turtle as an "edge" species, and Compton et al. (2002) hypothesized that thermoregulation and feeding demands required turtles to cross between open- and closed-canopy habitats routinely.

Results were similar for habitat associations based on local availability and landscape availability habitat classes. Both indicated significant associations for males with respect to still water (+) and mixed forest (−). Of the six classes, coefficient signs were the same in four and five cases for males and females, respectively, and classes with opposite signs were not significant in one or either analysis. Testing both habitat type and habitat class associations in the landscape-availability analyses yielded useful information for future classification schemes. In this study, we classed forested habitat by dominant cover type to facilitate comparisons to other spatial data sets, but it appears forest age/structure (i.e., young, mature, semiopen) was an important predictor, with males appearing to prefer young upland deciduous forest, and females appearing to prefer semiopen lowland coniferous forest (but note females also had a positive association with mature upland mixed forest). Further, with respect to semiaquatic habitat types, males appeared to prefer shrub swamps to marshes and sedge meadows, whereas females showed the opposite preferences. Hence, a single marshy class appeared to obscure some finer habitat associations. These apparent preference differences between sexes warrant further investigations with a more robust data set.

In conclusion, this study provided baseline metrics for Wood Turtle management regulations and future research in Minnesota and other populations in the northwestern portion of the upper Great Lakes states. There was general consistency between our results and studies conducted in the northern and eastern portions of the species' range, but with a possible difference in distance and timing of movements away from flowing water, indicating that managers of western populations can consult and adapt the broader Wood Turtle literature for conservation initiatives. Finally, although NLCD and LANDFIRE are convenient data sets that provide wide coverage areas for classifying and assessing use of habitat, we recommend not using them for Wood Turtle management and research because of the lack of accuracy at the landscape scale used by Wood Turtles.

Acknowledgments.—We thank B. Brecke and L. Hanson for assistance with field data collection, and R. Moen and J. Tamplin for providing helpful draft manuscript comments. Two anonymous reviewers provided comments that improved the quality of this manuscript. Funding and resources were provided by the Minnesota Department of Natural Resources (Collection Agreement No. NC-90-C11), and the U.S. Forest Service (Study No. NC-4202-90-3). This study was conducted under Minnesota Department of Natural Resources special permits 5412, 6098, and 6922.

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Accepted: 14 November 2015.