Herpetological Conservation and Biology 13(1):257–272.
Submitted: 11 January 2017; Accepted: 24 February 2018; Published 30 April 2018.

Bog Turtle (*Glyptemys muhlenbergii*) Dispersal Corridors and Conservation in New York, USA

***Kristen Bell Travis*[1,4], *Ingrid Haeckel*[1,2], *Gretchen Stevens*[1], *Jason Tesauro*[3], and *Erik Kiviat*[1]**

[1]*Hudsonia Ltd., P.O. Box 5000, Annandale, New York 12504, USA*
[2]*Department of Natural Resources, Cornell University, and New York State Department of Environmental Conservation, 21 South Putt Corners Road, New Paltz, New York 12561, USA*
[3]*Jason Tesauro Consulting LLC, P.O. Box 908, Millbrook, New York 12545, USA*
[4]*Corresponding author, e-mail: bell@bard.edu*

Abstract.—**Identifying potential corridors for local movements and dispersal is an important but often difficult part of conservation planning for rare species. New spatial analysis tools facilitate mapping of potential movement pathways, provided sufficient detail is known about the habitat use, dispersal behavior, and threats to a species, and appropriately specific regional habitat and landscape feature data are available. Using previously collected detailed habitat data (mapped remotely and field-verified), we identified potential core habitat for endangered Bog Turtles in a 590-km^2 area in their northern range. We created a landscape resistance map based on habitats, roads, water bodies, and slope, and then calculated least-cost corridors for maintaining both population complex and regional network connectivity, identified points of vulnerability in these corridors, ascertained the relative importance of each core habitat and corridor for maintaining connectivity across the network, and mapped likely road-crossing sites. The model results were supported by records of Bog Turtles found away from core habitats. Our results can be used directly for prioritizing sites for acquisition and management, reviewing land development proposals, educating landowners, locating road signs or crossing aids, and other conservation measures. The results are particularly relevant as this species responds to both land use alterations and climate change.**

Key Words.—connectivity; fen; habitat; home range; landscape resistance; least-cost model; population complex; pinch point; wetland

Introduction

Bog Turtles (*Glyptemys muhlenbergii*) are among the most critically endangered turtles globally, in large part because of the loss, fragmentation, and degradation of their core habitats, groundwater-fed fens and wet meadows (Herman and Tryon 1997; Turtle Conservation Coalition 2011). Changes in land use, particularly away from pasture-based agriculture and toward residential development, continue to degrade and isolate Bog Turtle wetlands (Tesauro and Ehrenfeld 2007; Kiviat et al. 2010). Climate change also threatens to further alter the sensitive groundwater hydrology and plant communities that characterize these habitats (Duval and Waddington 2012). There has been a substantial effort to locate and, in some cases, monitor populations of Bog Turtles, and to manage selected habitats, but little is known about turtle movement between core habitats or away from deteriorating wetlands.

Mark-recapture and radio tracking studies in both the disjunct northern and southern populations indicate that Bog Turtles spend most of their time in fairly small wetland areas that include nesting, foraging, and overwintering habitat (U.S. Fish and Wildlife Service [USFWS] 2001). Mean home range reported in the literature ranges from 0.06 ha to 1.33 ha (although methods for estimating home range vary; Gemmell 1994; Carter et al. 1999; Morrow et al. 2001; Shoemaker 2011; Sirois et al. 2014; and sources in Table 1). Most recorded movements are < 350 m and fall within the core wetland complex. However, occasional dispersal events (up to 4 km) have also been recorded, either along stream corridors or far into upland habitats (Table 1). Maximum movement distances tend to be greater in the southern population (North Carolina, Tennessee, Virginia, USA) than in the northern population (New York, Massachusetts, Pennsylvania, Delaware, USA; Table 1). Henceforth we refer to these movement events as dispersal, although with this we include regular travel between distant parts of a multi-wetland home range (as in Feaga 2010) as well as permanent relocations. Recent genetic analysis of Bog Turtles in seven clustered and four more distant sites in southeastern New York found that populations within 1–2 km of each other experience a regular exchange of individuals and are effectively one demographic unit, or population complex. Because Bog Turtles are long-lived (approximately 40 y; USFWS 2001), genetic connectivity is achieved with an estimated rate of only 1% of each population dispersing each year (Shoemaker and Gibbs 2013). This

Table 1. Maximum dispersal distances traveled by Bog Turtles (*Glyptemys muhlenbergii*) reported in the literature, including number of turtles followed, movement description, study duration and location, and source. If known, tracking method was included (MR: mark-recapture, RT: radio tracking). Maximum movements within a core wetland, not included here, ranged from 59–335 m (Arndt 1977; Ernst 1977; Chase et al. 1989; Lovich et al. 1992; Carter et al. 2000; Whitlock 2002). State abbreviations are NC = North Carolina, NY = New York, PA = Pennsylvania, TN = Tennessee, and VA = Virginia.

Maximum distance, m	Turtles followed; Tracking method	Type of movement	Study duration	U.S. State	Source
400	1 MR	Displaced turtle returning to home wetland, in one day	Not stated	PA	Ernst 1977
530	35 RT	Three turtles moved to neighboring wetland and back for part of season (1 y only)	2 y	VA	Carter et al. 2000
556	11	Apparent dispersal – crossed powerline, railroad track, and residential area	1 y	NC	Pittman and Dorcas 2009
585	53 RT	Largest movement not within stream corridor; crossed road, found dead in residential area	2 y	VA	Feaga 2010
750	Not stated; RT	Overland migration	4 y	NY	Eckler et al. 1990
800–1,600	15 RT	Dispersal among wetlands within one valley, mainly across farmland	15 y	TN	Michael Ogle, Zoo Knoxville, pers. comm.
956	53 RT	Linear home range along a string of six wetlands (0.7–8.5 km apart)	2 y	VA	Feaga 2010
1,500	10 pairs of first-degree relatives	Genetic analysis showed that a mother and daughter were nesting in separate wetlands about 1.5 km apart	5 y (single most recent nest location used)	NY	Macey 2015
2,700 (MR), then RT an additional 375	35 MR RT	Apparent dispersal across upland habitats	Found 2.7 km from its location in previous year	VA	Carter et al. 2000
2,700 (inferred)	1	Apparent dispersal - juvenile turtle found in completely forested, previously unoccupied wetland, 2.7 km from nearest known occupied wetland	2 y	VA	Feaga et al. 2012
3,600 (inferred); 800 (RT)	1	Found in stream 3.6 km from nearest appropriate habitat, then tracked downstream until lost	Single incident	NC	Somers et al. 2007
ca. 4,000	15 RT	Dispersal across mountain, killed on road	15 y	TN	Michael Ogle, Zoo Knoxville, pers. comm.

figure is consistent with the paucity of evidence of such dispersal through radio tracking or recapture of marked turtles. Additionally, there is evidence of some genetic exchange across longer distances (at least 10 km), most likely via intermediate populations that are either undiscovered or no longer extant (Shoemaker and Gibbs 2013). Even with low rates of dispersal and fairly small populations, such regional networks can theoretically maintain genetic diversity and demographic stability in our study region (Shoemaker and Gibbs 2013). This conclusion is strengthened by demographic modeling based on 10 y of mark-recapture data, indicating that Bog Turtle populations with as few as 20 females have a 95% chance of persisting > 100 y (Shoemaker et al. 2013). It also highlights the critical importance of identifying and protecting potential (occupied or unoccupied) core habitats and connecting corridors to ensure that successful dispersal can occur.

Conservation plans for threatened animals increasingly rely on analysis of the species-specific connectivity among their core habitats. Protected corridors ideally allow gene flow among populations (preventing harmful genetic drift or inbreeding depression), allow for successful escape from degraded habitats and colonization of newly suitable habitats, and minimize mortality of dispersing individuals. Landscape connectivity (the degree to which the landscape impedes or facilitates movements among source patches) is a concept that takes into account the structural components of the landscape as well as the mobility of one or more focal species (Adriaensen et al. 2003). Least-cost modeling is a widely used approach to predict the best connecting corridors among high-quality habitats for a single species, multiple species, or ecological integrity in general (Beier et al. 2008, 2011). For single species analysis, the landscape is represented by a raster grid, with each cell given an estimated numeric resistance value that reflects the cost or difficulty (usually due to avoidance and/or mortality risk) associated with crossing a landscape feature. The cost of crossing each cell is its length in actual (Euclidean) distance multiplied by its resistance value. The resulting Cost-Weighted Distance (CWD) is longer for paths crossing high-resistance areas and shorter for paths crossing low-resistance areas. Least-Cost Paths (LCPs; single lines) and Least-Cost Corridors (LCCs; raster grids) can be calculated among all or a subset of neighboring core habitats using this method (Washington Wildlife Habitat Connectivity Working Group [WHCWG] 2010). Circuit theory-based analyses for modeling habitat connectivity provide an alternative and often complementary approach to CWD models (McRae et al. 2008; McClure et al. 2016). Running a theoretical electrical current among connected core habitats shows areas of highest current density (pinch points) in the LCCs: places where dispersers have a high probability of passing, and which are therefore disproportionately critical to connectivity (Pelletier et al. 2014; Lechner et al. 2017). Core habitats and least-cost corridors can also be assigned relative values for their roles in mediating flow between all other cores, called centrality (a higher value means greater importance for overall network connectivity; Beier et al. 2011).

As with any model, meaningful least-cost model results are obtained only when ecologically accurate inputs and parameters are used. Constructing a resistance layer specific to the species is important (Adriaensen et al. 2003), although highly generalized models including only developed, disturbed, and natural areas may predict movement frequencies for multiple species (Koen et al. 2014). Ideally, resistance values, corridor length, and corridor width should be determined based on empirical habitat association, movement, or genetic data rather than expert opinion (Sawyer et al. 2011; Zeller et al. 2012). Existing descriptions and quantitative analysis of Bog Turtle habitat use are almost entirely based on local movements within their core wetlands and do not apply to dispersal movements (but see the few exceptions in Table 1). Thus, we have little empirical evidence for assigning resistance values.

Nevertheless, we have an in-depth understanding of core habitat features and suitability based on decades of Bog Turtle work (e.g., Kiviat 1978; Tesauro and Ehrenfeld 2007; Kiviat et al. 2010), and uniquely detailed landscape feature data (for identification of core and matrix habitat; Hudsonia, unpubl. data) for a New York study area that supports a critical part of the northern population. These resources, along with recent genetic analysis of a nearby population (to inform corridor length maxima; Shoemaker and Gibbs 2013), provide sufficient ecological detail to predict best corridors and important places to maintain habitat connectivity for Bog Turtles in this region where it is so urgently needed. Our goals were to analyze the connectivity of our study landscape for Bog Turtles by predicting least-cost movement corridors, identifying areas within those corridors most critical for maintaining connectivity, and ranking core habitats and LCPs for importance in maintaining the network.

Materials and Methods

Study area.—Our study area, approximately 590 km^2 in New York, USA, supports one of the largest concentrations of potential Bog Turtle habitats and known (historical and extant) Bog Turtle populations in the northern population. Because of the threat of illegal collecting, we have omitted precise locations from this paper. Fine-scale habitat data are available for this area, because all ecologically significant habitats were identified and mapped between 2004 and 2009 (Hudsonia, unpubl. data). These detailed habitat maps (scale 1:10,000) have been extensively field-checked, and make distinctions among wetland types important for Bog Turtles such as fen and calcareous wet meadow. They also provide more comprehensive wetlands and small streams data than sources such as the National Wetlands Inventory, National Land Cover Dataset, and National Hydrography Dataset. The landscape is one of roughly north-south trending ridges and valleys, with predominantly acidic bedrock forming the ridges and calcareous bedrock underlying the valleys. Surficial material is largely glacial till, with some areas of recent alluvium, kame (mounds of glacially-deposited sand and gravel), and outwash. Upland forest, primarily deciduous, makes up about 43% of the study area; 29% is upland meadow (managed and unmanaged, including farm fields); approximately 3% is nonforested wetland;

and 5% is forested wetland. Historically, this was a dairy-farming region. Current land uses are primarily agricultural and residential, with several small villages and hamlets but no large human population centers; most of the land is privately owned. Although it is scattered, residential development is rapidly fragmenting the significant areas of open space present.

Core habitats.—In this part of New York, Bog Turtles almost exclusively inhabit groundwater-fed, calcareous fen and wet meadow habitats (see descriptions of rich sloping fen, rich graminoid fen, rich shrub fen, and medium fen in Edinger et al. 2014) and adjacent shrub swamp, Red Maple (*Acer rubrum*) swamp, or deeper marsh areas. The highest-quality habitats are usually maintained in an open state by the inherent nutrient limitation of calcareous fens (Boyer and Wheeler 1989) or by habitat management practices including prescribed grazing or periodic clearing of shrubs and trees. Such high-quality habitats are characterized by soft, saturated soils, numerous small rivulets, and often subsurface flow. The vegetation is diverse, primarily herbaceous, and short-statured, and includes hummocks of sedge (*Carex*) or peat moss (*Sphagnum*). These wetlands are located within larger wetland complexes associated with headwater streams (Kiviat 1978; USFWS 2001). Bog Turtles generally overwinter in soft soils or watery channels beneath roots of woody vegetation, nest on top of hummocks in the wetland, and spend most of the active season within the core wetland habitat and adjacent wetland areas, rarely traveling more than 300–400 m from their hibernacula (Ernst et al. 1989; USFWS 2001; Whitlock 2002).

To identify potential core habitats in our study area, we referred to New York Natural Heritage Program records (acquired in 2013) of Bog Turtle populations and occurrences, ecologically significant habitat data (Hudsonia, unpubl. data), and field notes. We included fens with known or historical populations, as well as fens that seemed to offer adequate habitat despite no known Bog Turtle presence; many of the latter have not been surveyed for Bog Turtles. We only included fens that were part of a wetland complex of at least 2 ha. Although Bog Turtles in New York occur in wetlands smaller than 2 ha (Meyers and Gibbs 2013), we limited our analysis to larger wetlands for several reasons. To create maps most useful for practical conservation planning, we decided to prioritize those Bog Turtle habitats and populations most likely to persist in the long term. Larger wetlands are more likely to contain the habitat variation necessary to provide foraging, nesting, and overwintering habitat; may be more resistant to vegetation changes resulting from nutrient loading or other factors; and have the potential to support larger populations of Bog Turtles (Meyers and Gibbs 2013) that are less vulnerable to harmful effects of genetic drift (Shoemaker and Gibbs 2013). Each mapped core habitat included one or more of these fens plus all contiguous wetlands within 300 m of the fen perimeter. Based on literature records of Bog Turtle movements (Table 1), this distance is likely to encompass most (non-dispersal) movements of a population.

Resistance values.—Resistance values of landscape features generally reflect two things: the physical difficulty a turtle would have moving through that feature type and the mortality risk associated with the feature (in other words, the difficulty of emerging alive or without serious injury). One might assign a river high resistance for physical difficulty (and probable avoidance), and a highway high resistance for mortality risk, even if it would be easy to walk across. We used the One-stage Expert Approach (Zeller et al. 2012) to assign resistance values: discussion and consensus among authors Kiviat, Stevens, and Tesauro. In other studies, LCC models were quite robust with respect to the scale of resistance values within given ranks (Compton et al. 2007; Beier et al. 2009). Therefore, most discussion centered on rank and weight of each landscape feature. We used a resistance value scale ranging from 1 (core habitat) to 1,000 (divided highway and railroad), a scale used by others performing similar analyses (WHCWG 2010). After assigning resistance values to each feature, we determined the weight, or relative importance, of each feature for the model. Many of the landscape features did not overlap (e.g., wetland habitats, upland habitats, cropland), but some features did (e.g., riparian corridors, steep slopes, and some roads overlapped mapped habitats). In places where landscape features of differing resistance values overlapped, we used only the feature with the highest weight. In most cases, we gave higher weight to features with higher resistance, but there were a few exceptions: we assigned riparian corridors lower resistance but higher weight than upland habitats, so that near a stream, the riparian corridor resistance applied instead of the upland habitat resistance (Table 2). A great deal of the validity of the model rests on the assignment of resistance and weight, so we included a more detailed discussion in Appendix A. This appendix also contains more detail on the sources and treatment of landscape data.

Constructing the resistance raster.—We created a final vector (polygon) file consisting of all landscape feature data by successively layering features in increasing order of weight (Update tool in ArcMap). Therefore, areas with overlapping features only displayed the highest-weighted feature in the final file. We converted the final vector file to raster format, using resistance values for cell assignment, with a cell

Table 2. Values used to construct the resistance map for least-cost model connecting core Bog Turtle (*Glyptemys muhlenbergii*) habitats in New York. Landscape features; notes on data sources; resistance values representing avoidance and/or the difficulty of moving through or surviving a crossing of each landscape feature; rationale; and weight for each feature. Where landscape features of differing resistance overlapped on the map, only the resistance value with the higher weight was used. Notes on data sources: (1) NYS Streets. GIS streets data copyrighted by HERE North America LLC and licensed to the New York State Office of Information Technology Services. 2013. Available from NYS GIS Clearinghouse, gis.ny.gov [Accessed 2 March 2015]; (2) NYS Railroad Lines. New York State Department of Transportation. 2005. Available from NYS GIS Clearinghouse, gis.ny.gov [Accessed 2 March 2015]; (3) Traffic data for selected roads available from Dutchess County, http://www.dutchessny.gov/PlnRoadCnts/ [Accessed 2 March 2015]; (4) Digitized or classified for this project by authors; (5) Ecologically significant habitats data, Hudsonia. 2004–2009. Available on request from www.hudsonia.org; (6) Streams classifications from National Hydrography Dataset. Available from http://nhd.usgs.gov/ [Accessed 22 October 2015]; (7) Steep Slopes grid produced from 10 m Digital Elevation Model published by US Geological Survey. 2003. Part of Dutchess County Infrastructure dataset. Available from NYS GIS Clearinghouse, gis.ny.gov [Accessed 2 March 2015].

Landscape Feature	Notes	Resistance	Rationale	Weight
Divided highway (each lane 18 m wide)	1	1,000	Mortality risk associated with vehicles, entrapment.	10
Railroad (18 m wide)	2	1,000		10
Highway with > 3,000 cars/day (18 m wide)	1,3	800		9
Village/hamlet center	4	800	Avoidance; mortality risk from vehicles, entrapment, collecting.	9
Large streams, open water, ponds, lakes	5	800	Avoidance of deep water, strong current.	9
Other perennial streams	5,6	700		8
Road or highway with 1,000-3,000 cars/day (12 m wide)	1,3	600	Mortality risk from vehicles.	7
Steep slopes (> 25%)	7	600	Inability to climb rock ledges, which are common at this slope.	7
Road with < 1,000 cars/day or no traffic data (9 m wide)	1,3	400		6
Mapped developed areas, including buildings, driveways, paved or gravel areas, lawns	5	300	Mortality risk associated with vehicles, mowing, entrapment, collecting.	4
Mapped cultural areas, including large lawns, golf courses	5	230		1
Driveway, unnamed road, small or private road (6 m wide)	1	210		5
Cropland, hayfield	4,5	170	Mortality risk associated with mowing and farm machinery.	1
Riparian corridors (14 m on each side of streams) through cultural areas, cropland, and hayfield	4,5	130		3
Upland habitats (forest, shrubland, oldfield, pasture, oak-heath barren, cool ravine, waste ground)	5	90	Ability to travel through most undisturbed uplands and wetlands; slight preference for wetlands and riparian corridors.	1
Intermittent streams and their riparian corridors, and riparian corridors along perennial streams (14 m on each side of streams), excluding wetlands	4,5	50		2
Wetland habitats (non-core fens, wet meadows, marsh, swamps, etc.)	5	30		1
Core fen (and surrounding contiguous wetlands within 300 m)	4,5	1	Preferred habitat – easiest to travel through.	11

(grain) size of 4 m, which was the largest cell size that preserved our narrowest linear features without diagonal gaps. This cell size is smaller than those generally used for least cost analyses, but we chose it to improve the accuracy of our results. In an analysis of resistance surface error, enlarging grain size resulted in the largest errors (compared to changing resistance values, changing the number of categories, or misclassified edges between categories; Simpkins et al. 2017).

Data analysis.—We conducted all analysis in Esri ArcMap 10.3.0 with Linkage Mapper Connectivity Analysis Software 1.0.9 toolbox add-ins (McRae, B.H., and D.M. Kavanagh. 2011. The Nature

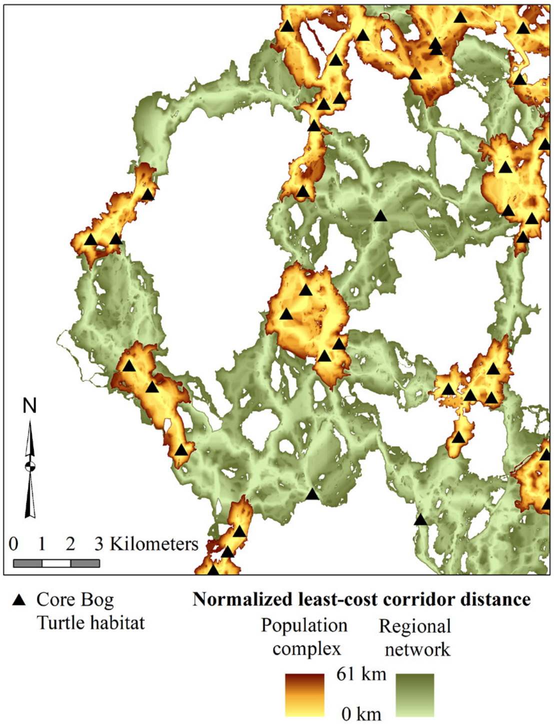


Figure 1. Normalized least-cost corridors among potential Bog Turtle (*Glyptemys muhlenbergii*) core habitats within maximum straight-line Euclidean distances of 2 km (population complex) and 10 km (regional network) in part of the New York study area (white). We instructed the model to connect each core to its three nearest neighbors and then to connect neighboring constellations. Corridor width was limited to 61 km cost-weighted distance. Exact locations protected due to the threat of poaching.

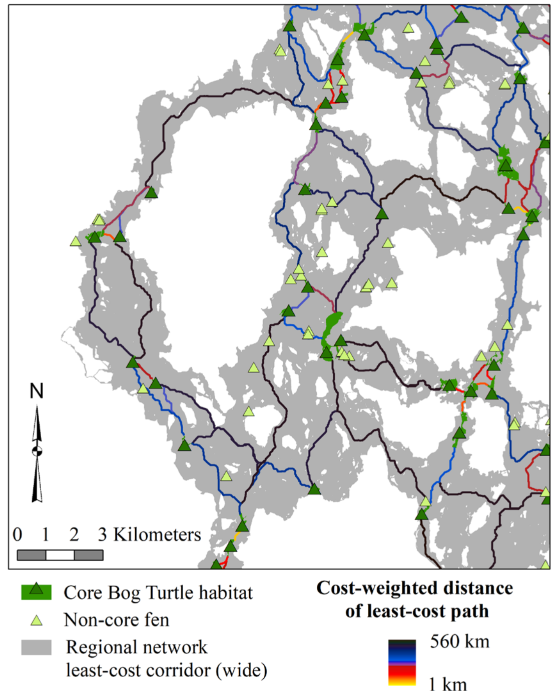


Figure 2. Cost-weighted distances of least-cost paths among potential Bog Turtle (*Glyptemys muhlenbergii*) core habitats within a maximum straight-line Euclidean distance of 10 km (regional network) in part of the New York study area. We instructed the model to connect each core to its three nearest neighbors and then to connect neighboring constellations. Corridor width was limited to 61 km cost-weighted distance. Exact locations protected due to the threat of poaching.

Conservancy. Available from http://www.circuitscape.org/linkagemapper [Accessed 19 May 2015]), including the Pinch Point Mapper and Centrality Mapper tools (McRae, B.H. 2012. The Nature Conservancy. Available from http://www.circuitscape.org/linkagemapper [Accessed 19 May 2015]). We used Linkage Mapper to identify neighboring core areas and construct a straight-line network among them. We then ran the model twice, limiting the straight-line Euclidean distances to maxima of 2 km and 10 km so that least-cost paths and corridors would only be calculated between pairs of core wetlands less than 2 km (population complex) and 10 km (regional network) apart. Within those parameters, we set each model to connect each core to its three nearest neighbors (measured in either cost-weighted or Euclidean distance), and then to connect neighboring constellations (discrete clusters of neighboring core areas). The resulting two linkage maps were rasters of the entire study area. To create linkage zones of widths relevant for conservation planning, we truncated corridors by maximum cost-weighted distances of 60.96 km (200,000 ft, approximately 3% of total calculated CWD; wide) and 7.62 km (25,000 ft, approximately 0.4%; narrow). Although no methods for determining optimal corridor width have been developed (Beier et al. 2008, Sawyer et al. 2011), these maxima were within the range used by other studies (e.g., WHCWG 2010). Resulting widths were generally 500–2,500 m Euclidean distance (wide) and 50–400 m (narrow). We chose the wide corridor to reflect uncertainty in resistance values and other parameters, and the narrow corridor for usefulness in setting land protection priorities. To characterize the modeled corridors, we compared the proportion area of different landscape cover types between corridors and the entire study area.

Using the Linkage Mapper results, we ran the Pinch Point Mapper tool to determine the most restricted (or vulnerable) parts of those connecting corridors, for both the population complex and regional network models. We set the cost-weighted distance to 7.6 km (to correspond with the narrower Linkage Mapper corridor width) and calculated adjacent pair pinch points. This method runs a hypothetical electrical current between all pairs of nodes (core areas), with one node connected to ground and the other to a one ampere current source. The result is a raster of current density with the value of each cell summed for all pairwise iterations. To perform

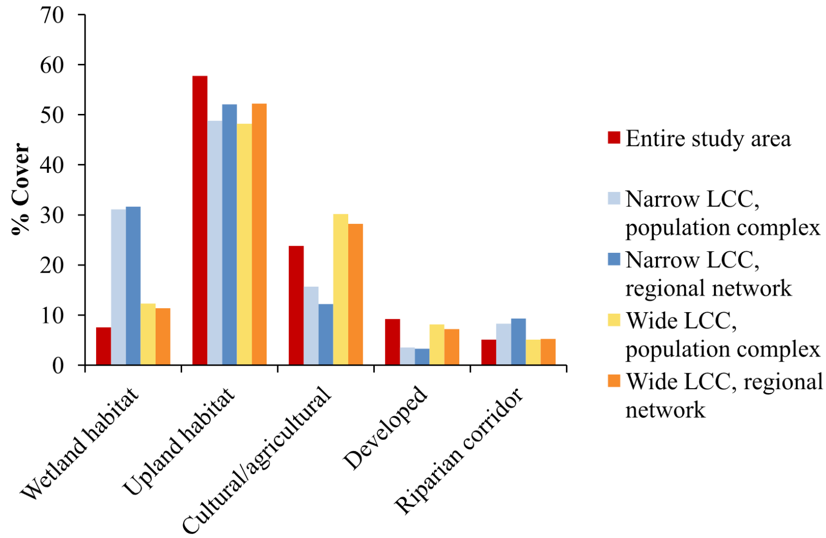


Figure 3. Percentage cover of select landscape features within two modeled least-cost corridors (population complex and regional network; see Fig. 1) connecting core Bog Turtle (*Glyptemys muhlenbergii*) habitats in the New York study area, and within the study area as a whole (590 km^2). Narrow corridors (maximum cost-weighted distance [CWD] width of 7.6 km) were generally 50–400 m and wide corridors (maximum CWD of 61 km) were generally 500–2,500 m in width.

this function, Pinch Point Mapper calls on a separate program, Circuitscape 4.0 (McRae, B.H., V.B. Shah, and T.K. Mohapatra. 2013. The Nature Conservancy. Available from http://www.circuitscape.org [Accessed 19 May 2015]). We defined current values > 0.082 (90th percentile) as pinch points. We used the Centrality Mapper tool to assign relative values to each core and least-cost path, with higher values representing greater importance to overall connectivity of the network. Where least-cost paths crossed roads (excluding driveways), we mapped the intersections. More detail on settings, parameters, and analysis is in Appendix B.

Results

We identified 62 potential Bog Turtle core wetlands in our study area, ranging in area from 2–53 ha. To protect Bog Turtles from collectors, our maps show only part of the study area and omit identifying features (study results have been shared with U.S. Fish and Wildlife Service, New York State Department of Environmental Conservation, other agencies and organizations, and bog turtle researchers). For the population complex model (cores within 2 km), Linkage Mapper generated 67 least-cost corridors. The analysis yielded eight discrete clusters of connected core habitats, and three unconnected core wetlands (Fig. 1). For the regional network model (cores within 10 km), Linkage Mapper generated 100 least-cost corridors, including all the population complex corridors but one (see omitted least-cost path in Fig. 3D, compared with Fig. 3A–C). All core habitats in the study area were connected in this model, including the three left out of the population complex clusters (Fig. 1). Least-cost paths were symbolized by the total cost-weighted distance of each path (Fig. 2). Within the population complex, 47 (70%) corridors connected core wetlands within a given watershed, while 20 (30%) corridors connected core wetlands in adjacent watersheds. The regional network had an additional 10 (total 57%) corridors within a single watershed and 23 (total 43%) corridors crossing into another watershed.

We simplified the LCCs for conservation planning applications by extracting wide and narrow corridors (with different maximum cost-weighted distances) for both models. Narrow corridors generally ranged in width from 50–400 m Euclidean distance, and wide corridors from approximately 500–2,500 m. Corridors tended to be narrower when a narrow low-resistance area was bounded by higher-resistance areas (such as a riparian corridor bounded by steep slopes, or a linear wetland crossing cropland), and wider where low-resistance areas such as wetland or upland forest were wide. Where corridors crossed linear high-resistance features, they were often constricted, but sometimes widened at the crossing, depending on surrounding landscape resistance. The narrow corridors encompassed proportionally more wetland habitat, non-core fen, and riparian corridor area and less upland habitat, cultural and agricultural land, and developed area than the study area overall. The wide corridors more closely approximated the entire study area in land cover composition, although they contained proportionally less upland habitat and more cultural and agricultural land (Fig. 3). For both the population complex and regional network models, both narrow (0.17%, 0.09%) and wide (0.07%, 0.05%)

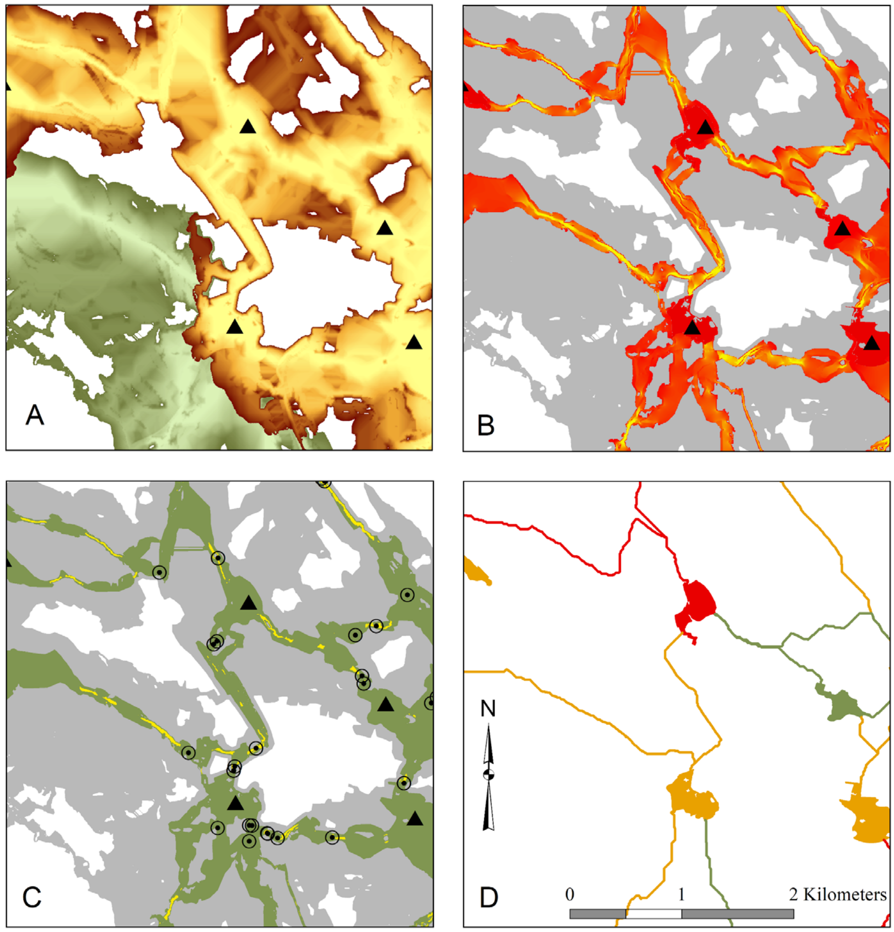


Figure 4. (A) Least-cost corridors among potential core Bog Turtle (*Glyptemys muhlenbergii*) habitats (black triangles) in part of New York study area for population complex model (lowest resistance routes in yellow, highest in brown) and regional network model (lowest resistance routes in light green, highest in dark green; see Fig. 1). (B) Current flow for both models constrained to a narrow version of the same least-cost corridors (maximum cost-weighted distance [CWD] width of 7.6 km), with highest current densities in yellow. Gray area corresponds to wide corridors (maximum CWD of 61 km) for both models. (C) Pinch points (yellow) defined as highest 10% of current values, and corridor outlines of wide (gray) and narrow (green) least-cost corridors. Intersections of corridors and roads marked with circled black points. (D) Core habitats and least-cost paths classified by centrality, the importance of each in keeping the whole network connected (lower centrality in green, higher in red), for the regional network model.

corridors had higher proportions of non-core fen habitat than the entire study area (0.02%).

Corridors appeared to be traversable by Bog Turtles. In several places, narrow corridors crossed large streams, highways with > 3,000 cars/d (and one railroad track), and narrow steep hillsides; but they circumvented ponds and lakes, village centers, and extensive steep areas. Based on records of Bog Turtles found far from core wetlands, these turtles are capable of traversing upland and sometime steep habitats (including meadow, shrubland, and forest), streams and riparian corridors, and disturbed or developed areas (including pasture, cropland, powerline right-of-way, road, railroad track, and residential area; sources in Table 1, New York Natural Heritage Program records).

To illustrate results on a fine scale, we depicted the same least-cost corridors for a smaller part of the study area (see Fig. 4A, an area mostly omitted in Fig. 1). Current flow analysis using the Pinch Point Mapper tool was constrained to the narrower least-cost corridor (Fig. 4B). For conservation planning applications, we extracted pinch points corresponding to the highest 10% of current flow values (Fig. 4C). Pinch points were generally located at corridor constrictions, including places where narrow wetlands (or other low-resistance habitats) were bounded by higher-resistance features (such as perennial streams, ponds, agricultural fields, or development), places where corridors crossed roads, and some places where narrow wetlands were bounded by higher but still moderately low-resistance upland habitat. The population complex model had 94 road crossing points; for the regional network model an additional 92 crossings were identified (Fig. 4C). Results of centrality analysis show a relative ranking of cores and least-cost paths in order of importance for maintaining whole-network connectivity (Fig. 4D).

We examined New York Natural Heritage Program records of Bog Turtles found outside core wetlands in our study area (590 km^2 total area), which comprised 11 turtles found in eight locations. Of these, nine turtles in six locations occurred within the narrow least-cost corridors (44 km^2 total area, including core wetlands). One occurred about 25 m from a corridor and another occurred adjacent to a core wetland but near the study area boundary (i.e., where corridors leading to Bog Turtle sites outside the study area were not mapped). Five of these 11 turtles were adjacent to a core wetland, on the road; the remaining six were approximately 380, 460, 780, 2,200, and 3,160 m from the nearest core wetland.

Discussion

Any Bog Turtle populations within the < 2-km population complex clusters can likely be considered one demographic unit as described by Shoemaker and Gibbs (2013), although genetic exchange would probably be slower between the far ends of the largest cluster (which extends 16 km in Euclidean straight line-distance). The 62 core habitats include extant Bog Turtle populations and locations with no known Bog Turtles to date; many of the latter have yet to be surveyed for turtles. Any unoccupied core habitats in a cluster may function as refuges when conditions (such as vegetation, land use, or climate) change in an occupied core. The more numerous corridors in the regional network model represent possible longer-distance dispersal pathways for genetic exchange over a longer time frame. They include the three core habitats that were not part of clusters in the population complex model, indicating that these could be important intermediate habitats for longer-distance dispersal (Shoemaker and Gibbs 2013). Because we assigned relatively low resistance values to undeveloped upland habitats (with slopes < 25%), many of the resulting least-cost corridors crossed ridges, traversed fairly steep slopes, and departed extensively from riparian zones. This may contradict widely held perceptions of Bog Turtles as restricted to wetlands and streams, even when moving long distances. Because clusters of core wetlands are often found within a single watershed, stream corridors are hypothesized to be important for dispersal (Morrow et al. 2001; USFWS 2001), and there is some direct evidence from the southern population that Bog Turtles use stream corridors for dispersal (Somers et al. 2007; Feaga 2010). However, there are also documented instances of Bog Turtles moving long distances across upland habitats, including deciduous and coniferous forests, agricultural lands, and developed areas (Carter et al. 2000; Pittman and Dorcas 2009; Feaga 2010), as well as records of Bog Turtles found on roads far from wetlands or streams (e.g., Buhlman et al. 1997; New York Natural Heritage Program, unpubl. data).

Although we are fairly confident in our identification of potential core habitats, additional cores could exist. Efforts were made during habitat assessment to visit every potential fen, but access was limited by landowner cooperation, and some fens could have been missed. Fens in wetland complexes of < 2 ha total area (our minimum cutoff) could still support Bog Turtles (Meyers and Gibbs 2013). Interestingly, 84% of non-core fens fell within modeled corridors. Different methods of assigning resistance values to the landscape have been found to result in different corridor locations. In particular, reliance on expert opinion, rather than empirical habitat use data or genetic data, to assign resistance rank could result in incorrect corridor mapping. However, reliance on known habitat associations for core habitats may underestimate connectivity because organisms may select different habitats for dispersal. We think this would be especially true for Bog Turtles, which is in part why we relied on expert opinion rather than empirical (core) habitat association data. Until habitat association data can be collected for dispersing bog turtles, the urgent need for bog turtle conservation action can justify the use of expert opinion for model construction (Zeller et al. 2012).

Some habitat connectivity studies have assessed how uncertainty in setting resistance values affected modeled corridor locations or total resistance (Beier et al. 2009). Performing such a time-intensive sensitivity analysis was not within the scope of this study; however, in other systems varying the resistance values and/or weights of landscape features (within the same rank order) did not greatly change corridor locations or total resistance (Compton et al. 2007, Beier et al. 2009). Uncertainties in geospatial layers, particularly errors in land cover assignment, resulted in the largest LCC errors (Beier et al. 2009; Zeller et al. 2012). The fine-scale mapping of our landscape and use of a small grain size in the resistance raster both enhanced model accuracy. For example, instead of using proxies for land development (e.g., human population density), we used residential development mapped at the scale of each lawn and driveway. Instead of streams, wetlands, and other land cover types mapped remotely, we used field-verified maps with precise habitat distinctions.

One measure of support for our modeled least-cost corridors comes from New York Natural Heritage Program records of Bog Turtles found within the study area but outside core wetlands. Of the 11 individuals in eight locations, we found nine turtles in six locations within our narrow least-cost corridors (which comprised 7.5% of the total study area). Five locations were

380–3,160 m away from the nearest core wetland. This is circumstantial evidence, but it does support the assumption of dispersal (including long-distance dispersal) among wetlands, and indicates our predicted corridors are likely used by those dispersing individuals.

There are several ways the model results can be used by agencies, organizations, and local government to prioritize land conservation and management to benefit Bog Turtles. Core wetlands often need restoration (e.g., cutting woody vegetation, reducing robust herbaceous vegetation) and ongoing management (e.g., low-intensity grazing or periodic burning) to provide high-quality habitat for Bog Turtles (Tesauro and Ehrenfeld 2007; Sirois et al. 2014). Maintenance of hydrologic regimes and limitation of nutrient loading, while more difficult to address, are also critical for preserving vegetation structure, plant diversity, and Bog Turtle habitat in fens (Drexler and Bedford 2002; Kiviat et al. 2010; Feaga et al. 2012). Such preservation and restoration efforts have been focused on wetlands with known Bog Turtle populations, but our results could help conservation planners prioritize other fen complexes for Bog Turtle presence-absence surveys or for fen restoration as intermediate habitats whether or not turtles are present. Core wetlands could be ranked by size, proximity (in cost-weighted distance) to other cores or to known populations, or centrality, their relative importance in contributing to the connectivity of each population complex or the whole regional network. Results of the centrality analyses should be interpreted with caution because additional core habitats and known populations occur immediately outside our study area. Thus, the centrality ranking within our study area would change if these were considered. Cores and paths ranked high for centrality within our study area would likely remain important at a wider scale, but additional cores and paths on the edges of our study area may also be important for connectivity in the larger region.

Similarly, least-cost corridors can be ranked in several ways to set priorities for conservation. Corridors connecting cores within each population complex could be ranked according to shortest least-cost distance, highest centrality of paths, or those crossing the fewest number (or lowest assessed value) of parcels. Larger complexes (such as the northernmost one in Fig. 1) might also be prioritized over smaller ones, for the potential of longer-term stability due to easier migration. For regional network corridors, priorities could focus on the one or two shortest paths between each pair of population complex clusters. Within each least-cost corridor, pinch points (areas of highest current flow in circuit modeling) are disproportionately important for maintaining connectivity in that corridor. Pinch point analysis is a good complement to least-cost corridor analysis, which shows the most efficient path but not the most vulnerable points along that path (McRae et al. 2008). Conservation measures for these vulnerable pinch points (other than roads, discussed below) include land protection, management recommendations for landowners, and possibly habitat restoration (for example, streambank restoration).

Many pinch points were places where LCCs crossed roads. We marked all places where LCCs intersected roads as possible places for corridor protection or improvement. Roads pose a great threat to turtle populations, especially those of terrestrial and semi-terrestrial species (including Bog Turtles). In a simple model using actual road and traffic data, and assuming random travel patterns, semi-terrestrial turtle populations were expected to lose > 5% of individuals annually in the northeastern region of the U.S. (Gibbs and Shriver 2002). A more detailed gravity model using actual travel patterns of Spotted Turtles (*Clemmys guttata*) and Blanding's Turtles (*Emydoidea blandingii*) found the greatest risk of road mortality where distances between wetlands were short and wetland habitat quality high, and this mortality risk was high enough to cause population declines (Beaudry et al. 2008). Road mortality risk may be less overall for Bog Turtles because of their reluctance to leave core habitats, but it would still be one of the greatest risks for dispersing Bog Turtles. Most roads in our study area are small, low-traffic roads, but they are numerous (crossing LCCs 186 times). Furthermore, the loss of adults or juveniles (through exogenous factors such as road mortality or collecting) disproportionately affects the viability of Bog Turtle populations (Whitlock 2002). Mitigation measures for potential road-crossing zones could include culvert improvement, exclusionary fencing, seasonally reduced speed limits, traffic re-routing, volunteer patrolling, or zonal signage (Beaudry et al. 2008). Some Bog Turtles will use appropriately placed culverts: six adult turtles (both sexes) at three sites in New Jersey and Pennsylvania were observed crossing under roads or driveways via 0.46–0.66 m diameter metal pipes (Robert Zappalorti, pers. comm.; full description in Appendix A). One adult male in Virginia used two different large culverts (both ends of each were below grade; Feaga 2010). Other freshwater and terrestrial turtles have been documented using culverts as small as 0.3 m diameter (Dodd 2004; Aresco 2005; Woltz et al. 2008). To reduce road mortality, exclusionary fencing must be installed and maintained in conjunction with existing (or improved) culverts (Aresco 2005); inadequate fencing can actually increase mortality (Baxter-Gilbert et al. 2015). As with Spotted and Blanding's turtles, the width of potential movement corridors for Bog Turtles limits the usefulness of single-point solutions such as culverts or road signs (Beaudry et al. 2008).

Protection of corridors for Bog Turtle dispersal would probably enhance habitat connectivity for a host of other species, although even other fen-adapted species would likely have different least-cost movement corridors. More comprehensive regional connectivity analyses consider core habitats and dispersal behaviors of multiple species (Beier et al. 2011), and such analysis would be extremely valuable here as elsewhere. However, even within a broader conservation context, the specific habitat and life history requirements and vulnerabilities of Bog Turtles would necessitate a specific conservation plan. We recognize that corridors could also facilitate the spread of pathogens, predators, or weeds (Simberloff 1988), but the maintenance of connections between small, threatened populations of Bog Turtles in an era of increasingly fragmented habitat and changing climate is likely critical for Bog Turtle persistence in the region (Shoemaker and Gibbs 2013).

Although our modeled LCCs represent a starting point for connected preserve design for Bog Turtles, several further analyses would add clarity and complement our results. Ongoing efforts to identify new populations and study Bog Turtle movement and habitat use in the region remain essential. To assess alternate dispersal pathways, it would be useful to run an electrical current model with a greatly simplified resistance landscape of only three values (developed, disturbed, natural; Koen et al. 2014). The resulting current map would be a more generalized map predicting potential movement frequencies of many terrestrial animals, and would show, in effect, all potential connecting corridors instead of a single least-cost corridor between two cores. Corridor locations and values can also be quite different when genetic data are used instead of habitat association data (Mateo-Sánchez et al. 2015). Our analysis would be greatly strengthened by a comparison with genetic similarity of populations across our study area, even though the probable presence of undiscovered populations in some of the many potential core wetlands might bias results. Also, in long-lived species (including Bog Turtles), measures of genetic connectivity could reflect historical landscape conditions rather than present-day ones. Nevertheless, a combination of genetic analysis and least-cost modeling could be employed to help predict which habitats are preferred for dispersal (Wang et al. 2009). This could be a more accurate way to build a resistance layer for dispersing Bog Turtles.

The main constraints on feasibility and replicability in using these methods for other regions or species include the time necessary to identify, map, field check, and categorize relevant landscape feature types and combine them into a single resistance layer, and the processing time for Linkage Mapper to run a single model iteration (approximately 24 h in this case, for an area of 590 km^2 at a resolution of 4 m). The time commitment could be reduced by simplifying landscape features (fewer categories, for instance). It would be useful to use this dataset to test the similarity of results obtained by using lower-resolution, less accurate, but publicly available data on land cover. Similarly, the processing time could be reduced by using a larger grain size for the resistance raster; the effect of enlarging grain size could also be tested with our data.

Conservation plans should be based on analysis of core reserves and corridors done at multiple scales, because analysis at each scale gives different results (Huber et al. 2010). Here, we have explored two scales relevant for Bog Turtle population dynamics, the population complex (< 2 km between core wetlands) and the regional network (< 10 km) within our study area. Corridors allowing for longer-distance movement north may be particularly important as climate warms during the next century (Howard and Schlesinger 2012). In the future, as more is known about the demographics, genetics, behavior, and habitat use of dispersing Bog Turtles, we recommend re-running these analyses. In the meantime, we hope these models, built on our best understanding to date, can guide specific and targeted conservation measures.

Acknowledgments.—We thank Brad McRae for help with Linkage Mapper and for comments on the manuscript. We also benefitted from conversations with the New York State Department of Environmental Conservation (NYS DEC), the U.S. Fish and Wildlife Service (USFWS), and participants at the Northeast Natural History Conference (2012) and a NYS DEC (2013) presentation. We sincerely thank the Andrew Sabin Family Foundation, the Geoffrey C. Hughes Foundation, and the USFWS, each of whom provided funding for this project. This paper is a Bard College Field Station-Hudsonia contribution.

Literature Cited

Adriaensen, F., J.P. Chardon, G. De Blust, E. Swinnen, S. Villalba, H. Gulinck, and E. Matthysen. 2003. The application of 'least-cost' modeling as a functional landscape model. Landscape and Urban Planning 64:233–247.

Aresco, M.J. 2005. Mitigation measures to reduce highway mortality of turtles and other herpetofauna at a north Florida lake. Journal of Wildlife Management 69:549–560.

Arndt, R.G. 1977. Notes on the natural history of the Bog Turtle, *Clemmys muhlenbergii* (Schoepff), in Delaware. Chesapeake Science 18:67–76.

Baxter-Gilbert, J.H., J.L. Riley, D. Lesbarrères, and J.D. Litzgus. 2015. Mitigating reptile road mortality: fence failures compromise ecopassage effectiveness.

PLoS ONE 10:e0120537. doi:10.1371/journal.pone.0120537

Beaudry, F., P.G. deMaynadier, and M.L. Hunter, Jr. 2008. Identifying road mortality threat at multiple spatial scales for semi-aquatic turtles. Biological Conservation 141:2550–2563.

Beier, P., D.R. Majka, and S.L. Newell. 2009. Uncertainty analysis of least-cost modeling for designing wildlife linkages. Ecological Applications 19:2067–2077.

Beier, P., D. Majka, and W. Spencer. 2008. Forks in the road: choices in procedures for designing wildlife linkages. Conservation Biology 22:836–851.

Beier, P., W. Spencer, R.F. Baldwin, and B.H. McRae. 2011. Toward best practices for developing regional connectivity maps. Conservation Biology 25:879–892.

Boyer, M.L.H., and B.D. Wheeler. 1989. Vegetation patterns in spring-fed calcareous fens: calcite precipitation and constraints on fertility. Journal of Ecology 77:597–609.

Buhlman, K.A., J.C. Mitchell, and M.G. Rollins. 1997. New approaches for the conservation of Bog Turtles, *Clemmys muhlenbergii*, in Virginia. Pp. 359–363 *In* Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles - An International Conference. Van Abbema, J. (Ed.). New York Turtle and Tortoise Society and the WCS Turtle Recovery Program, New York, New York, USA.

Carter, S.L., C.A. Haas, and J.C. Mitchell. 1999. Home range and habitat selection of Bog Turtles in southwestern Virginia. Journal of Wildlife Management 63:853–860.

Carter, S.L., C.A. Haas, and J.C. Mitchell. 2000. Movements and activity of Bog Turtles (*Clemmys muhlenbergii*) in southwestern Virginia. Journal of Herpetology 34:75–80.

Chase, J.D., K.R. Dixon, J.E. Gates, D. Jacobs, and G.J. Taylor. 1989. Habitat characteristics, population size, and home range of the Bog Turtle, *Clemmys muhlenbergii*, in Maryland. Journal of Herpetology 23:356–362.

Compton, B.W., K. McGarigal, S.A. Cushman, and L.R. Gamble. 2007. A resistant-kernel model of connectivity for amphibians that breed in vernal pools. Conservation Biology 21:788–789.

Dodd, C.K., Jr, W.J. Barichivich, and L.L. Smith. 2004. Effectiveness of a barrier wall and culverts in reducing wildlife mortality on a heavily traveled highway in Florida. Biological Conservation 118:619–631.

Drexler, J.Z., and B.L. Bedford. 2002. Pathways of nutrient loading and impacts on plant diversity in a New York peatland. Wetlands 22:263–281.

Duval, T.P., and J.M. Waddington. 2012. Landscape and weather controls on fine-scale calcareous fen hydrodynamics. Hydrology Research 43:780–797.

Eckler, J.T., A.R. Breisch, and J.L. Behler. 1990. Radio telemetry techniques applied to the Bog Turtle (*Clemmys muhlenbergii* Schoepff 1801). Pp. 69–70 *In* Ecosystem Management: Rare Species and Significant Habitats. Mitchell, R.S., C.J. Sheviak, and D.J. Leopold (Eds.) New York State Museum Bulletin 471, Albany, New York, USA.

Edinger, G.J., D.J. Evans, S. Gebauer, T.G. Howard, D.M. Hunt, and A.M. Olivero (Eds.). 2014. Ecological Communities of New York State. 2nd Edition. A Revised and Expanded Edition of Carol Reschke's Ecological Communities of New York State. New York Natural Heritage Program, New York State Department of Environmental Conservation, Albany, New York, USA.

Erb, L. and M.T. Jones. 2011. Can turtle mortality be reduced in managed fields? Northeastern Naturalist 18:489–496.

Ernst, C.H. 1977. Biological notes on the Bog Turtle, *Clemmys muhlenbergii*. Herpetologica 33:241–246.

Ernst, C.H., R.T. Zappalorti, and J.E. Lovich. 1989. Overwintering sites and thermal relations of hibernating Bog Turtles, *Clemmys muhlenbergii*. Copeia 1989:761–764.

Feaga, J.B. 2010. Wetland hydrology and soils as components of Virginia Bog Turtle (*Clemmys muhlenbergii*) habitat. Ph.D. Dissertation, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA. 225 p.

Feaga, J.B., C.A. Haas, and J.A. Burger. 2012. Water table depth, surface saturation, and drought response in Bog Turtle (*Glyptemys muhlenbergii*) wetlands. Wetlands 32:1011–1021.

Gemmell, D.J. 1994. The natural history and ecology of the Bog Turtle, *Clemmys muhlenbergii*. Ph.D. Dissertation, Rutgers University, New Brunswick, New Jersey, USA. 214 p.

Gibbs, J.P., and W.G. Shriver. 2002. Estimating the effects of road mortality on turtle populations. Conservation Biology 16:1647–1652.

Herman, D.W., and B.W. Tryon. 1997. Land use, development, and natural succession and their effects on Bog Turtle habitat in the southeastern United States. Pp. 364–371 *In* Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles - An International Conference. Van Abbema, J. (Ed.). New York Turtle and Tortoise Society and the WCS Turtle Recovery Program, New York, New York, USA.

Howard, T.G., and M.D. Schlesinger. 2012. Pathways: wildlife habitat connectivity in the changing climate of the Hudson Valley. New York Natural Heritage Program, Albany, New York, USA.

Huber, P.R., S.E. Greco, and J.H. Thorne. 2010. Spatial scale effects on conservation network design: tradeoffs and omissions in regional versus local scale planning. Landscape Ecology 25:683–695.

Kiviat, E. 1978. Bog Turtle habitat ecology. Bulletin of the Chicago Herpetological Society 13:29–42.

Kiviat, E., G. Mihocko, G. Stevens, P.M. Groffman, and D. Van Hoewyk. 2010. Vegetation, soils, and land use in fens of eastern New York and adjacent Connecticut. Rhodora 112:335–354.

Koen, E.L., J. Bowman, C. Sadowski, and A.A. Walpole. 2014. Landscape connectivity for wildlife: development and validation of multispecies linkage maps. Methods in Ecology and Evolution 5:626–633.

Lechner, A.M., D. Sprod, O. Carter, and E.C. Lefroy. 2017. Characterising landscape connectivity for conservation planning using a dispersal guild approach. Landscape Ecology 32:99–113.

Lovich, J.E., D.W. Herman, and K.M. Fahey. 1992. Seasonal activity and movements of Bog Turtles (*Clemmys muhlenbergii*) in North Carolina. Copeia 1992:1107–1111.

Macey, S. 2015. Bog Turtle (*Glyptemys muhlenbergii*) nesting ecology: implications for conservation and management. Ph.D. Dissertation, Fordham University, New York, New York, USA. 142 p.

Mateo-Sánchez, M.C., N. Balkenhol, S. Cushman, T. Pérez, A. Domínguez, and S. Saura. 2015. Estimating effective landscape distances and movement corridors: comparison of habitat and genetic data. Ecosphere 6:59.

McClure, M.L., A.J. Hansen, and R.M. Inman. 2016. Connecting models to movements: testing connectivity model predictions against empirical migration and dispersal data. Landscape Ecology 31:1419–1432.

McRae, B.H., B.G. Dickson, T.H. Keitt, and V.B. Shah. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712–2724.

Meyers, A.T., and J.P. Gibbs. 2013. Landscape-level factors influencing Bog Turtle persistence and distribution in southeastern New York State. Journal of Fish and Wildlife Management 4:255–266.

Morrow, J.L., J.H. Howard, S.A. Smith, and D.K. Poppel. 2001. Home range and movements of the Bog Turtle (*Clemmys muhlenbergii*) in Maryland. Journal of Herpetology 35:68–73.

Pelletier, D., M. Clark, M.G. Anderson, B. Rayfield, M.A. Wulder, and J.A. Cardille. 2014. Applying circuit theory for corridor expansion and management at regional scales: tiling, pinch points, and omnidirectional connectivity. PLoS ONE 9: e84135. doi:10.1371/journal.pone.0084135.

Pittman, S.E., and M.E. Dorcas. 2009. Movements, habitat use, and thermal ecology of an isolated population of Bog Turtles (*Clemmys muhlenbergii*). Copeia 2009:781–790.

Saumure, R.A., T.B. Herman, and R.D. Titman. 2007. Effects of haying and agricultural practices on a declining species: the North American Wood Turtle, *Glyptemys insculpta*. Biological Conservation 135:565–575.

Sawyer, S.C., C.W. Epps, and J.S. Brashares. 2011. Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes? Journal of Applied Ecology 48:668–678.

Shoemaker, K.T. 2011. Demography and population genetics of the Bog Turtle (*Glyptemys muhlenbergii*): implications for regional conservation planning. Ph.D. Dissertation, College of Environmental Science and Forestry, State University of New York, Syracuse, New York, USA. 210 p.

Shoemaker, K.T., and J.P. Gibbs. 2013. Genetic connectivity among populations of the threatened Bog Turtle (*Glyptemys muhlenbergii*) and the need for a regional approach to turtle conservation. Copeia 2013:324–331.

Shoemaker, K.T., A.R. Breisch, J.W. Jaycox, and J.P. Gibbs. 2013. Reexamining the minimum viable population concept for long-lived species. Conservation Biology 27:542–551.

Simberloff, D. 1988. The contribution of population and community ecology to conservation science. Annual Review of Ecology and Systematics 19:473–511.

Simpkins, C.E., T.E. Dennis, T.R. Etherington, and G.L.W. Perry. 2017. Effects of uncertain cost-surface specification on landscape connectivity measures. Ecological Informatics 38:1–11.

Sirois, A.M., J.P. Gibbs, A.L. Whitlock, and L.A. Erb. 2014. Effects of habitat alterations on Bog Turtles (*Glyptemys muhlenbergii*): a comparison of two populations. Journal of Herpetology 48:455–460.

Somers, A.B., J. Mansfield-Jones, and J. Braswell. 2007. In stream, streamside, and under stream bank movements of a Bog Turtle, *Glyptemys muhlenbergii*. Chelonian Conservation and Biology 6:286–288.

Tesauro, J., and D. Ehrenfeld. 2007. The effects of livestock grazing on the Bog Turtle [*Glyptemys* (= *Clemmys*) *muhlenbergii*]. Herpetologica 63:293–300.

Turtle Conservation Coalition (Rhodin, A.G.J., A.D. Walde, B.D. Horne, P.P. van Dijk, T. Blanck, and R. Hudson [Eds.]). 2011. Turtles in Trouble: The World's 25+ Most Endangered Tortoises and Freshwater Turtles—2011. International Union for the Conservation of Nature/Species Survival Commission Tortoise and Freshwater Turtle Specialist Group, Turtle Conservation Fund, Turtle Survival Alliance, Turtle Conservancy, Chelonian Research Foundation, Conservation International, Wildlife Conservation Society, and San Diego Zoo Global, Lunenburg, Massachusetts, USA. 54 p.

U.S. Fish and Wildlife Service (USFWS). 2001. Bog Turtle (*Clemmys muhlenbergii*) northern population recovery plan. U.S. Fish and Wildlife Service, Hadley, Massachusetts, USA. 78 p. + appendices.

Wang, I.J., W.K. Savage, and H.B. Shaffer. 2009. Landscape genetics and least-cost path analysis reveal unexpected dispersal routes in the California Tiger Salamander (*Ambystoma californiense*). Molecular Ecology 18:1365–1374.

Washington Wildlife Habitat Connectivity Working Group (WHCWG). 2010. Washington connected landscapes project: statewide analysis. Washington Departments of Fish and Wildlife, and Transportation, Olympia, Washington, USA. 187 p. + appendices.

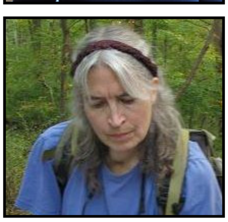
Whitlock, A.L. 2002. Ecology and status of the Bog Turtle (*Clemmys muhlenbergii*) in New England. Ph.D. Dissertation, University of Massachusetts, Amherst, Massachusetts, USA. 147 p.

Woltz, H.W., J.P. Gibbs, and P.K. Ducey. 2008. Road crossing structures for amphibians and reptiles: informing design through behavioral analysis. Biological Conservation 141:2745–2750.

Zeller, K.A., K.McGarigal, and A.R. Whitely. 2012. Estimating landscape resistance to movement: a review. Landscape Ecology 27:777–797.

Kristen Bell Travis is a Biologist with the nonprofit research organization Hudsonia Ltd., in New York's Hudson Valley, although she currently works from her farm in northwestern North Carolina, USA. She holds a B.S. in biology from Oberlin College, Oberlin, Ohio, USA, and an M.S. from Florida International University, Miami, Florida, USA, for her work on frog and lizard communities in tropical forest fragments and has 14 y experience combining species- and habitat-focused ecology with GIS analysis to further biodiversity conservation. (Photographed by David Travis).

Ingrid Haeckel is a Conservation and Land Use Specialist at the Hudson River Estuary Program of the New York State Department of Environmental Conservation through a partnership with Cornell University. She provides extension programs, tools, and technical assistance to municipal and regional partners in the Hudson Valley to promote conservation of important habitats and wildlife. Ingrid previously worked as a Biologist with Hudsonia and earned a B.A. from Columbia University, New York, New York, USA, and an M.A. from the University of Texas at Austin, Texas, USA. (Photographed by Othoniel Vazquez Dominguez).



Gretchen Stevens is a Biologist with Hudsonia and Director of Hudsonia's Biodiversity Resource Center, Annandale, New York, USA. She has 37 y experience studying the plants, animals, and habitats of northeastern North America. She oversees Hudsonia's Habitat Mapping and Biodiversity Education programs, conducts biological assessments and rare plant surveys, and curates the Bard College Field Station Herbarium, Annandale, New York, USA. (Photographed by Laura Heady).

Jason Tesauro is a Wildlife Ecologist specializing in research, surveying, and conservation of freshwater turtles and other herpetofauna in the northeastern U.S. He is considered a national expert on the ecology, habitat restoration, and recovery of the federally listed as threatened Bog Turtle, a species with which he began working in 1994. He earned his M.S. in Ecology and Evolution from Rutgers University, New Brunswick, New Jersey, USA, under Dr. David Ehrenfeld, studying the relationship between domestic livestock grazing and bog turtles. Jason has been collaborating with Hudsonia on herpetofaunal studies for 20 y. (Photographed by Jason Tesauro).

Erik Kiviat is a Co-founder and Executive Director of Hudsonia, and formerly taught Natural History and Environmental Studies at Bard College, Annandale, New York, USA. He holds a B.S. in Natural Sciences from Bard College, an M.A. in Biology from State University of New York at New Paltz, USA, and a Ph.D. in Ecology from Union Institute, Cincinnati, Ohio, USA. Erik has studied turtles since a high school volunteer at an American Museum of Natural History field station in 1964. He also conducts research on wetland habitats, biota associated with nonnative weeds, urban biodiversity, and human ecology. (Photographed by Peter Mauney.)

Appendix A

More detail on data sources.—Developed areas mapped as part of Hudsonia's habitat mapping projects included all roads, buildings, paved or gravel areas, and surrounding lawns or other intensively managed areas. To further differentiate levels of risk associated with different types of developed areas, we created five roads categories by applying county traffic volume data (for selected roads) to the state roads layer. Roads (or individual lanes of divided highways) were buffered to a total width that approximated the width of the pavement plus shoulders (6-18 m). Village and hamlet centers were digitized for this project and included the most densely developed areas in population centers.

Open upland habitat distinctions among old field, pasture, hayfield, and cropland were made in 2014 using recent orthophotos available through ESRI World Imagery basemap layers (Sources: Esri, DigitalGlobe, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community). There is some level of error in these categorizations both due to the difficulty of distinguishing land use remotely and the fact that these land use types often change from year to year, but we thought the distinction in mortality risk between more and less intensively used agricultural lands warranted consideration. A test run on a sample area of the study site revealed that corridor location would be influenced by a modest difference in resistance among these agricultural land types.

Stream locations were derived from Hudsonia's habitat data, and riparian corridors were delineated for this project (14 m on either side of all streams). Streams were classified as perennial or intermittent by Hudsonia in approximately 3/5 of the study area. In the remaining area, streams were mapped by Hudsonia but mostly not classified, so National Hydrography Dataset (NHD; http://nhd.usgs.gov/) classifications were used to categorize streams as perennial or intermittent (defined as anything not called perennial or not mapped by NHD). NHD was more liberal in its use of the perennial classification (where classifications overlapped, 87% of Hudsonia-mapped perennial stream length was also called perennial by NHD [174.3/200.3 km], whereas only 60% of NHD-mapped perennial stream length was also called perennial by Hudsonia [181.3/300.9]). We were not overly concerned with this discrepancy because continuous narrow features with high resistance (such as perennial streams and roads) tended not to influence the general locations of corridors much in our study area (on a scale of several kilometers, a few meters with high resistance does not add disproportionately to CWD).

Several instances of Bog Turtle culvert use were described by Robert T. Zappalorti (Herpetological Associates, Pemberton, NJ, pers. comm.); we were unable to find any such records in the published literature (with the sole exception of Feaga [2010]). At his long term study area in Sussex County, New Jersey, he observed an adult male use a 0.66-m (26-in) metal pipe to cross under a road. (There was suitable habitat on both sides.) On the same road, he subsequently found a dead Bog Turtle, which had apparently not learned to use the culvert. Several Bog Turtles of both sexes consistently used a roadside ditch at this location as well. At a site in Lancaster County, Pennsylvania, he observed two adult Bog Turtles (one male and one female) use a 0.51-m (20-in) metal pipe that went under a paved road. The pipe was later removed and the road was dismantled to protect the Bog Turtle population. At another site in Lancaster County, three adult Bog Turtles used an 18-inch metal pipe that went under a driveway near the wetland. A 76-m (250-ft) long wet, flowing roadside ditch ran along the edge of the road at this location, but there was no culvert under the road. Two Bog Turtles were found dead on this road over a 5-year period, and two others were killed when the local township dredged the ditch to remove silt and debris.

More detail on setting resistance weights and values.—We assigned wetland habitats the lowest resistance (next to core habitats) because Bog Turtles are almost always found in wetlands (e.g., Carter et al. 1999). We do not know, however, whether wetlands are preferred for dispersal movements. Stream habitats adjacent to or within core wetlands can be used during normal conditions or as refuges during drought (Pitman and Dorcas 2009). There is some direct evidence from the southern population that Bog Turtles use riparian corridors for dispersal (Somers et al. 2007; Feaga 2010 [defined stream corridors as 80 m wide]), but there are also documented instances of Bog Turtles moving long distances across upland habitats without streams, including deciduous and coniferous forests, agricultural lands, and developed areas (Carter et al. 2000; Pittman and Dorcas 2009; Feaga 2010), as well as records of Bog Turtles found on roads far from wetlands or streams (e.g., New York Natural Heritage Program). One individual spent two weeks in an upland pasture (Pitman and Dorcas 2009). We decided to assign low resistance values both to relatively undisturbed upland habitats and to riparian corridors (where they cross undisturbed habitats), with riparian corridors having lower resistance than other uplands. We erased riparian corridors where they crossed wetlands, to avoid increasing the low resistance of wetlands along streams. We assigned higher weights to riparian corridors than to habitats and cultural and agricultural lands, so that where they overlapped, the lower riparian resistance was used.

Although Bog Turtles are clearly able to travel across uplands, some uplands are riskier than others. We assigned higher resistance to hayfield and cropland compared to pasture and oldfield, because of the significant mortality risks for turtles associated with farm machinery (Saumure et al. 2007; Erb and Jones 2011). Hayfields in the region are often mowed three or more times per year, and most crop production involves the use of heavy machinery several times per year, for fertilization, tilling, sowing, pesticide application, and harvesting. We also gave a higher resistance value to riparian corridors crossing these agricultural lands, relative to riparian corridors crossing less-disturbed uplands. Mapped cultural areas, including large lawns and golf courses, presumably pose an even greater risk to turtles due to much more frequent mowing, and perhaps higher visibility to predators. We gave cultural areas a slightly higher resistance value than driveways and small, private roads (risk of road mortality). Driveway locations were obtained from two data sources: most from the habitat map (where they were not differentiated from other developed areas) and some from the roads layer. We wanted to assign lower resistance to driveways than other developed areas, because they are usually narrow and used at slower speeds and less frequently than, e.g., parking lots and roads, and less risky than lawns for lawnmower encounters. Driveways mapped from the roads layer were given a higher weight than developed areas, so that where they overlapped the lower resistance was used.

We assigned higher resistance to mapped developed areas, including buildings, parking lots, and lawns. While Bog Turtles may try to avoid such areas, they have certainly been found in residential areas (Pitman and Dorcas 2009; Feaga 2010; New York Natural Heritage Program), so the higher resistance mainly reflects increased mortality risk from vehicles, mowers, predators (including pets), entrapment, and collecting. Although Bog Turtles seem to cross roads less frequently than other turtle species, they are found on roads with some frequency (Morrow et al. 2001; Feaga 2010; Pitman and Dorcas 2009), and road crossing is risky for any turtle (Beaudry et al. 2008). We put roads into four categories of increasing traffic volume with resistance values ranging from 400 to 1,000.

It is unclear what role topographic position or slope play in Bog Turtle route choice; we suspect not much. Bog Turtles have been found on ridges and crossing watersheds. Of course, cliffs, rock outcrops, and some talus slopes would be impossible for turtles to cross. We gave a relatively high resistance value to areas with slopes greater than 25% because these areas are more likely to contain steep, rocky outcrops. Bog Turtles avoid open water (Sirois et al. 2014, Jason Tesauro, pers. comm.), so we assigned high resistance to large perennial streams, lakes, and ponds. We hypothesized that village and hamlet centers, with their stores, parking lots, and closely-spaced houses, might be avoided more than scattered residential development, as well as posing a higher mortality risk. We assigned the highest resistance values to divided highways and railroads. Railroad tracks seem to be a particular risk, whether because of steep berms, entrapment between ties, or some other reason (Pitman and Dorcas 2009).

Appendix B

Run settings used for data analysis in the Linkage Mapper and Pinch Point toolbox applications.

“Population Complex” (LMBT15): Least-cost corridor analysis using Linkage Mapper

Start time: Wed Feb 03 11:51:25 2016

Parameters: ['C:\\GIS\\LinkageMapper1_0_9\\toolbox\\scripts\\lm_master.py', 'C:\\LMBT15', 'C:\\GIS\\Bog Turtle Connectivity\\KT_2015_1\\BT_connect_2015KT.gdb\\Core_fen_complex', 'Core_id', 'C:\\LMBT15\\resistance', 'true', 'true', 'Cost-Weighted & Euclidean', 'C:\\LMBT15\\Core_fen_complex_dists.txt', 'true', 'true', 'true', '3', 'Cost-Weighted', 'true', 'true', '#', '#', '6562']

Linkage Mapper Version 1.0.9 on ArcGIS Desktop 10.3 Service Pack N/A

Setting data frame spatial reference to that of core area feature class.

“Population Complex” (LMBT15): Pinch point analysis using Circuitscape

Linkage Mapper log file: Circuitscape

Start time: Thu Feb 18 20:31:58 2016

Parameters: ['C:\\GIS\\LinkageMapper1_0_9\\toolbox\\Scripts\\circuitscape_master.py', 'C:\\LMBT15', 'C:\\GIS\\Bog Turtle Connectivity\\KT_2015_1\\BT_connect_2015KT.gdb\\Core_fen_complex', 'Core_id', 'C:\\LMBT15\\resistance', '25000', 'false', 'true', '#', 'All-to-one']

“Regional Network” (LMBT16): Least-cost corridor analysis using Linkage Mapper

Linkage Mapper log file: Linkage Mapper

Start time: Sat Feb 13 22:18:54 2016

Parameters: ['C:\\GIS\\LinkageMapper1_0_9\\toolbox\\scripts\\lm_master.py', 'C:\\LMBT16', 'C:\\GIS\\Bog Turtle Connectivity\\KT_2015_1\\BT_connect_2015KT.gdb\\Core_fen_complex', 'Core_id', 'C:\\LMBT15\\resistance', 'true', 'true', 'Cost-Weighted & Euclidean', 'C:\\LMBT15\\Core_fen_complex_dists.txt', 'true', 'true', 'true', '3', 'Cost-Weighted', 'true', 'true', '#', '#', '32808']

Linkage Mapper Version 1.0.9 on ArcGIS Desktop 10.3 Service Pack N/A

“Regional Network” (LMBT16): Pinch point analysis using Circuitscape

Linkage Mapper log file: Circuitscape

Start time: Thu Feb 18 15:40:50 2016

Parameters: ['C:\\GIS\\LinkageMapper1_0_9\\toolbox\\Scripts\\circuitscape_master.py', 'C:\\LMBT16', 'C:\\GIS\\Bog Turtle Connectivity\\KT_2015_1\\BT_connect_2015KT.gdb\\Core_fen_complex', 'Core_id']