

Habitat Characteristics That Influence the Occurrence of Wood Turtles at the Southern Limits of Their Range in the Central Appalachians

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ABSTRACT.—Topographical features and environmental variables form geographic range boundaries and limit species' distributions. Studies of Wood Turtle (*Glyptemys insculpta*) limitations in the northern reaches of their geographic range are fairly well documented; however, few studies exist that investigate ecological factors that affect distribution at the southern extent of their range. Our objectives were to 1) determine aquatic and terrestrial habitat characteristics relevant to Wood Turtle presence or absence and 2) determine the approximate southern geographic boundary of Wood Turtles in the Cacapon River Watershed, West Virginia, USA. We conducted random surveys of 100 sites along the Lost and North rivers during summer 2010, and 64% contained Wood Turtles. Proximity to the Cacapon River, elevation, soil pH, canopy cover, and slope influenced the presence of Wood Turtles. In addition, Wood Turtles occurred at sites with higher herbaceous species richness and diversity, especially in locations along the North River. Vegetative community composition differed between terrestrial sites associated with these two rivers in the field and shrub layers (regardless of turtle presence), and differed in the site \times river interaction in the tree layer. Wood Turtles on the Lost and North rivers, at their southern range limits in West Virginia, are associated with lower elevation, gentler slopes, higher soil pH, and higher tree canopy cover, and also are located closer to the confluence of the Cacapon River. We recommend creating and managing riparian buffers along waterways where Wood Turtles occur to provide essential terrestrial habitat and to promote adult survivorship and population stability.

The geographic range of a species can be considered the primary unit of biogeography (Brown et al., 1996). Barriers such as mountains, coastlines, deserts, and cold temperatures greatly influence features of geographic ranges, including size, shape, and position (Hecnar, 1999). These features also are influenced by environmental variables and ecological functions that limit a species' distribution and abundance, a combination that contributes to the dynamic nature of geographic range borders (Brown et al., 1996). Reptile and amphibian populations affected by range edge effects may be vulnerable to extirpation at faster rates than interior range populations located in environments that are more stable and suitable for the species (Channell and Lomolino, 2000; Lehtinen et al., 2003). Peripheral populations can serve an important role in increasing genetic diversity and species persistence, however, by serving as allelic reservoirs for conservation, because peripheral populations may be locally adapted to environmental and climatic conditions typically found at the edge of their geographic range (Hunter and Hutchinson, 1994; Lesica and Allendorf, 1995; Spradling et al., 2010).

Although the population ecology of Wood Turtles (*Glyptemys insculpta*) has been studied in the northern portion of their range (Quinn and Tate, 1991; Kaufmann, 1992), its habitat use and population dynamics in its southern range need to be better understood for regional conservation efforts to be effective (Bodie, 2001). The geographic range of Wood Turtles extends north from eastern West Virginia and northern Virginia, USA, through the Atlantic states to Nova Scotia, Canada, and west past the Great Lakes to eastern Minnesota (Ernst and Lovich, 2009), with a peripheral isolated population that occurs in Iowa (Spradling et al., 2010). Habitat destruction and alteration over the past several hundred years, however, have resulted in the

decline of this species throughout its range (Ernst and Lovich, 2009).

Studies of Wood Turtles have focused mainly on life history traits and behaviors to determine why the species' distribution may be limited at the northern extent of its range (Arvisais et al., 2002, 2004; Walde et al., 2007; Greaves and Litzgus, 2009). Few have focused on habitat characteristics to explain distributional limits of the species, although dependence on highly oxygenated, flowing water for hibernation has been suggested as a range limitation (Greaves and Litzgus, 2008). In addition, although there are a limited number of ecological studies that characterized other nearby populations (Niederberger and Seidel, 1999; Spradling et al. 2010; Curtis and Vila, 2015), no previous studies have been conducted that specifically determine which factors affect distribution of the species at the southern extent of its range. Dispersal barriers may limit occurrence in distant, but suitable, habitat and may influence where the southern range of Wood Turtles ends (Brown et al., 1996). Turtle distributions often follow large river systems and lie within specific drainage basins (Iverson, 1986; Hecnar, 1999). The objectives of our study were to 1) determine aquatic and terrestrial habitat characteristics relevant to Wood Turtle presence or absence and 2) determine the approximate southern geographic boundary of Wood Turtles in the Cacapon River Watershed, West Virginia.

MATERIALS AND METHODS

Study Site.—The Cacapon River Watershed, composed of the Lost, North, and Cacapon rivers (Fig. 1), occurs within the Ridge and Valley physiographic province of West Virginia; it is 79% forested; 19% agriculture; and 2% residential, barren, or water cover (National Park Service, 1982). The Ridge and Valley region annually receives an average of 76 cm of precipitation (Kozar and Mathes, 2001). The upstream half of the Cacapon River Watershed is heavily farmed, with row crops and grass or

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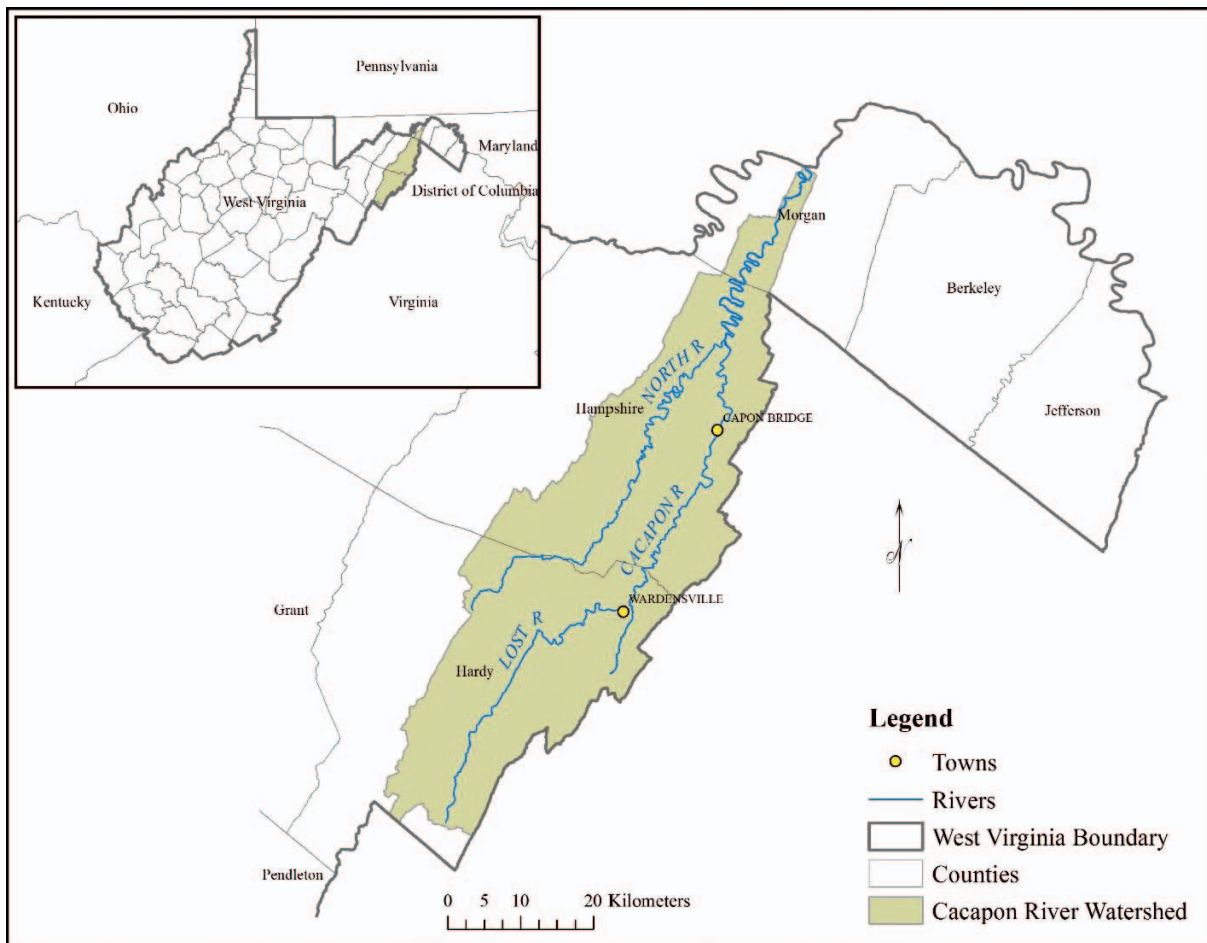


FIG. 1. The Cacapon River watershed occurs in the eastern panhandle of West Virginia, USA. It is composed of the Cacapon, North, and Lost rivers. The watershed drains into the Potomac River that flows into the Chesapeake Bay watershed.

forested pastures occurring up to the edge of the river (Constantz et al., 1995; Niederberger and Seidel, 1999). Within the surveyed areas along the Lost River, about 10% consisted of cultivated crops and about 26% was pasture/hayfield. The North River survey area consisted of about 5% cultivated crops and 13% pasture/hayfield. The temperature (average \pm SD) of the three rivers was $23.7 \pm 2.34^\circ\text{C}$ ($18.4\text{--}30.7^\circ\text{C}$) and the average pH was 8.1 ± 0.43 ($7.2\text{--}9.3$) (Constantz et al., 1995). Riparian overstory vegetation is dominated by coniferous and deciduous species, including American sycamore (*Platanus occidentalis*), red maple (*Acer rubrum*), yellow-poplar (*Liriodendron tulipifera*), black walnut (*Juglans nigra*), white pine (*Pinus strobus*), and chestnut oak (*Quercus prinus*) (Constantz et al., 1995; Niederberger and Seidel, 1999).

Wood Turtle Surveys.—We conducted initial surveys for Wood Turtles within the Cacapon River watershed during spring and summer 2009. These surveys indicated that the species became less abundant upstream of the Cacapon River along the North and Lost rivers. To determine the proportion of 100 random sites that would be surveyed during summer 2010 for Wood Turtles along both the North and Lost rivers, we divided the individual river lengths by the combined length of both rivers. We determined site locations by randomly generating 61 survey sites for the North River, which accounted for 61% of the combined river lengths, and 39 survey sites for the Lost River, from their headwaters to confluence with the Cacapon River. We plotted the survey sites in ArcMap (Environmental Systems

Research Institute, Inc. [ESRI], Redlands, CA) to obtain universal transverse mercator coordinates to locate the sites on the ground. The survey sites were separated by 30.2 to 6,752.8 m ($x = 1,329.1 \pm 135.4$ SE).

We sampled for presence of Wood Turtles from 17 June to 6 August 2010, when the Wood Turtles were primarily terrestrial (Ernst, 1986; Niederberger and Seidel, 1999; McCoard, 2012). At each sampling location, we established a 100-m radius survey circle with the central point occurring in the middle of the river. To determine presence of Wood Turtles, one observer intensively surveyed the entire circle on foot and captured turtles by hand or net. For each capture, we recorded date, time, and location coordinates by using a Garmin Global Positioning System 72™ (accuracy ± 3 m), weather conditions, observed activity when captured, perpendicular distance from the river's edge, and depth if in water. Because presence of the species was the factor of interest, we did not mark the turtles for recapture. After data collection, we released the turtles at their original capture locations. To estimate detection probability, we followed an independent-observer, double sampling method in August 2011 (Mazerolle et al., 2007); however, the primary observer documented more turtles than the two-member alternate team, yielding an estimated detection probability of 1.0.

Habitat Surveys.—Within the 100-m radius survey circle at each Wood Turtle sampling location, we measured terrestrial and aquatic habitat characteristics. We conducted vegetation surveys within a $10 \times 10\text{-m}$ plot within the survey circle (McCoard, 2008).

We generated two random integers from the set {1,2} to determine whether we would begin at the upstream (1) or downstream (2) end of the survey circle and which side of the river (1, river right; 2, river left) to place the plot. We generated two additional random integers between 1 and 50 to select the number of meters along the river and the number of meters perpendicular from the river to place the plot.

We identified and recorded diameter at breast height (dbh) of all trees within the plot with dbh > 5 cm. In addition, we identified and counted the number of stems for all shrubs within the plot, including saplings taller than 1 m and <5 cm in dbh. We surveyed the field layer (woody and herbaceous plants <1 m in height) in 1-m² subplots in the four corners of the 10 × 10-m plot. We identified and estimated percentage of cover of each species, as well as leaf litter, woody debris, and bare ground/rock (Daubenmire, 1959), and averaged the four values for the whole plot. At the center of each subplot, we used a Robel pole to determine vertical density from visual obstruction readings taken 4 m from the pole (1 m in height) in all four cardinal directions and determined the average for the plot (Robel et al., 1970). We measured percentage of canopy cover (Robert E. Lemmon Forest Densiometer Model C, Bartlesville, OK) and recorded a description of the local cover type (e.g., pasture, crop field, wetland, forest) from the center of the 10 × 10-m plot. We estimated cover class rankings for trees, shrubs, and the field layer for the entire 100-m radius survey plot by using the categorical variables of six cover class ratings (1–5% = 1, 6–25% = 2, 26–50% = 3, 51–75% = 4, 76–95% = 5, and 96–100% = 6; Daubenmire, 1959) to assess whether a general percentage of cover of the vegetation layers was preferred by Wood Turtles. We derived elevation, slope, and aspect from U.S. Geological Survey 3-m Digital Elevation Models (West Virginia GIS Technical Center, Morgantown, WV) ArcMap shapefiles (ESRI).

To gain close approximates of the environment being used, we recorded terrestrial data in the center of the vegetation plots when turtles were absent or aquatic and directly under the turtles when terrestrial. We collected a single reading (± 0.01) of soil pH (Oakton® double junction waterproof pH tester 30; Oakton Instruments, Vernon Hills, IL), soil moisture (1 = dry, 10 = saturated; 22.86-cm Lincoln soil moisture meter; Lincoln Irrigation, Lincoln, NE), air temperature ($\pm 1^\circ\text{C}$), and relative humidity ($\pm 5\%$; Oakton digital max-min thermohygrometer). When the turtles were present, we measured aquatic data directly over the turtles and at a randomly generated number (1 to 100) of meters from the upstream survey circle's edge in the river when the turtles were absent. The data recorded included depth (centimeters) and width (meters) of the stream, water temperature ($^\circ\text{C}$; 15.24-cm Enviro-Safe® armor case pocket thermometer; H-B Instrument Company, Collegeville, PA), and water pH (± 0.01). We conducted a pebble count (modified from Wolman, 1954) by measuring 50 randomly selected rocks within the stream occurring in the survey circle to determine whether an average rock size was preferred by the turtles. Within the 100-m radius survey plot, we estimated a cover class ranking for exposed rocks within the stream bed by using a similar scoring system as for the vegetation surveys.

Statistical Analyses.—We performed statistical analyses in R 2.10.1 (R Development Core Team, available from www.r-project.org) or SAS® 9.2 (SAS Institute, Inc., Cary, NC), with $\alpha = 0.05$. For each analysis, we checked for normality and equal variances, transformed data, and removed outliers as necessary, based on visual examination and results of Shapiro-Wilk tests.

We calculated overall (natives and exotics) and natives-only vegetative species diversity (H) and richness (S) ('diversity' and 'specnumber' functions, 'vegan' package, R) for the field, shrub, and tree layers, testing between site types (e.g., presence or absence of turtles), rivers, and site × river interactions by using univariate analyses of variance with Bonferroni multiple comparison adjustments (Dunn, 1961; $\alpha = 0.05/6$ tests = 0.008) and Tukey tests, if significant effects occurred. Normality and equal variances were checked on all models; to approximate normality in the overall vegetation, we exponentially transformed field diversity, removed three outliers, and square-root (plus 1) transformed shrub richness, tree diversity, and tree richness. In the native vegetation, we exponentially transformed field diversity, square-root transformed field richness, shrub diversity and richness, square-root (plus 1) transformed tree diversity, and log (plus 1) transformed tree richness. We reduced the vegetation community datasets by excluding species that accounted for <5% of all observations. To compare community composition of the three vegetation layers between sites, rivers, and site × river interactions, we used permutational multivariate analysis of variance (PerMANOVA, 1,000 permutations, Euclidean distance; 'adonis' function, 'vegan' package, R), because our abundances were skewed with many zeros present (Tuyo et al., 2005). PerMANOVA is robust to departures from parametric distribution assumptions and suitable for community composition analysis (Walters and Coen, 2006; Lorion and Kennedy, 2009). If the community composition was significant among sites or rivers, we used indicator species analysis ('indval' function, 'labdsv' package, R) to determine characteristic species, calculating the indicator values (IVs) for each species by taking the product of its relative frequency and its relative average abundance within each category (Dufrêne and Legendre, 1997). We used an indicator value threshold of 0.25 and $\alpha = 0.05$ (P -values generated through randomization procedures; Dufrêne and Legendre, 1997) to determine which species characterized the site types and rivers. We plotted the characteristic species with their significant main effects (i.e., site type, river) by using nonmetric multidimensional scaling ordination ('metaMDS' and 'envfit' functions, 'vegan' package, R).

To determine which variables were important in determining the presence of Wood Turtles, we considered an initial 28 terrestrial and aquatic habitat variables for logistic regression model membership. We centered and scaled all quantitative predictor variables. An eigenanalysis revealed mild issues with multicollinearity; therefore, we removed stream order, land use, and river from the pool of possible variables. Because of small sample size with respect to the initial number of independent variables, we proceeded with logistic regression using Firth's penalized maximum likelihood estimation. For the same reason, we did not include interaction effects in the model. Using least absolute shrinkage and selection operator (LASSO) regression, a penalized method used for variable selection in high-dimensional data (Zhang and Huang, 2008), in conjunction with corrected Akaike Information Criterion (AIC_c; Hurvich and Tsai, 1989) and Bayesian Information Criterion (BIC), we selected an initial candidate set of 11 variables. We conducted penalized likelihood ratio tests on the log-odds ratios and computed 95% profile penalized likelihood confidence intervals for the odds ratios. We conducted model reduction and proceeded by sequentially pooling terms exhibiting the largest P -value until all term parameter estimates were significant at

TABLE 1. Penalized likelihood ratio tests on the log-odds ratios and 95% profile penalized likelihood confidence intervals (CI; original data scale) computed for a model containing microhabitat variables related to the presence of Wood Turtles along the Lost and North rivers, Cacapon River watershed, West Virginia, USA, during summer 2010. Distance refers to the distance (km) of the Lost and North rivers to the Cacapon River.

Variable	Presence		Absence		Penalized likelihood ratio tests on the log-odds ratios				95% profile likelihood CI	
	<i>x</i>	SE	<i>x</i>	SE	Coefficient	SE	95% CI	<i>P</i>	Estimate	95% CI
Distance (km)	24.8	1.3	48.3	2.3	-2.14	0.64	-3.69 to -1.01	≤0.001	0.85	0.76–0.93
Elevation (m)	299.9	8.9	430.0	16.1	-1.42	0.48	-2.45 to -0.56	≤0.001	0.98	0.97–0.99
Soil pH	7.2	0.02	7.0	0.02	0.61	0.35	-0.04 to 1.37	0.068	25.65	0.80–999.0
Canopy cover (%)	52.9	3.6	44.9	5.5	0.99	0.40	0.26–1.89	0.006	1.03	1.01–1.06
Slope (°)	8.4	0.8	10.1	1.4	-1.27	0.44	-1.69 to -0.16	0.014	0.89	0.79–0.98

the (uncorrected) 0.10 level. We used logistic regression diagnostics to verify the fit of the model.

To determine the Wood Turtles' range within the study area, we used an adaptive local convex hull ('a-LoCoH', Adehabitat package, R [Getz et al., 2007]) to form an isopleth around all turtle locations. We compared values and areas of the utilization distributions (UDs) by using \hat{a} , (asymptote of the UD construction) and a_1 (maximum distance between any two turtle capture points) between 95 and 100% isopleths. We calculated the value of \hat{a} , by plotting the UD area against increasing values of the parameter a until an asymptote was reached at 50,000 m. We calculated the value of a_1 by measuring the distance between the two most separated points, at about 71,000 m. To determine the most accurate UD, we imported the UD and capture locations into ArcMap (ESRI) and overlaid them on elevation and hillshade shapefile layers (West Virginia GIS Technical Center).

RESULTS

Wood Turtle Occurrence.—We confirmed the presence of Wood Turtles at 64 sites. We did not locate any turtles at the remaining 36 sites. Two Wood Turtles were captured at one site, but single turtles were observed in all other locations with the confirmed presence of the turtles.

Vegetation.—We recorded 125 (72% native) species in total within the field ($n = 112$), shrub ($n = 29$), and tree ($n = 26$) layers; some species were recorded in multiple layers (see McCoard, 2012, for species lists). Mean \pm SE overall (natives and exotics) field diversity, mean native field diversity, mean overall field richness, and mean native field richness were greater at sites with turtles (overall field diversity: 2.27 ± 0.07 ; native field diversity: 1.89 ± 0.07 ; overall field richness: 15.34 ± 0.71 ; native field richness: 10.44 ± 0.53) than sites without turtles (overall field diversity: 1.79 ± 0.09 , $F_{1,93} = 22.02$, $P < 0.001$; native field diversity: 1.38 ± 0.11 , $F_{1,96} = 9.25$, $P = 0.003$; overall field richness: 11.11 ± 0.92 , $F_{1,96} = 10.12$, $P = 0.002$; native field richness: 7.58 ± 0.053 , $F_{1,96} = 9.23$, $P = 0.005$). Mean overall field diversity, mean native field diversity, mean overall field richness, and mean native field richness were also greater along the North River (overall field diversity: 2.37 ± 0.05 ; native field diversity: 1.96 ± 0.07 ; overall field richness: 16.84 ± 0.639 ; native field richness: 11.54 ± 0.49) than the Lost River (overall field diversity: 1.68 ± 0.09 , $F_{1,93} = 53.20$, $P < 0.001$; native field diversity: 1.28 ± 0.09 , $F_{1,96} = 46.42$, $P < 0.001$; overall field richness: 9.10 ± 0.65 , $F_{1,96} = 61.22$, $P < 0.001$; native field richness: 6.08 ± 0.47 , $F_{1,96} = 55.89$, $P < 0.001$). Overall field community composition was similar between the rivers and in the site \times river interaction ($P \geq 0.055$), but differed among sites with and without turtles (pseudo- $F_{1,96} = 8.81$, $P = 0.001$). Native field composition was similar among the sites and in the site \times river interaction ($P \geq 0.166$), but differed among

rivers (pseudo- $F_{1,96} = 8.84$, $P = 0.002$). Wingstem (*Verbesina alternifolia*; IV = 0.55, $P = 0.018$) and Reed Canary Grass (*Phalaris arundinacea*; IV = 0.40, $P = 0.013$) characterized the Lost River compared to the North River, but no species differentiated sites with Wood Turtles from those without the turtles.

Mean overall shrub diversity was similar among all variables ($F_{1,96} \geq 0.00$, $P \geq 0.041$ [Bonferroni correction: $\alpha = 0.05/6$ tests = 0.008]). Mean overall shrub richness differed in the site \times river interaction, with mean shrub richness being higher in sites with turtles (2.00 ± 0.26) than without (1.06 ± 0.30) along the Lost River ($F_{1,96} = 13.20$, $P \leq 0.001$). Mean native shrub richness ($F_{1,96} = 14.61$, $P < 0.001$) was higher along the North River (1.05 ± 0.14) than the Lost River (0.38 ± 0.13). Overall shrub community composition did not differ between sites or rivers ($P \geq 0.068$). Native shrub composition did not differ between sites (pseudo- $F_{1,96} = 1.19$, $P = 0.318$), but differed between rivers (pseudo- $F_{1,96} = 3.09$, $P = 0.014$). Spicebush (overall, IV = 0.28, $P = 0.005$; native, IV = 0.28, $P = 0.004$) differentiated the North River from the Lost River, but no indicator species occurred to differentiate the sites overall.

The overall tree layer did not differ in mean diversity or mean richness ($P \geq 0.117$) among any of the variables. Mean native tree diversity ($F_{1,96} = 9.86$, $P = 0.002$) and mean native tree richness ($F_{1,96} = 20.66$, $P \leq 0.001$) were higher along the North River (diversity: 0.57 ± 0.07 ; richness: 2.18 ± 0.19) than the Lost River (diversity: 0.26 ± 0.07 ; richness: 1.08 ± 0.18). Overall tree community composition was similar among sites (pseudo- $F_{1,96} = 2.53$, $P = 0.022$ [Bonferroni correction: $\alpha = 0.05/3$ tests = 0.017]) and rivers (pseudo- $F_{1,96} = 2.05$, $P = 0.067$), and native tree composition was similar among sites (pseudo- $F_{1,96} = 2.53$, $P = 0.026$) and rivers (pseudo- $F_{1,96} = 2.05$, $P = 0.046$). Witch-hazel (*Hamamelis virginianus*; overall, IV = 0.08, $P = 0.048$; native, IV = 0.08, $P = 0.043$) and ironwood (*Ostrya virginiana*; IV = 0.08, $P = 0.049$) were more likely to be located in sites without turtles than those with turtles. No indicator species occurred to differentiate the rivers.

Environmental Variable Model.—Sites with Wood Turtles were compared to sites without the turtles to determine, through generating a logistic regression model, which variables influenced the presence of the turtles. The final, reduced habitat variable model using LASSO regression and AIC_c contained five variables: elevation, distance from the Cacapon River, soil pH, canopy cover, and slope (Table 1). The full model containing all 11 terms had an AIC_c = 50.082 and a BIC = 81.344. The reduced model had an AIC_c = 59.105 and a BIC = 74.736. The generalized coefficient of determination per Nagelkerke (1991) for the reduced model was 0.7115. The Hosmer-Lemeshow goodness-of-fit test was not significant ($P = 0.46$), suggesting that the logistic response function was appropriate. Logistic regression diagnostics also verified the fit of the model.

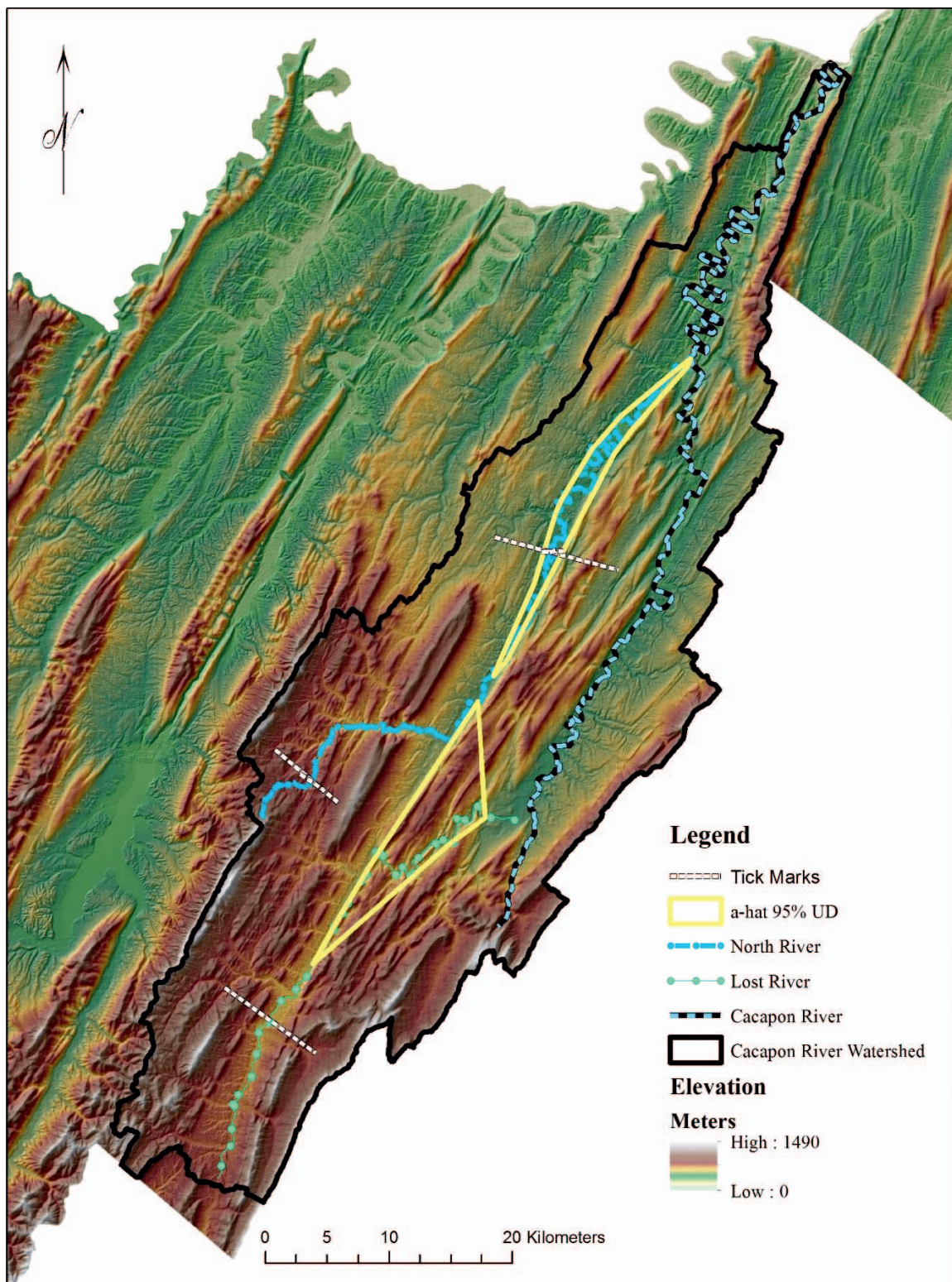


FIG. 2. A 95% UD (adaptive local convex hull, Adehabitat package, R) for Wood Turtles was generated from North and Lost river, West Virginia, USA, sampling efforts during summer 2010. Model-driven cutpoints (tick marks) for 50 and 0% predicted probabilities of site occupancy along the North and Lost rivers are overlaid on the map.

Site Occupancy Probability.—The 95 and 100% isopleths for \hat{a} , and a_1 were similar in distribution and area. Area of the \hat{a} , 100% UD was 13,400 ha and covered more occupied lowland habitat than the a_1 100% UD at 14,000 ha; however, 95% isopleths are more commonly used and gave a more representative UD consistent with field observations of Wood Turtle locations than

the 100% isopleths. Area of the \hat{a} , 95% UD was about 11,800 ha and covered more occupied lowland habitat than the a_1 95% UD at an area of 11,700 ha. We considered the \hat{a} , 95% UD to be representative of the actual Wood Turtle distribution along the North and Lost rivers among the four UD's generated (Fig. 2). Based on the UD produced from field surveys, the approximate

termination of the Wood Turtles' range within the Cacapon River watershed occurs where the two rivers lose their floodplains and flow primarily through upland habitat; this result did not coincide with the absence of agricultural lands, as agriculture was present further along the river headwaters than the turtles were found.

DISCUSSION

Vegetation.—Wood Turtles were present in sites with high field layer richness and diversity compared to sites without the turtles. Vegetative complexity possibly provided a greater variety of edible plant matter and cover for the turtles. The field layer seemed to have a greater influence on the presence of the turtles than shrubs or trees, because no differences were observed between sites with and without turtles in regard to the tree layer. Results of the shrub analyses were mixed, however, with higher shrub richness at sites with turtles on the Lost River, but not the North River. The North River sites were higher in overall vegetative species diversity and richness than the Lost River sites. This result may have been related to the North River's larger and more forested floodplain (McCoard, pers. obs.), which supported greater plant species diversity. Riparian zones, where Wood Turtles are primarily found, tend to support greater wildlife richness and diversity than surrounding uplands (Doyle, 1990; McComb et al., 1993; Palmer and Bennett, 2006). The high use of riparian zones by wildlife is closely associated with complex vegetative structure and composition (Stauffer and Best, 1980; Giuliano and Homyack, 2004), as may be reflected in the Wood Turtles occurring in sites with greater vegetative diversity.

Environmental Influences Acting as Southern Range Limitations.—Hecnar (1999) suggested that turtle ranges are influenced by the positions of coastlines, mountain ranges, deserts, and extreme temperatures on each continent. Wood Turtles in our study tended to occur at lower elevations (300 m [present] vs. 430 m [absent]; also noted by Strang, 1983; Jones and Sievert, 2009; Tingley et al., 2009, 2010) and at slightly gentler slopes (8.4° vs. 10.1°). In Massachusetts, Jones and Sievert (2009) determined that the majority of Wood Turtles exhibited home ranges with stream gradients <1%, possibly to avoid displacement by flooding in high-relief areas. Generally, they were not located on dry, open, and hilly terrain (also noted by Carroll and Ehrenfeld, 1978). Soil pH was higher in sites where Wood Turtles were present (7.2) and lower (7.0) where they were not found. Wood Turtles may be indirectly influenced by soil pH as plant species richness has been shown to increase with higher levels of soil pH (Gough et al., 2000; Partel, 2002). Gough et al. (2000) hypothesized this may be a result of greater nutrient availability and diversity in soils with higher pH compared to those with lower pH.

Wood Turtles were absent from points within the Cacapon River watershed where the Lost and North rivers lost their wide floodplains and instead flowed primarily through upland habitat. Even beyond where this change occurred, similar cover types (e.g., forests, pastures, row crops) continued, indicating that cover type was not the driving factor in Wood Turtle presence or absence. From our results, the primary factors that appear to limit Wood Turtles at the southern limits of their range in West Virginia include the inability to disperse over high elevations and steeper slopes. Wood Turtles are declining throughout their range, primarily because of habitat destruction and fragmentation (Harding and Bloomer, 1979); to prevent the status of the species from becoming more critical, conservation and management of local populations, and education of

landowners about the needs of Wood Turtles on their properties, are essential for the species' persistence (Kaufmann, 1992; Channell and Lomolino, 2000; Remsberg et al., 2006). Our study focused on environmental conditions that are associated with the presence or absence of Wood Turtles along the southern border of their range (Brown et al., 1996). The information gained is valuable for better understanding how to protect and promote populations of Wood Turtles occurring in West Virginia.

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