

HABITAT SELECTION BY WOOD TURTLES (*CLEMMYS INSCULPTA*): AN APPLICATION OF PAIRED LOGISTIC REGRESSION

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Abstract. Models of habitat selection have been developed primarily for mobile animals with well-defined home ranges. The assumptions made by traditional techniques about habitat availability are inappropriate for species with low mobility and large home ranges, such as the wood turtle. We used paired logistic regression, typically used in medical case – control studies, to model selection of habitat within activity areas in a population of wood turtles in a watershed in western Maine. We also modeled selection of activity areas within the watershed, using nonpaired logistic regression. Within activity areas, wood turtles selected nonforested locations close to water with low canopy cover. Within the watershed, they selected activity areas close to streams and rivers with moderate forest cover and little open water. The difference between selection at these two scales suggests that wood turtles select forest edges to balance thermoregulatory and feeding needs. The model of selection of activity areas within the watershed correctly classified 84% of activity areas and random areas. This model may be useful for identifying wood turtle habitat across the landscape as part of regional conservation efforts. We suggest that paired logistic regression shows promise for analysis of habitat selection of species with movement patterns that violate the assumptions of traditional habitat selection models.

Key words: case – control; *Clemmys insculpta*; *Emydidae*; habitat selection; Maine; matched-pairs logistic regression; wood turtles.

INTRODUCTION

Models of habitat selection have typically been developed for mobile animals with well-defined home ranges, such as many mammals and passerine birds. Traditional use-vs.-availability analyses determine “available” habitat by measuring mapped cover types or sampling habitat within a fixed study area or home range, and assume that an animal’s entire home range is available to it between successive observations (Arthur et al. 1996). This assumption is clearly false for animals with low mobility and large home ranges such as wood turtles.

Arthur et al. (1996) describe an approach that allows for fluctuating habitat availability by defining available habitat separately for each animal location. Hjermmann (2000) provides a modification that refines estimates of available habitat, allowing availability to vary continuously, rather than assuming that all habitat within a fixed-radius circle is equally available. These methods require mapping cover types, and thus are not appropriate for situations where habitat cannot be mapped, such as studies of microhabitat selection. We present an alternative approach, based on sampling one or more random locations paired with each animal lo-

cation and using paired logistic regression to analyze habitat selection (Breslow and Day 1980, Hosmer and Lemeshow 1989, Ormsbee and McComb 1998).

Habitat selection studies based on analysis of cover types assume that predefined cover types essentially reflect the first principal component of environmental variables that are important to the species being studied. Multivariate approaches avoid such assumptions by taking the more exploratory approach of modeling habitat selection based on a number of environmental variables of potential importance (Garshelis 2000). Habitat selection models based on measurements at animal locations and random locations are typically analyzed either using discriminant function analysis or logistic regression (e.g., Sherburne and Bissonette 1994, Mladenoff et al. 1995, Block et al. 1998). Logistic regression is a more robust technique than discriminant analysis, as it does not require multivariate normality, and it allows the use of categorical predictor variables (North and Reynolds 1996).

When one or more random locations can be explicitly paired with animal locations, random points and animal points can be measured at the same time, with the same resource availability and weather conditions. Paired logistic regression compares use with availability at the same place and time, not against everywhere (as in fixed home range models) or all times (as in discriminant analysis and nonpaired logistic regression). For species with limited mobility or without well-defined

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home ranges, paired analyses come closer to modeling the choices that animals are making.

The wood turtle, *Clemmys insculpta* (LeConte, 1830) is a riparian emydid found throughout the northeastern U.S. and southeastern Canada. Wood turtles hibernate and mate in streams and rivers, typically nest in riparian gravel bars, and forage during the summer throughout a variety of wetland and upland habitats. Their diets include fruits, fungi, slugs, earthworms, insects, carrion, amphibian larvae, and the leaves of a number of plant species (Ernst et al. 1994). Within riparian areas, they are known as habitat generalists, using alder swales, swamps, bogs, meadows, agricultural fields, and deciduous and mixed forests (Kaufmann 1992, Ernst et al. 1994, Foscarini and Brooks 1997). Their habitat use apparently varies across their geographic range, with midwestern populations being more aquatic than those in the east (Harding and Bloomer 1979, Ernst et al. 1994). In Pennsylvania, Kaufmann (1992) found that wood turtles select creek, alder, and grass-sedge-forb cover types, and avoid cornfields, hemlock, and deciduous forests; whereas in Ontario, Foscarini and Brooks (1997) found heavy use of agricultural fields. The variety of cover types used and differences among populations suggest that wood turtles may not be selecting habitat based upon cover types.

The objective of this study was to model wood turtle habitat selection at two scales. Individual wood turtles at our study site in western Maine use a succession of widely separated "activity areas" throughout the season. These movement patterns present a natural separation of scales for studying habitat selection: (1) selection within activity areas and (2) selection of activity areas within the watershed. We modeled selection within activity areas based on habitat features at turtle locations vs. paired random locations, where habitat was measured simultaneously to remove effects of differing availability by season, weather, and time of day. We also described seasonal selection of habitat comprising potential food items within activity areas. We modeled within-watershed selection of activity areas by comparing habitat features within activity areas with those in similar-sized circles placed randomly within the watershed, with a similar distribution of distances from the river and streams. At each scale, we measured habitat features with potential relevance to travel, thermoregulation, hydration, and feeding.

METHODS

Study site

Data for this study were collected in Somerset County, western Maine. We omit the exact study location because of the danger that illegal collection for the commercial pet trade poses to wood turtle populations. The study population inhabits the riparian zone of an ~6.5 km stretch of a river fed by three second-order and higher tributaries, as well as by several smaller

streams. The broad riparian zone is dominated by fens, bogs, sedge meadows, alder swales, and forested wetlands. Other features include marshes, beaver ponds, a complex of oxbow vernal pools, and several gravel bars and artificial gravel pits. Most of the surrounding land consists of mixed and coniferous forest, and is managed as industrial forest. Permanent human habitation in the immediate area is <0.2 persons/km², but people camp, fish, and boat in the area.

Capture and radiotelemetry

Adult wood turtles were caught opportunistically between October 1994 and September 1998 at hibernacula, nesting sites, during mating, and elsewhere. They were uniquely marked by shell notching, using a modified version of Cagle (1939). Lotek MBFT-6 transmitters (Lotek Engineering, Inc., Newmarket, Ontario, Canada) were attached to 37 animals (10 male; 27 female) with Biocryl acrylic cement (Great Lakes Orthodontic Products, Tonawanda, New York, USA). Transmitters (9 g) plus cement (total ~37 g) weighed 3–8% of turtle body weight. Transmitters and antennas were attached around the margin of the carapace to avoid increasing turtle carapace height and to minimize interference with mating in females. Transmitters were removed from turtles at the end of the study.

Each turtle was located by radiotelemetry one or two times per week during a pilot season in June–August 1997. Analysis of location data taken from this pilot season showed that the distance moved between locations was independent of the number of days between locations 1–7 d apart (Kruskal-Wallis test, $n = 679$, $df = 6$, $\chi^2 = 7.00$, $P = 0.32$). Therefore, locations were separated by at least one intervening day in 1998 to avoid serial autocorrelation within activity areas.

Relocation was increased to two to three times per week in June–August 1998 and additional locations were recorded one to two times per week in May and September 1998. Turtles were located between 0800 and 1800 (95% of locations were between 0900 and 1630). Locations of animals were recorded precisely, or to within 3 m when they were submerged and could not be located exactly. Locations were entered into Trimble Pathfinder GPS units (Trimble Navigation Ltd., Sunnyvale, California, USA) and post-processed with differential correction for a final precision of 3–5 m. Locations were converted to UTM coordinates on the 1927 North American Datum and entered into a geographic information system (GIS) as a point coverage.

Because nesting habitat is well known (Harding and Bloomer 1979, Buech et al. 1997), nesting females were excluded from habitat analysis from the time they moved to nesting sites until after they nested.

Activity areas

Activity areas for each animal were defined based on the distance from each successive location to the running mean of the previous five locations. As soon

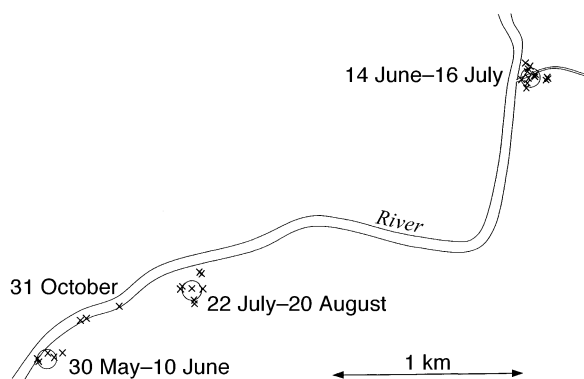


FIG. 1. Typical wood turtle movement patterns in a riparian landscape. Locations of female F15 during 1997 ($n = 32$), showing three distinct activity areas (circles) used from May through August.

as this distance exceeded a threshold of 100 m (this distance was chosen empirically as the approximate inflection point of an accumulation curve of number of locations within activity areas from turtle locations taken in 1997), a new activity area was started, and the running mean was restarted. After each activity area was defined for an animal, activity areas with center points (defined as the mean of all locations within the area) within 100 m of each other were merged. Finally, all activity areas with fewer than five points were considered travel points and were deleted. This procedure was calibrated to locations from the 1997 pilot season to define activity areas appropriately for individual animals with obvious separation among activity areas (Fig. 1), and to provide reasonable results for individuals with more ambiguous movement patterns. The procedure was then applied to 1998 locations to define

activity areas for each animal. Further analyses were restricted to observations within activity areas.

Habitat measurement

Each time a turtle was located in 1998, we measured a number of habitat features potentially important for travel, thermoregulation, hydration, and feeding (Table 1). We also recorded cover type for each location in the following categories: alder, bank, bog/fen, clearcut, forest, gravel, marsh, meadow, pond, river, scrub-shrub, stream, and vernal pool. Habitat was measured both at the turtle's location and at a nearby random location, based on a random bearing and a random distance selected uniformly from 12–50 m, the interquartile range of distances moved between locations within an activity area during the 1997 pilot season (Fig. 2).

Habitat variables were recorded as presence/absence, categorical (high, medium, low, none), or as paced distances (m). Open water was defined as any water body large enough for a wood turtle to submerge itself (≥ 10 cm deep). Running water was defined as any stream ≥ 10 cm deep. Distance to open water and distance to running water were estimated in the field for distances < 20 m and estimated from GIS if > 20 m. Distance to edges between National Wetland Inventory (NWI) classifications were estimated from GIS. Canopy was measured from a turtle's perspective, i.e., plant cover above 10 cm. Potential food items (raspberries, mushrooms, green plants, slugs, and earthworms) were based upon reports in the literature (Ernst et al. 1994); turtles were observed eating all of these items during the course of the study.

Thirty-two random areas were selected throughout the watershed at distances from the river and streams

TABLE 1. Variables included in activity area scale analysis of wood turtle habitat selection.

Variable	Description
<i>dist.lotie</i> †	Distance (m) to running water > 10 cm deep
<i>dist.water</i> †	Distance (m) to any open water > 10 cm deep
<i>dist.vp</i>	Distance (m) to the nearest vernal pool > 10 cm deep
<i>depth</i>	Depth of water (cm)
<i>sun</i>	Amount of sun of turtle: none (0), partial (1), full (2)
<i>canopy</i>	Canopy density: none ($< 2\%$), low (2–20%), medium (20–80%), high ($> 80\%$), from a turtle's perspective (i.e., closure above 10 cm), coded as midpoint of category
<i>razz</i>	Raspberry in fruit within 3 m: none (0), low (1), medium (2), high (3)
<i>shroom</i>	Mushrooms within 3 m: none (0), low (1), medium (2), high (3)
<i>herb</i>	Green plants within 15 cm of ground within 3 m: none (0), low (1), medium (2), high (3)
<i>slug</i>	Slugs within 3 m: presence (1), absence (0)
<i>worm</i>	Earthworms within 3 m: sum of presence (1)/absence (0) in each of five samples using bulb planter
<i>edge.fine</i> ‡§	Distance to nearest edge (full National Wetlands Inventory [NWI] specification)
<i>edge.coarse</i> ‡§	Distance to nearest edge (to NWI class)
<i>upland</i> ‡	1 if classified as upland on NWI
<i>forest</i>	1 if cover type = forest
<i>em</i>	1 if cover type = marsh or meadow
<i>ss</i>	1 if cover type = alder, scrub-shrub, bog, or fen
<i>wet</i>	1 if in water > 10 cm deep

† Estimated in field if ≤ 20 m; from GIS if > 20 m.

‡ Estimated from GIS.

§ Edge measures excluded river and stream banks.

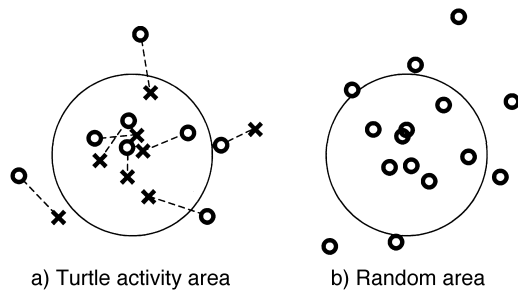


FIG. 2. Sampling design for habitat selection models. In turtle activity areas (a), habitat was sampled at turtle locations (X), and at a random location (O) paired with each turtle location. In random areas (b), habitat was sampled at 15 points (O) with a distribution matching that of random points in activity areas. Landscape metrics for within-watershed habitat analysis were calculated for 100 m diameter circles centered on each activity area and random area. Within-activity area analysis compared turtle locations with paired random locations. Within-watershed analysis compared random locations and landscape metrics in turtle activity areas with random locations and landscape metrics in random areas.

that matched quartiles of distances of activity areas of a subset of turtles from rivers and streams in 1997 (minimum = 0 m, $Q_{0.25}$ = 15 m, median = 60 m, $Q_{0.75}$ = 100 m, maximum = 300 m). Within each random area, habitat was measured at 15 random points in the same way as it was for turtle locations (Fig. 2). Random points within random areas were selected (based on random walks from uniform random points) to approximately match the distribution of random points within activity areas.

We tested for a bias in the placement of random points within activity areas vs. random points in random areas by simulating random points within each activity area, using the same method as for random points in random areas. We then calculated the distance from each random point to the nearest turtle point (excluding the turtle point it was based upon, which is not independent), and the distance from each simulated random point to the nearest turtle point. The distribution of distance (in meters) from turtle points to random points ($Q_{0.10}$ = 6.01, $Q_{0.25}$ = 10.27, median = 17.18, $Q_{0.75}$ = 28.07, $Q_{0.90}$ = 42.15; n = 937) and from simulated random points ($Q_{0.10}$ = 6.18, $Q_{0.25}$ = 10.20, median = 17.18, $Q_{0.75}$ = 28.26, $Q_{0.90}$ = 48.05) were similar; we conclude that no bias exists.

Values of several habitat variables were estimated from a GIS polygon coverage of digitized NWI maps for the state of Maine. These maps were supplemented with an arc coverage of streams (USGS DLG stream coverage, 1:24 000). Streams too small to be mapped on USGS 7.5' topographic maps were mapped in the field by walking them with a GPS unit, and then creating a smoothed arc coverage.

Activity area scale analysis

Matched-pairs logistic regression was used to analyze selection of habitat within activity areas (Table 1),

because it is more appropriate and powerful than standard logistic regression for analyzing paired data such as observed location vs. random location data (Breslow and Day 1980, Hosmer and Lemeshow 1989). Paired logistic regression is analogous to a paired t test. Values of all variables for each "control" (random point) are subtracted from the values for each paired "case" (turtle location). Standard logistic regression software is then used to fit a response vector of all 1's (presence – absence) to a matrix of predictor variables (case – control). A constant term is excluded from the model. Interactions and higher order terms must be calculated before subtracting the paired observations.

Each estimated coefficient β_i is interpreted as usual for logistic regression: an n -unit increase in an explanatory variable results in a $e^{n\beta_i}$ increase in the odds ratio. For low-probability events (such as the presence of a wood turtle), the odds ratio approximates the relative risk, i.e., the ratio of the probability of event x (e.g., a turtle being present) given A to the probability of x given B (Hosmer and Lemeshow 1989). Because explanatory variables in paired logistic regression are differences between paired case vs. control observations, the model is interpreted in terms of differences in habitat rather than absolute measured values of habitat variables.

Models were fit separately for each of the 37 animals, producing a vector of coefficients for each habitat variable. After some preliminary exploratory analysis, 20 candidate models were selected. The fits of models including each member of sets of highly intercorrelated predictor variables ($r \geq 0.70$) were compared against each other to prevent less significant variables from "shadowing" correlated variables in the candidate models. Once candidate models were selected, residuals were examined for linearity of the logit, and adjusted if necessary (Hosmer and Lemeshow 1989:88–91). These candidate models were tested with Akaike's Information Criterion (corrected for small sample sizes), AIC_c (Burnham and Anderson 1998). The model with the minimum AIC_c and all models with AIC_c within two of the minimum were considered to be supported.

Overall significance across animals was tested for each variable in each supported model by testing the coefficient vector against zero using individual Wilcoxon signed-rank tests, with a Bonferroni adjustment to hold α to a nominal value of 0.05. Final model(s) were those for which all coefficients were significant. Positive coefficients represent selection for a particular habitat feature across animals; negative coefficients represent "avoidance." Coefficient vectors were compared between sexes with Wilcoxon rank-sum tests. Fit of the models was assessed with McFadden's ρ^2 , which is analogous to the multiple correlation coefficient R^2 (McFadden 1974).

Selection of habitat comprising seasonal food items (raspberries, mushrooms, green plants, slugs, and

TABLE 2. Variables included in watershed scale analysis of wood turtle habitat selection.

Variable	Description
<i>open.water</i>	Proportion with open water ≥ 10 cm deep
<i>depth</i>	Mean water depth (cm)
<i>up</i>	Distance (m) from plot center to nearest vernal pool
<i>canopy</i>	Mean canopy density: none ($>2\%$), low (2–20%), medium (20–80%), high ($>80\%$), from a turtle's perspective (i.e., closure above 10 cm), coded as midpoint of category
<i>razz</i>	Mean raspberry: none (0), low (1), medium (2), high (3)
<i>shroom</i>	Mean mushroom: none (0), low (1), medium (2), high (3)
<i>herb</i>	Mean herb: none (0), low (1), medium (2), high (3)
<i>slug</i>	Mean slug: presence (1), absence (0)
<i>worm</i>	Mean earthworm abundance: sum of presence (1)/absence (0) in each of five samples using bulb planter
<i>forest</i>	Proportion in forest
<i>em</i> †	Proportion classified as emergent on National Wetland Inventory [NWI]
<i>fowet</i> †	Proportion classified as forested wetland on NWI
<i>riv</i> †	Proportion classified as river on NWI
<i>ss</i> †	Proportion classified as scrub–shrub on NWI
<i>ub</i> †	Proportion classified as unconsolidated bottom on NWI
<i>upland</i> †	Proportion classified as upland on NWI
<i>edge.fine</i> †‡	Length of edge (m) between NWI cover types (full NWI specification)
<i>edge.coarse</i> †‡	Length of edge (m) between NWI cover types (to NWI class)
<i>strlen</i> †	Total stream length (m) in plot
<i>dist.fowet</i> †	Distance (m) from plot center to forested wetland
<i>dist.upland</i> †	Distance (m) from plot center to upland

† Estimated from GIS.

‡ Edge measures excluded river and stream banks.

earthworms) was described by plotting weekly mean selection indices of each food item separately. Each selection index was calculated as the difference between the abundance code at a turtle location and the abundance code at the paired random location. A positive selection index indicates selection for habitat containing a particular food item, and a negative index indicates “avoidance.” Weekly means were estimated for each animal and then across animals.

Watershed scale analysis

Within the watershed, each turtle activity area was characterized by the mean of each habitat variable across the random points within that activity area, and each random area was characterized by the mean of the 15 random points measured in that area. Landscape metrics were obtained from GIS based on 100 m circles centered on both activity areas and random areas. We chose 100 m to match the empirically determined size threshold of activity areas. These 100 m circles encompassed $\sim 50\%$ of turtle and random points within activity areas and random areas. Because the area of a circle increases with the square of its diameter, increasing these circles to include a higher percentage of turtle locations would have included increasingly more non-habitat.

Landscape metrics included the proportion of each NWI wetland type, total length of streams within each area, and total length of edges among NWI types (Table 2). Random areas that overlapped with any turtle activity area were dropped from the analysis. To maintain independence of activity areas, means were taken across all activity areas for each animal. Standard (non-

paired) logistic regression was used to compare turtle activity areas with random areas, both by sex and overall. Twenty candidate models were selected based on exploratory analyses, and adjusted for linearity as for the activity area analysis. Models were ranked using AIC_c , and a final model was selected from the models with the lowest AIC_c , based on the stability of parameter estimates (i.e., the best model for which the 95% confidence intervals of each parameter did not include zero). The stability of the final model was validated by performing 1000 random bootstrap replications (Efron and Gong 1983).

Statistical analyses were done using S-Plus version 4.5 (MathSoft, Inc., Cambridge, Massachusetts, USA), JMP IN version 3.2.1 (SAS Institute, Inc., Cary, North Carolina, USA), and programs written by BWC in APL*Plus II version 5.2 (Manugistics, Inc., Rockville, Maryland, USA). Arc/Info (version 7.2.1, Environmental Systems Research, Inc., Redlands, California, USA) was used for GIS analysis. We used $\alpha = 0.05$ in statistical tests unless stated otherwise.

RESULTS

Habitat was measured at 1155 turtle locations and paired random points during May–September, 1998. Overall, $\sim 77\%$ of locations occurred in forest, scrub–shrub, bog–fen, and emergent cover types (Table 3); on average, 69% of locations for males and 80% of locations for females occurred within these four cover types. Males were located in water about twice as often as females. The number of activity areas ($n = 78$) used by individual turtles varied from one to four (median = 2). Habitat data were collected at 4–31 locations

TABLE 3. Cover types used by wood turtles in 1998, excluding females during the nesting season.

Cover type	Females (<i>n</i> = 27)		Males (<i>n</i> = 10)		Both (<i>n</i> = 37)	
	%	(<i>n</i>)	%	(<i>n</i>)	%	(<i>n</i>)
Lotic (river, stream)	11	(99)	20	(56)	13	(155)
Lentic (pond, vernal pool)	3	(28)	4	(12)	3	(40)
Emergent (marsh, meadow)	19	(169)	11	(32)	17	(201)
Fen/bog	16	(137)	22	(61)	17	(198)
Scrub-shrub (alder, other scrub-shrub)	22	(191)	19	(53)	21	(244)
Forest	23	(205)	17	(47)	22	(252)
Other (bank, gravel, clearcut)	5	(46)	7	(19)	6	(65)
Total	100	(875)	100	(280)	100	(1155)

(separated by ≥ 36 h) per activity area (median = 9.5). Each turtle had 9–32 (median = 27) locations among all activity areas throughout the year, for a total of 936 locations within activity areas. Individual animals generally used the same activity areas in both 1997 and 1998.

Activity area scale

Seven models selected by Akaike's Information Criterion had all coefficients significant across animals (Wilcoxon signed-rank tests, adjusted $P < 0.05$). The coefficients of these models were similar to each other (Table 4). No interactions among these variables contributed significantly to the model, nor was there any significant difference between sexes.

Coefficients of the best model (*dist.water* + *forest* + *canopy*; see Table 1 for description of model components) suggest that, within activity areas, a turtle tends to select nonforested areas that are close to water and have low canopy cover. The median odds ratios (Table 5) indicate that every 10 m of additional distance from water results in a 25% decrease in selection, that a 10% increase in canopy closure results in a 10% decrease in selection, and that when both forested and nonforested habitat is available, a turtle is about one-third as likely to select forested as nonforested areas (Fig. 3).

Although this was the best overall model in terms of predicting within-activity area selection of all turtles in the population, there was considerable variation

among individual turtles. The odds ratios varied widely across animals (Table 5). Overall, these models do not show strong predictive power (McFadden's $\rho^2 = 0.04$ – 0.57 , median = 0.25). For example, individuals varied in their selection of forest. One group (7 females, 4 males) strongly avoided forest, never selecting it when nonforested areas were available (median odds ratio = 0.0001), while a larger group (20 females, 6 males) weakly avoided forest (median odds ratio = 0.76).

Turtles selected locations with raspberries from mid-July through mid-August, and high densities of green plants within 15 cm of the ground through much of the summer (Fig. 4). More equivocally, they may have selected for mushrooms late in the season and for both worms and slugs in spring and again late in summer.

Watershed scale

Six random areas that overlapped one or more turtle activity areas were dropped from analysis, leaving 26 random areas and 37 mean turtle activity areas in the model. The best eight models all included proportion of open water and a quadratic term for proportion of forest (Table 6). Seven of these models contained an additional variable (*depth*, *slug*, *worm*, *edge.coarse*, *strlen*, *edge.fine*, and *dist.upland*); the 95% confidence interval of the odds ratios for all of these variables included 1.0, suggesting unstable parameter estimates. Furthermore, the magnitude of odds ratios from several of these parameters (those for *depth*, *slug*, and perhaps *worm*) are biologically unrealistic. These results sug-

TABLE 4. Paired logistic regression models of within-activity area habitat selection by wood turtles supported by AIC_c (*n* = 37).

Model	AIC _c	Median			
		<i>dist.water</i>	<i>dist.lotic</i>	<i>forest</i>	<i>canopy</i>
<i>dist.water</i> + <i>forest</i> + <i>canopy</i>	34.1	-0.0315		-1.12	-0.0141
<i>dist.lotic</i> + <i>forest</i>	34.5		-0.0304	-1.40	
<i>dist.lotic</i> + <i>forest</i> + <i>canopy</i>	34.7		-0.0318	-1.28	-0.0138
<i>dist.water</i>	34.9	-0.0317			
<i>forest</i>	35.2			-1.39	
<i>dist.water</i> + <i>forest</i>	35.4	-0.0331		-1.29	
<i>forest</i> + <i>canopy</i>	35.4			-1.24	-0.0155

TABLE 5. Paired logistic regression model that best explains within-activity area selection across all wood turtles ($n = 37$).

Variable	Coefficient (median)	Odds ratio (median)	Odds ratio (interquartile range)
<i>dist.water</i>	-0.032	0.74 (10 m)	(0.47, 1.0)
<i>canopy</i>	-0.014	0.90 (10%)	(0.74, 1.0)
<i>forest</i>	-1.12	0.33	(0.0002, 0.90)

gest that the models selected as “best” by AIC are too rich for reliable estimates of parameters, given the sample size, although the direction of parameters is probably meaningful. We therefore chose the more robust $forest + forest^2 + open.water$ ($n = 63$; McFadden’s $\rho^2 = 0.75$) as the best predictive model (Table 7). Bootstrapping gave tighter 95% confidence intervals for the odds ratios than those from the original logistic regression; this indicates that parameter estimates are reliable. Again, habitat selection did not differ significantly between males and females.

Because the random areas were selected from the same distribution of distances from the river and streams as turtle activity areas, the strong effect of distance to running water was controlled for in this model. The model must therefore be interpreted in the context that turtle activity areas were located a median of 29 m from rivers and streams (the interquartile range was 11–72 m) and 95% were within 304 m from rivers and streams. The watershed model thus suggests that wood turtles select activity areas near streams and rivers, with a low proportion of open water, and a moderate (~10–50%) forest cover (Fig. 5). This model correctly classified 81% of the original 78 turtle activity areas and 92% of random areas, for an overall correct classification rate of 84%.

DISCUSSION

Logistic and paired logistic regression effectively modeled habitat selection of wood turtles. When

viewed at the watershed scale, turtles placed their activity areas near rivers and streams, in relatively dry areas with moderate forest cover. Within these activity areas, selection was for nonforested locations near water with low canopy cover. Thus, habitat selection differed between these two scales. When selecting activity areas within the landscape, partially forested areas are favored, but forest is selected against within-activity areas. This conflict in habitat selection likely reflects the trade-off between feeding and thermoregulation. Many important food items are found in deciduous and mixed forests (slugs, earthworms, and mushrooms, and raspberries in forest clearings and on forest edges). In contrast, high canopy cover of forests provides few basking sites. Turtles at our study site were observed basking during 35–80% of morning locations (between 0800 and 1200) from late April to mid-June. From mid-June on, they basked fairly consistently ~15–30% of the morning. Thus, turtles must balance selecting food-rich areas with available basking sites. The solution is to select forest edges and fragmented forests. Although alder swales were not significant habitat types in the models, they may play a role similar to forests: they have abundant slugs, earthworms, and raspberries (although not mushrooms); and also have high canopy closure.

The conflict between forest selection at the two scales suggests wood turtles select for forest edges, providing some support for Kaufmann’s (1992) suggestion that wood turtles are an “edge species,” even though “edge” as defined from NWI maps did not enter the activity area model and was not strongly supported by the watershed model. Our analysis suggests that, rather than generically selecting “edges,” the conflicting demands of thermoregulation and feeding often require turtles to travel back and forth across edges between forests and open areas such as meadows and fens.

The second conflict between activity area and watershed scales involves open water. Within the watershed, wood turtles selected areas near the river and

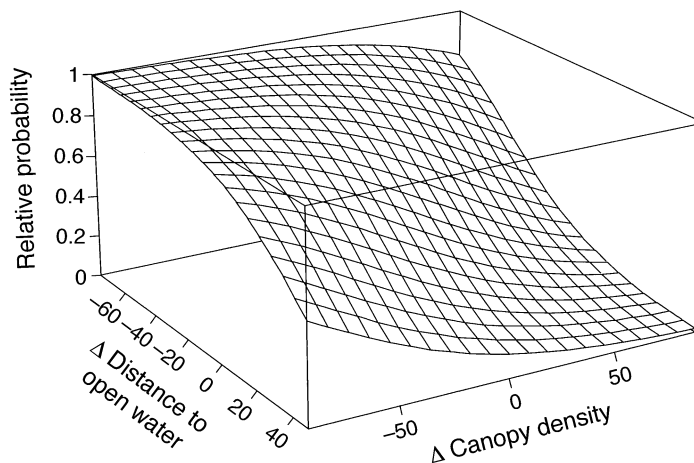


FIG. 3. Within-activity area model, showing the relative probability of occurrence of a turtle given the difference between values for canopy density and distance to open water between turtle locations and paired random locations. The odds ratio for Δ forest (not shown) is 0.33.

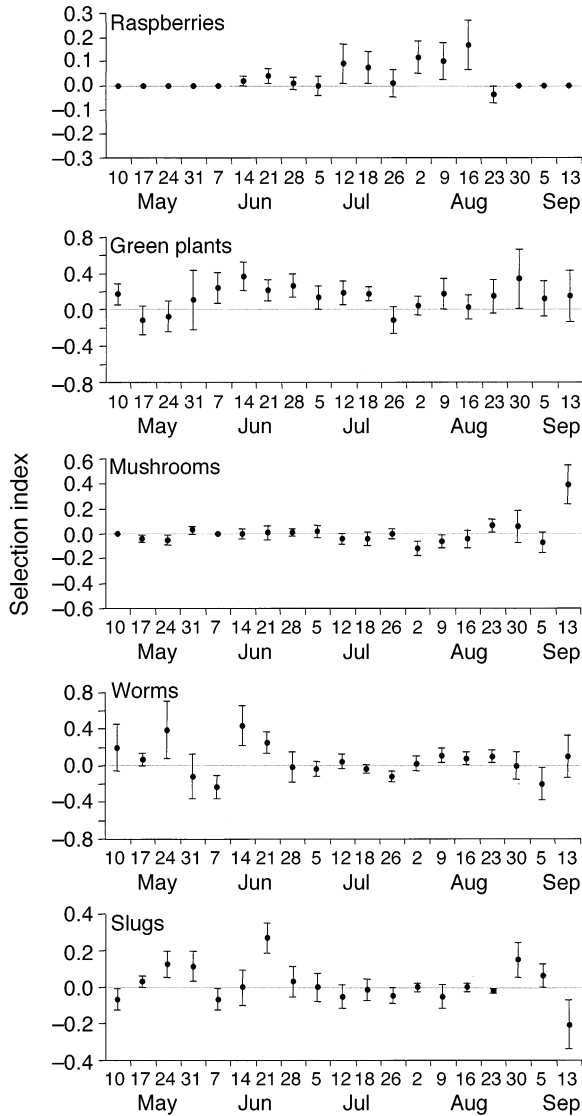


FIG. 4. Mean weekly seasonal selection (± 1 SE) of potential food items by wood turtles ($n = 11\text{--}36$ animals per week, median = 27).

streams with a relatively low proportion of open water deeper than 10 cm, while within activity areas, they selected locations near water. It is important to note that none of the GIS-based measures of water were significant in the watershed analysis (except for *strlen*, which was equivocally supported), therefore this effect is primarily driven by water bodies too small to be mapped, such as open pools in fens and wet meadows.

The watershed model shows strong predictive power, and is potentially useful for modeling wood turtle habitat across the landscape. The within-activity area model is not as effective as a predictive model. This is probably because wood turtles select different micro-habitat features depending upon their activity, e.g., open areas for basking, and forests for foraging. Presumably, stratification by activity would be required for a strongly predictive within-activity area model.

As noted by Kaufmann (1992), individual wood turtles displayed considerable variation in habitat use. For instance, five animals (four females, one male) spent >50% of their time in meadows from late June through mid-August, while 10 animals (eight females, two males) were never observed in meadows. Some of the strongest individual variation was observed in selection of raspberries. Seven females accounted for nearly 60% (38 of 66) of all observations of animals within 3 m of fruiting raspberries, while 15 of the 37 turtles were never found near raspberries. One possible explanation for this wide disparity in habitat selection is that, as long-lived food generalists, food resource selection has a strong learned component in wood turtles. Learned behavior, coupled with limited mobility in the terrestrial environment, may limit the ability of turtles to sample terrestrial habitats. This may result in idiosyncratic habitat selection by individuals with high site fidelity.

Paired logistic regression

Unlike pooled techniques such as standard logistic regression, paired logistic regression controls for both known and unknown confounding factors. Uncontrolled variables can result in incorrect null models of habitat selection. Rosenberg and McKelvey (1999) provide an example of the bias resulting from inappropriate null models in habitat selection studies of central place foragers. They suggest explicitly including the

TABLE 6. Logistic regression models of habitat selection at the watershed scale.

Model	AIC _c	ρ^2	constant	forest	forest ²	open. water	Additional variables
forest + forest ² + open.water + depth	25.62	0.83	-8.91	62.1	-89.6	-34.6	13.5 × depth
forest + forest ² + open.water + slug	29.11	0.79	-1.51	30.1	-47.0	-14.4	17.9 × slug
forest + forest ² + open.water + worm	29.21	0.79	-0.52	34.5	-59.5	-12.7	10.6 × worm
forest + forest ² + open.water	30.32	0.75	0.26	33.5	-52.2	-14.5	
forest + forest ² + open.water + edge.coarse	30.48	0.77	-1.59	37.5	-61.1	-15.0	0.020 × edge.coarse
forest + forest ² + open.water + strlen	30.73	0.77	-0.46	30.5	-48.2	-12.4	0.026 × strlen
forest + forest ² + open.water + edge.fine	31.37	0.76	-1.27	34.0	-54.2	-15.8	0.014 × edge.fine
forest + forest ² + open.water + dist.upland	32.24	0.75	1.54	27.1	-44.5	-13.9	-0.003 × dist.upland

TABLE 7. Logistic regression model that best predicts wood turtle habitat selection at the watershed scale.

Variable	Coefficient	SE	Odds ratio (10% change)	95% CI odds ratio (10% change)	Bootstrapped 95% CI odds ratio (10% change)
<i>constant</i>	0.26	1.68			
<i>forest</i>	33.46	12.22			
<i>forest</i> ²	-52.23	17.67	0.15†	(0.062, 0.44)†	(0.096, 0.41)†
<i>open.water</i>	-14.54	4.60	0.23	(0.095, 0.58)	(0.16, 0.52)

† These values are for *forest* and *forest*² combined.

distance to the central place (e.g., nest site) as a covariate. However, this approach requires sufficient knowledge of both species biology and an individual animal's habits to locate the central place. Although central place foraging is a well-understood phenomenon, seasonal, diurnal, and weather-related factors affect animal behavior in ways that researchers often do not fully understand. For instance, we often observed wood turtles feeding on slugs on rainy days, when slugs were out in the open. Thus, weather confounds wood turtle selection of slugs. Such relationships can be complex. The variable *dist.water*, which was significant in the overall within-activity area selection model, measures the distance to any open water >10 cm deep, including ephemeral ponds and puddles such as bog pools or flooded meadows. Such water sources vary seasonally and in response to recent weather. Explicitly controlling for all such confounding factors requires understanding them, measuring them, and increasing sample sizes to avoid loss of statistical power. A paired approach, such as paired logistic regression, controls for temporal (and to some extent spatial) confounding factors.

An important assumption of paired habitat selection models is that the random points adequately represent "available" habitat for each animal. Analysis is therefore sensitive to the method used to select random

points: distances between animal locations and random points must be based on knowledge of the species' biology and observed movement patterns, and the distribution of random points should match those of animal movements between successive observations. Estimates of available habitat can be improved by sampling multiple random locations for each animal location. A drawback to the paired logistic approach is that results can be more difficult to interpret than those of standard logistic regressions, because paired logistic regression is interpreted in terms of relative differences in habitat variables rather than absolute terms.

As James and McCulloch (1990:150–152) point out, habitat selection models based on the difference in multivariate means between used and available habitat will fail to find selection when the mean habitat values at used locations coincide with the mean at available locations, even if animals are strongly selecting habitat. This critique applies to any use of discriminant analysis, multiple regression, or logistic regression to model used vs. available habitat, because these techniques do not test for differences in variance. This problem can be mitigated by either choosing multiple study sites that vary along the first principal component of habitat variables (James and McCulloch 1990), or by modeling selection separately for each animal when there is wide

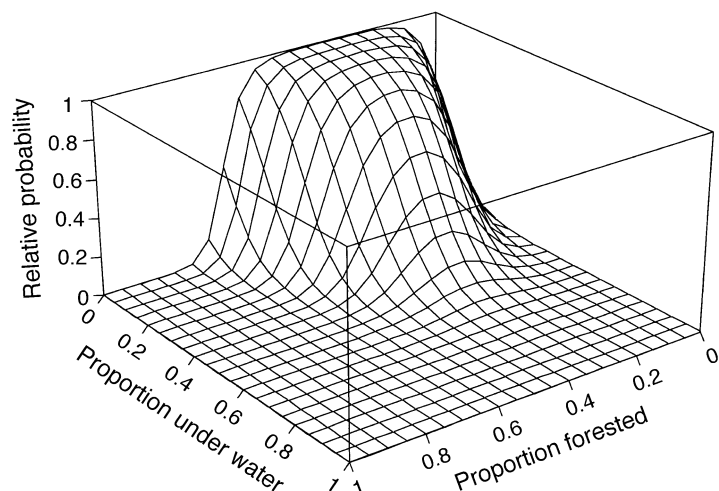


FIG. 5. Watershed model, showing the relative probability of occurrence of a turtle activity area with respect to the proportion forested and proportion of open water. Ninety-five percent of activity areas were located within 304 m of rivers and streams (median = 29 m).

variation in habitat availability among animals, as we have done in the within-activity area model.

Paired logistic regression shows promise for modeling habitat selection of animals that do not have well-defined home ranges or do not use their territories uniformly. Examples include animals with low mobility relative to home range size, such as the wood turtle; nomadic species, such as opossums (*Didelphis virginiana*; Hunsaker 1977); nomadic life-stages, such as dispersing juvenile birds (e.g., Ovenbirds; *Seiurus aurocapillus*; D. I. King, *personal comment*); and migratory animals during migration.

Conservation implications

Wood turtle populations have declined or been extirpated throughout their range (Harding and Bloomer 1979, Klemens 1989, Ernst and McBreen 1991, Harding 1991, Garber and Burger 1995; Harding et al., *in press*). They face a number of threats, including degradation of riparian habitat. A better understanding of habitat selection would help focus conservation efforts.

While the wood turtle's primary habitat, rivers, are protected to some extent in many states (e.g., in Maine, Compton 1999), the extensive movements of northern wood turtles (Quinn and Tate 1991, Foscarini and Brooks 1997) may make protection of large riparian areas necessary in order to protect populations. Refinement of our understanding of wood turtle habitat will allow them to be more effectively included in multispecies and ecosystem-based conservation efforts, and support surveys that are more efficient. If the within-watershed habitat selection model presented here is supported by studies of other populations, it may be applied in conjunction with a model of nest site selection (Buech et al. 1997) to predict likely wood turtle habitat using remote sensing data across broad areas.

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LITERATURE CITED

- Arthur, S. M., B. F. J. Manly, L. L. McDonald, and G. W. Garner. 1996. Assessing habitat selection with availability changes. *Ecology* **77**:215–227.
- Block, W. M., M. L. Morrison, and P. E. Scott. 1998. Development and evaluation of habitat models for herpetofauna and small mammals. *Forest Science* **44**:430–437.
- Breslow, N. E., and N. E. Day. 1980. Statistical methods in cancer research. Volume I: the analysis of case-control studies. International Agency for Research on Cancer, Lyon, France.
- Buech, R. R., L. G. Hansen, and M. D. Nelson. 1997. Identification of wood turtle nesting areas for protection and management. Pages 383–391 in J. Van Abbema, editor. Conservation, restoration, and management of tortoises and turtles—an international conference. July 11–16, 1993. State University of New York, Purchase. New York Turtle and Tortoise Society, New York, New York, USA.
- Burnham, K., and D. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.
- Cagle, F. R. 1939. A system of marking turtles for future identification. *Copeia* **1939**:170–173.
- Compton, B. W. 1999. Ecology and conservation of the wood turtle (*Clemmys insculpta*) in Maine. Thesis. University of Maine, Orono, Maine, USA.
- Efron, B., and G. Gong. 1983. A leisurely look at the bootstrap, the jackknife, and cross-validation. *American Statistician* **37**:36–48.
- Ernst, C. H., J. E. Lovich, and R. W. Barbour. 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington, D.C., USA.
- Ernst, C. H., and J. F. McBreen. 1991. Wood turtle. *Clemmys insculpta* (LeConte). Pages 455–457 in K. Terwilliger, editor. Virginia's endangered species. McDonald and Woodward, Blacksburg, Virginia, USA.
- Foscarini, D. A., and R. J. Brooks. 1997. A proposal to standardize data collection and implications for management of the wood turtle, *Clemmys insculpta*, and other freshwater turtles in Ontario, Canada. Pages 203–209 in J. Van Abbema, editor. Conservation, restoration, and management of tortoises and turtles—an international conference. July 11–16, 1993. State University of New York, Purchase. New York Turtle and Tortoise Society, New York, New York, USA.
- Garber, S. D., and J. Burger. 1995. A 20-year study documenting the relationship between turtle decline and human recreation. *Ecological Applications* **5**:1151–1162.
- Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. Pages 111–164 in L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, New York, USA.
- Harding, J. H. 1991. A twenty-year wood turtle study in Michigan: implications for conservation. Pages 31–35 in K. R. Beaman, F. Caporaso, S. McKeown, and M. D. Graff, editors. Proceedings of the first international symposium on turtles and tortoises: conservation and captive husbandry. Chapman University, Orange, California, USA.
- Harding, J. H., J. L. Behler, R. J. Brooks, and M. W. Klemens. *In press*. *Clemmys insculpta* (LeConte, 1830) wood turtle. In P. C. H. Pritchard and A. G. J. Rhodin, editors. The conservation biology of freshwater turtles. Chelonian research monographs, Number 3. Lunenburg, Massachusetts, USA.
- Harding, J. H., and T. J. Bloomer. 1979. The wood turtle, *Clemmys insculpta* . . . a natural history. *HERP, Bulletin of the New York Herpetological Society* **15**:9–26.
- Hjermann, D. Ø. 2000. Analyzing habitat selection in animals without well-defined home ranges. *Ecology* **81**:1462–1468.
- Hosmer, D. W., and S. Lemeshow. 1989. Applied logistic regression. Wiley, New York, New York, USA.
- Hunsaker, D. I. 1977. Ecology of new world marsupials. Pages 95–156 in D. I. Hunsaker, editor. The biology of marsupials. Academic Press, New York, New York, USA.

- James, F. C., and C. E. McCulloch. 1990. Multivariate analysis in ecology and systematics: panacea or Pandora's box? *Annual Review of Ecology and Systematics* **21**:129–166.
- Kaufmann, J. H. 1992. Habitat use by wood turtles in central Pennsylvania. *Journal of Herpetology* **26**:315–321.
- Klemens, M. W. 1989. The methodology of conservation. Pages 1–4 in I. R. Swingland and M. W. Klemens, editors. *The conservation biology of tortoises. Occasional papers of the IUCN/SSC. Volume 5.* Gland, Switzerland.
- McFadden, D. 1974. Conditional logit analysis of qualitative choice behavior. Pages 105–142 in P. Zarembka, editor. *Frontiers in econometrics.* Academic Press, New York, New York, USA.
- Mladenoff, D. J., T. A. Sickley, R. G. Haight, and A. P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. *Conservation Biology* **9**:279–294.
- North, M. P., and J. H. Reynolds. 1996. Microhabitat analysis using radiotelemetry locations and polytomous logistic regression. *Journal of Wildlife Management* **60**:639–653.
- Ormsbee, P. C., and W. C. McComb. 1998. Selection of day roosts by female long-legged myotis in the central Oregon Cascade Range. *Journal of Wildlife Management* **62**:596–603.
- Quinn, N. W. S., and D. P. Tate. 1991. Seasonal movements and habitat of wood turtles (*Clemmys insculpta*) in Algonquin Park, Canada. *Journal of Herpetology* **25**:217–220.
- Rosenberg, D. K., and K. S. McKelvey. 1999. Estimation of habitat selection for central-place foraging animals. *Journal of Wildlife Management* **63**:1028–1038.
- Sherburne, S. S., and J. A. Bissonette. 1994. Marten subnivean access point use: response to subnivean prey levels. *Journal of Wildlife Management* **58**:400–405.