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Multi-scale habitat selection model assessing potential gray wolf den habitat and dispersal corridors in Michigan, USA

Heather K. Stricker[a,*], Thomas M. Gehring[a], Deahn Donner[b], Tyler Petroelje[c]

[a] Department of Biology, Central Michigan University, Mount Pleasant, MI, United States
[b] USDA Forest Service, Northern Research Station, Institute for Applied Ecosystem Studies, Rhinelander, WI, United States
[c] College of Forest Resources, Mississippi State University, Mississippi State, MS, United States

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ABSTRACT

Following decades of absence, the gray wolf (*Canis lupus*) has recolonized much of the northern Great Lakes region from Canada and remnant populations in northern Minnesota. The wolf population in Michigan's Upper Peninsula may now be reaching saturation, with evidence that some dispersing individuals have traversed the Straits of Mackinac during ice-over winter conditions indicating potential recolonization of northern Lower Michigan. While previous research suggests suitable habitat exists in northern Lower Michigan to support a small wolf population, habitat availability at other hierarchical levels, including den habitat and the ability of individuals to disperse successfully among suitable habitat patches, has not been assessed. We evaluated the den habitat availability and landscape connectivity using a multi-scale modeling approach that integrates hierarchical habitat selection theory as well as spatial structure to assess whether corridors exist for wolves to successfully recolonize and raise pups in northern Lower Michigan. We used expert opinion, scientific literature, and geographical information systems to develop models of landscape suitability, resistance, and least-cost path analysis to identify dispersal corridors throughout the Upper and northern Lower Peninsulas of Michigan. Based on our models, the Upper Peninsula was almost entirely amenable to wolves for both denning and dispersing, particularly in the western portion of the peninsula. Our estimates indicate that over 1900 km^2 of high quality den habitat exists in northern Lower Michigan, but landscape permeability between these habitat patches appeared relatively low relative to Upper Michigan. We delineated several corridors of high quality habitat in the Upper Peninsula that may facilitate dispersal in to Lower Michigan. Dispersal corridors were of moderate quality in northern Lower Michigan, representing higher mortality risk but potentially capable of promoting recolonization of high-quality habitat areas. Conservation efforts within these identified corridors may further increase the potential for successful recolonization and establishment of viable long-term breeding populations of gray wolves in northern Lower Michigan.

1. Introduction

The selection of habitats by animals is a multilevel, multi-decision process that can be broken down into 3 general orders: 1) First-order selection is a coarse scale selection, pertaining to selection of the physical or geographical range of a species; 2) Second-order selection is found within the range of the first, and determines the home range of an individual or social group; 3) Third-order selection pertains to the use of various habitat components within the home range (Johnson, 1980). As such, analyzing habitat selection within a hierarchical framework can identify differences in habitat preferences among levels (Weaver et al., 2012; Zeller et al., 2017). Multi-scale habitat modeling often produces stronger and more reliable inferences than using a single level alone (Johnson et al., 2004; Holland et al., 2004; Wasserman et al., 2012; DeCesare et al., 2012; Zeller et al., 2014; McGarigal et al., 2016). However, many studies of gray wolf (*Canis lupus*) habitat and/or probability of occurrence in the Great Lakes region have focused solely on second-order selection at the home range level (e.g. Mladenoff et al., 1995; Mladenoff and Sickley, 1998; Mladenoff et al., 1999; Wydeven et al., 2001; Potvin et al., 2005; Gehring and Potter, 2005). Much of this research has centered on the influence of road density on gray wolf occurrence and survivability, whereby road density serves as a proxy for potential human contact. While human presence is important in predicting wolf habitat and occupancy, other landscape factors (e.g. cover type, terrain, etc.) are clearly of significance to wolves to fulfill basic life history requirements. Furthermore, models of wolf habitat

* Corresponding author at: University of Wisconsin – Stevens Point, 2100 Main St, Stevens Point, WI 54481, United States.
E-mail address: heather.stricker@uwsp.edu (H.K. Stricker).

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solely focused at the home range level may be too simplistic, neglecting to assess limiting factors or habitat preferences at other scales of selection.

Within Johnson's (1980) hierarchical habitat selection theory, it is likely that wolves travel through and select a region on the landscape, then select an area to establish a home range, and lastly select the microscale location to birth and raise pups (den and rendezvous sites; Unger et al., 2009). Therefore, assessing landscape habitat suitability requires not only identifying suitable habitat for the establishment of a home range, but also identifying potential barriers to dispersal (first-order) and habitat suitable for the successful birthing and rearing of young (third-order). Arctic tundra wolves (*Canis lupus albus*), for example, have shown a strong association with eskers as den habitat, therefore availability of suitable of den site habitat may be a limiting factor affecting habitat selection patterns at higher levels (McLoughlin et al., 2004). Houle et al. (2010) and Lesmerises et al. (2012) found similar patterns of habitat selection at the within-home-range level in Canada, where wolf occurrence and activity was influenced more by timber harvesting and other anthropogenic activity during denning/rendezvous season than during other life events (e.g. nomadic periods).

Relatively less is known about the mechanisms behind long distance wolf dispersal (Linnell et al., 2005), however advancements in landscape genetics techniques have provided some evidence that natural and anthropogenic landscape barriers do exist for these highly mobile habitat generalists. Carmichael et al. (2001) showed that physical barriers (in that case, the Mackenzie River in the Northwest Territories, Canada) and prey specialization may govern large-scale wolf movements. Geffen et al. (2004) found patterns of genetic isolation at a continental scale in North American wolf populations that appeared to be related to habitat and climate. Anthropogenic barriers to wolf dispersal often include high-volume and/or high density road systems, as wolves tend to avoid areas of high human activity and disturbance (Jensen et al., 1986; Mech, 1989; Whittington et al., 2005; Oakleaf et al., 2006). In fact, relatedness within packs has been found to be greater near major roads suggesting decreased dispersal from natal packs with proximity to roads (Cullingham et al., 2016).

Given the complexities of habitat selection and movement for a highly-mobile mammal, we integrated expert opinion into a hierarchical modeling approach to better understand gray wolf habitat suitability and availability in Michigan. Our model assessed habitat suitability at multiple levels in both Michigan's Upper Peninsula (UP), where wolves currently exist, and Michigan's northern Lower Peninsula (NLP) where wolves may potentially recolonize if adequate habitat corridors are maintained. This approach allowed us to compare quality and quantity of habitat in known wolf range with habitat in potential wolf range. The UP wolf population is estimated at > 600 individuals and is likely near carrying capacity (Michigan Department of Natural Resources, 2015). As the UP population becomes saturated, the likelihood for individuals to disperse into the NLP may increase. Gehring and Potter (2005) estimated that enough suitable land area exists to support the home range level occupancy of 50–100 wolves in the NLP, although other hierarchical levels of habitat in Michigan has not been evaluated until now. As saturated wolf populations expand and re-inhabit greater portions of their former range, it will be imperative to identify not just suitable home range habitat, but also critical breeding patches and the landscape permeability between them. This is particularly germane in human-dominated areas of wolf recolonization such as the NLP, where habitat is fragmented and the potential for wolf-human conflict is high (Unger et al., 2009).

This study therefore assessed and integrated habitat suitability at multiple scales, bridging first-order landscape permeability to second-order home range suitability (based on past work by Mladenoff et al., 1995 and Gehring and Potter, 2005), and finally third-order selection (den/rendezvous site habitat) to better understand habitat suitability and permeability at large-scales. To our knowledge, hierarchical models of wolf habitat suitability are scarce, and ours is the first of its kind in the Great Lakes region.

2. Methods

2.1. Study area

Our study area included the entire Upper Peninsula of Michigan, as well as the northern Lower Peninsula which is considered to be all areas north of Michigan highway M-55. The UP is a 42,896 km^2 area dominated by boreal forest and mesic conifer and deciduous stands, with interspersed agricultural lands. The NLP covers 27,656 km^2 of land, and is a mosaic of northern hardwood forests and boreal coniferous wetlands, interspersed with intermittent agriculture and urban areas. State-owned public land dominates ownership of large tracts of land in the NLP, including the Pigeon River Country State Forest (PRCSF), a 477.5 km^2 multi-use managed forest tract. In addition, a vast expanse (approximately 583 km^2 combined area) of privately-owned club properties lie approximately 60 km to the south-east of the PRCSF, creating a contiguous tract of near-roadless forest.

2.2. Modeling overview

We used a modeling approach that combines expert opinion, best available knowledge from literature, and environmental spatial data. Peer-reviewed literature and expert information can be used with computer technologies such as geographic information systems (GIS) to develop predictive habitat models in a relatively short period of time (Store and Kanagas, 2001, Clevenger et al., 2002; Yamada et al., 2003; Perera et al., 2012). While empirical studies of den and dispersal habitat selection patterns in the Great Lakes exist (e.g. Thiel, 1985; Thiel et al., 1998; Wydeven et al., 2001; Norris et al., 2002; Treves et al., 2009), it was necessary to use expert opinion to quantify the relative importance of habitat variables to wolves when dispersing through the landscape and selecting critical den habitat. Furthermore, an important aspect of our study was to assess availability of critical habitat and the permeability of the NLP for dispersing wolves, an area that has not had an established wolf population for nearly 100 years (Stebler, 1944), therefore empirical data for this area does not currently exist. Expert-opinion data and GIS evaluations have been used to study large carnivores and habitat potential in the past, including black bears (*Ursus americanus*; Clevenger et al., 2002), Florida panthers (*Puma concolor coryi*; Thatcher et al., 2006), and cougars (*Puma concolor;* LaRue and Nielsen, 2008). Using these techniques, we developed models of habitat suitability, landscape permeability (resistance), and least-cost paths, a technique often used for determining dispersal corridors (Meegan and Maehr, 2002; Schad et al., 2002; Larkin et al., 2004; Kautz et al., 2006; Penrod et al., 2006).

2.3. Expert surveys

We created a survey to obtain expert opinion on variable importance. Variables were chosen from published literature on the ecological and life-history requirements of wolves, focusing specifically in the Lake States region. We distributed the survey to 13 species experts working for university, state, and federal agencies in the U.S. Great Lakes region and Ontario, Canada. Den/rendezvous habitat variables that were ranked by experts included distance to water (Joslin, 1967; Unger, 1999; Norris et al., 2002; Trapp, 2004), association with sandy soil (Pulliainen, 1965; Joslin, 1967; Ballard and Dau, 1983; Fuller, 1989; Unger, 1999; Trapp, 2004), land cover type (Fuller, 1989; Norris et al., 2002, Theuerkauf and Jedrzejewski, 2003, Trapp, 2004), and distance to roads (Unger, 1999; Wydeven et al., 2001, Theuerkauf and Jedrzejewski, 2003). "Distance-to-roads" was chosen for the den model rather than road density because distance to a road may be more appropriate for sensitive and spatially static den sites where we predicted distance from human influence is highly critical. Variables related to travel corridors presented for expert ranking included: road density (Mladenoff et al., 1995; Houts, 2002), land cover type (Fritts and Mech, 1981; Licht and Fritts, 1994; Wydeven et al., 2001; Whittington et al., 2004), prey density (Mech, 1977; Boyd and Pletscher, 1999; Potvin et al., 2005), and topographic position (Ream et al., 1985).

Species experts were asked to quantify the relative importance of each habitat variable by assigning a weight (i.e. percentage of 100) to each variable, and rank the attribute classes within each variable (e.g., within the land cover variable, there are several land cover types such as upland deciduous, lowland deciduous, barren, urban, etc.). Weights identified the importance of each variable in relation to the other landscape characteristics, where 100% would identify a deterministic habitat variable in which no other landscape variables are required for suitability. Attribute class ranks identify suitabilities of a range of data or attribute specific to a given variable, based on a biological suitability score ranging from 0 to 100 (but do not need to equal 100; Appendix A, adapted from Beier et al., 2007). Weights and ranks were averaged to obtain a final value (see Appendices B and C).

2.4. Geospatial data

Modeling processes were completed in ArcGIS 10.1 (ESRI, Redlands, CA.) using raster data with minimum mapping unit of 30 m. Michigan land cover data was obtained from the Michigan Center for Geographic Data online Data Library Catalog (www.mcgi.state.mi.us/mgdl/; accessed May 2007) and reclassified from its original 32 classifications to 11 based on expert survey responses. Reclassification was conducted because the scientific literature for wolves and many other species often does not distinguish between the suitabilities of highly related land cover types (Beier et al., 2007). Additionally, wolves have not been shown to actively select for specific types of habitat, but rather exhibit avoidance of areas of high human disturbance (Thiel, 1985; Mladenoff et al., 1995). Areas with high human influence typically include cropland, urban areas, roads, etc., which are represented in the simplified classifications. The open water landcover type was considered to be static; i.e. conversion to ice in winter months was not considered. Soil data were obtained from the Natural Resource Conservation Service (NRCS) online Soil Data Mart (http://soildatamart.nrcs.usda.gov/). Soil physical properties (percent sand) were extracted using the NRCS Soil Data Viewer 5.1.

Road data were obtained from the Michigan Center for Geographic Data online Data Library Catalog MGF Version 7 (May 2007) framework. Unimproved forest roads were removed as these roads are readily used by wolves and are often incorporated into their home ranges (Mladenoff et al., 1995; Gehring, 1995). Euclidean distance was used to estimate distance from a road. Road density was calculated using 10 km moving window neighborhood analysis (following Mladenoff et al., 1995; Gehring and Potter, 2005). Road densities were categorized for ranking according to Mladenoff et al.'s (1995) corresponding likelihood of wolf occurrence.

Distance to water was calculated from Michigan river, stream, and lake data obtained from MGF Version 7 hydrography framework (www.mcgi.state.mi.us/mgdl/; May 2007). Lake polygons originated from the Michigan Department of Natural Resources Institute for Fisheries Research. Relatively "small" water features (e.g. ephemeral, narrow, and/or shallow streams and small lakes/ponds) are often more associated with den and rendezvous sites than large or rapidly moving waters (Joslin, 1967; Norris et al., 2002), therefore major water bodies were excluded from analysis. Small rivers and streams data were considered features classified as H31 and H32 from MIRIS Level 7 (L. Blastic, Michigan Department of Natural Resources, *pers. comm.*). Small lakes and ponds were considered to be ≤1 ha in size, per largest documented lake size in Joslin (1967). Euclidean distance tools (up to 10,000 m) were run separately on lake and river shapefiles, and the resulting raster outputs were combined using Erdas IMAGINE (Hexagon Group, Inc., Sweden) for a single distance-to-water dataset.

A topographic position raster was derived from the digital elevation model (DEM; Michigan Center for Geographic Data online Data Library Catalog). Topographic position for each cell was classified as valley, ridgetop, flat, or slope in relation to neighborhood cells within 200 m. Valley was defined as an elevation of at least 12 m less than the average of the neighborhood cells, ridgetop as an elevation of at least 12 m greater than the average of the neighborhood cells, and flat as having a slope < 6 °, and did not fit the valley or ridgetop classification. Slope was defined as > 6 °, and did not fit valley or ridgetop classification. Topographic classifications followed Beier et al., 2007.

2.5. Habitat suitability modeling

Habitat suitability index (HSI) rasters were created for den habitat and landscape permeability using the ArcGIS extension tool CorridorDesigner (Beier et al., 2007). We used weighted geometric mean to incorporate weighted factors and ranked classes, as weighted geometric mean has the ability to incorporate deterministic factors (Beier et al., 2007). A deterministic habitat factor is one that has to be present in high-quality habitat, while a non-deterministic factor has a trade-off with some other factor (Store and Kanagas, 2001). This concept can also be applied to a limiting deterministic factor where the presence of a particular landscape characteristic (e.g. urban) may render the pixel as absolute non-habitat, even if all other factors (e.g. topography, distance to water, etc.) are ideal. Geometric mean accomplishes this because it is calculated using the product of the terms to the n^{th} root, thereby retaining an overall score of 0 if any of the terms are rated as such. The algorithm used for combining weighted habitat factors was therefore:

$$\text{Suitability or Permeability} = \Pi\ (S_n * W_n)$$

where S_n is the score for each factor and W_n is the weight for that factor and Π represents the geometric mean. The resultant HSI rasters contained pixels that contained a single index value to represent the relative suitability of that area. Raster data of habitat suitability/permeability was normalized on a scale of 0–100 to represent biological interpretations of habitat suitabilities (Appendix A).

2.6. Den/Rendezvous site habitat

We identified den/rendezvous site habitat patches from the den HSI raster using neighborhood analysis with a 250 m circular moving window on cells with a HSI score ≥ 60. Basis for removal of habitat < 60 HSI is to represent all den habitat patches that are suitable for denning on a consistent basis (per HSI definitions; Appendix A). We defined breeding patches as ≥1 ha, assuming highest frequency of wolf use at den sites occurs within an approximate 50 m radius (Unger, 1999, Theuerkauf and Jedrzejewski, 2003, Trapp, 2004). Habitat patches within the NLP were clipped to include only areas which lie within areas defined as suitable for general pack home range, based on Gehring and Potter (2005). This more accurately identifies suitable den habitat in the NLP, as third-order selection typically occurs within the range of second-order selection (Johnson, 1980). Euclidean distance nearest neighbor analyses were performed on UP and NLP den habitat patches using ArcGIS 10.1 spatial statistics tools.

2.7. Dispersal corridors

We used least-cost path methods to develop likely dispersal corridors, using the permeability raster as the "resistance" environment through which to move. This technique models the relative cost or ability for an animal to permeate the landscape between two suitable habitat patches (Penrod et al., 2006), based on how characteristics such as land cover, roads, or slope may affect the animal (Singleton et al., 2002; Penrod et al., 2006). Least-cost path (LCP) analyses will create a path with the least resistance (greatest permeability) and fewest barriers to movement (Larkin et al., 2004) and identify the best route for a dispersing animal (LaRue and Nielsen, 2008).

Large areas of suitable critical den habitat (developed from our den habitat patch model) were used as source and destination locations for our corridors. Within the UP, blocks of suitable den habitat found within Ottawa and Hiawatha National Forests were chosen as source and destination habitats. These habitat patches were chosen somewhat subjectively; while sufficiently large patches of suitable den habitat were identified within many ownership classifications (federal, state, private, etc.), we chose these patches both for their likely stability in ownership and natural status (i.e. likely to remain in federal National Forest ownership and thus likely to remain free from human development) as well as geographic location for constructing potential dispersal corridors. In other words, because a goal of our study was to assess how wolves might move across the landscape in the UP, it was necessary to choose suitable start and end points for LCP corridor modeling that would facilitate the simulation of a corridor that traversed the UP.

A final corridor was modeled to extend to the southeastern-most block of suitable habitat in the UP (near the Straits of Mackinac) to illustrate potential crossing locations into the NLP. Within the NLP, a corridor was modeled using den habitat within Wilderness State Park in Emmet County (the den habitat block nearest to UP populations) as the source. The destination for the corridor was the largest contiguous habitat block in the NLP, consisting of mostly private hunt/recreation club property in Alcona, Oscoda, and Montmorency Counties. While this is private land, much of it has remained unaltered for many years, and is surrounded by a matrix of public land (Pigeon River Country State Forest to the north; Huron National Forest to the south).

We used a neighborhood analysis to average neighboring pixels to determine a corridor with the least cost or greatest permeability. A 500 m circular moving window neighborhood analysis of all pixels > 60 HSI (permeability index) was used. Neighborhood effects are determined by species sensitivity to edge effects and perceptual range (Beier et al., 2007). It is likely that wolves have a broad perceptual range (Gehring and Swihart, 2003), therefore the maximum window size was chosen.

2.8. Evaluation of dispersal corridors

Our dispersal corridors are displayed in terms of permeability, with the various colored "slices" of least-cost paths, representing varying levels of permeability. For example, the 0.1% LCP represents the most permeable 0.1% of the landscape, up to the most permeable 10%. Corridors were also assessed for spatial bottlenecks, which were considered areas < 200 m in width to prevent close contact with human inhabitance (Boyd and Pletscher, 1999). Corridors were evaluated for maximum width so that no area of the corridor exceeded 10 km in width, based on the radius of an average summer home range for wolves in the Great Lakes region (Rossler, 2007). The latter was used to prevent establishing a corridor large enough for a wolf pack to become resident and prevent passage by other individuals (i.e. displaying territorial behavior within a corridor). Maximum widths were also assessed for purposes of feasibility from a management standpoint. Average widths were calculated using the "Bottleneck Statistics" tool, and least-distance analysis was performed using the "Patch-Distance Statistics" tool within the CorridorDesigner extension.

2.9. Validation of den model

We obtained (ex post facto) location data of field-verified wolf dens (n = 18) detected using satellite- and radio-collared wolves in the UP from 2009 to 2014 (Mississippi State University, *unpublished data*), and compared these locations to HSI values generated by our den model. Because much of the UP landscape contains suitable den habitat, we also compared the empirical data to the frequency at which random points would be within suitable den habitat patches from our model (HSI ≥ 60 and area ≥1 ha). To do this, we used ArcGIS 10.1 to generate 10 datasets of 18 random sites across the UP landscape. We compared known den location "successes" (den was located within a wolf den habitat patch from our model) and "failures" (point was not located within a wolf den habitat patch). We conducted the same comparison with the 10 iterations of 18 random points. We then performed Chi-Squared Goodness of Fit tests on the success/failure rate of the known wolf den locations compared with the 10 datasets of random sites to test if known den locations were within den patches developed by our model more than would be expected by random chance.

3. Results

3.1. Den/Rendezvous site habitat model

Averaged results of species expert surveys ($n = 8$) rendered distance to water as the most important variable in den habitat quality, followed by distance to roads, land cover, and sand composition in soil (Appendix B). Moderate to short distances (< 80 m) from water were considered the most suitable, and distances > 200 m were considered least suitable yet suitable enough for occasional to moderate use with a score of 40. Experts ranked distances from roads > 2000 m as having a high likelihood for den and pup success and areas < 500 m as least suitable. Mixed forest was identified as the most suitable cover type, followed by upland coniferous. The least suitable (and only limiting factor with a score of 0) habitat type was open water, followed by urban areas with a very low score of 1. A sand composition of 75–100% was considered as the most suitable class within the soil type factor. The least suitable class was non-sandy soil types, although still ranking high enough to support occasional wolf den activity.

Den habitat suitability modeling (Fig. 1) suggested widespread availability of high quality den habitat (HSI > 80) throughout the UP, but lower availability throughout the NLP. Available den habitat in the UP totaled 26,417 km^2, and is approximately 90% of the area identified by Mladenoff et al. (1995) as suitable for general home range habitat. Euclidean distance analysis (4 nearest neighbors) between UP den habitat patches (> 60 HSI) revealed a minimum inter-patch distance of 67 m, maximum of 54.9 km, and an average distance of 3.1 km. In the NLP, available den habitat was 1906 km^2, which is approximately 87% of the land area predicted as suitable for general home range set-up by Gehring and Potter (2005). Inter-patch distances between NLP den habitat patches were 778 m, 50.9 km, and 6.2 km, respectively. In the UP, the highest quality den habitat was concentrated in the western portion of the peninsula. Within the NLP, the majority of den habitat was distributed throughout private club country land to the southeast, however quality habitat was also identified in areas of public ownership such as in Wilderness State Park in the northwest and within the Pigeon River Country State Forest in the northeast.

Proportional analysis of HSI scores identified den habitat in the UP as being greater in both quality and quantity than within the NLP (Fig. 2). Most (35%) den habitat identified in the UP fell within the highest suitability index class of 80–100, and approximately 28% in the second highest suitability class (HSI 60–80). The largest proportion (46%) of den habitat in the NLP was identified as marginal quality (30–60 HSI) and 32% of habitat within the 60–80 HSI range. Only approximately 11% of the land area in the NLP is of the best habitat suitability (> 80 HSI) for denning.

3.2. Den model validation

Known den locations in the UP aligned well with our den habitat patch model, with 89% (n = 16) of the known points falling within modeled den habitat, with a mean HSI value of 78. Random point datasets had a mean "success" rate of 61% (range 8–13 "successes"). Chi-square Goodness of Fit Tests (Table 1) indicated that the observed

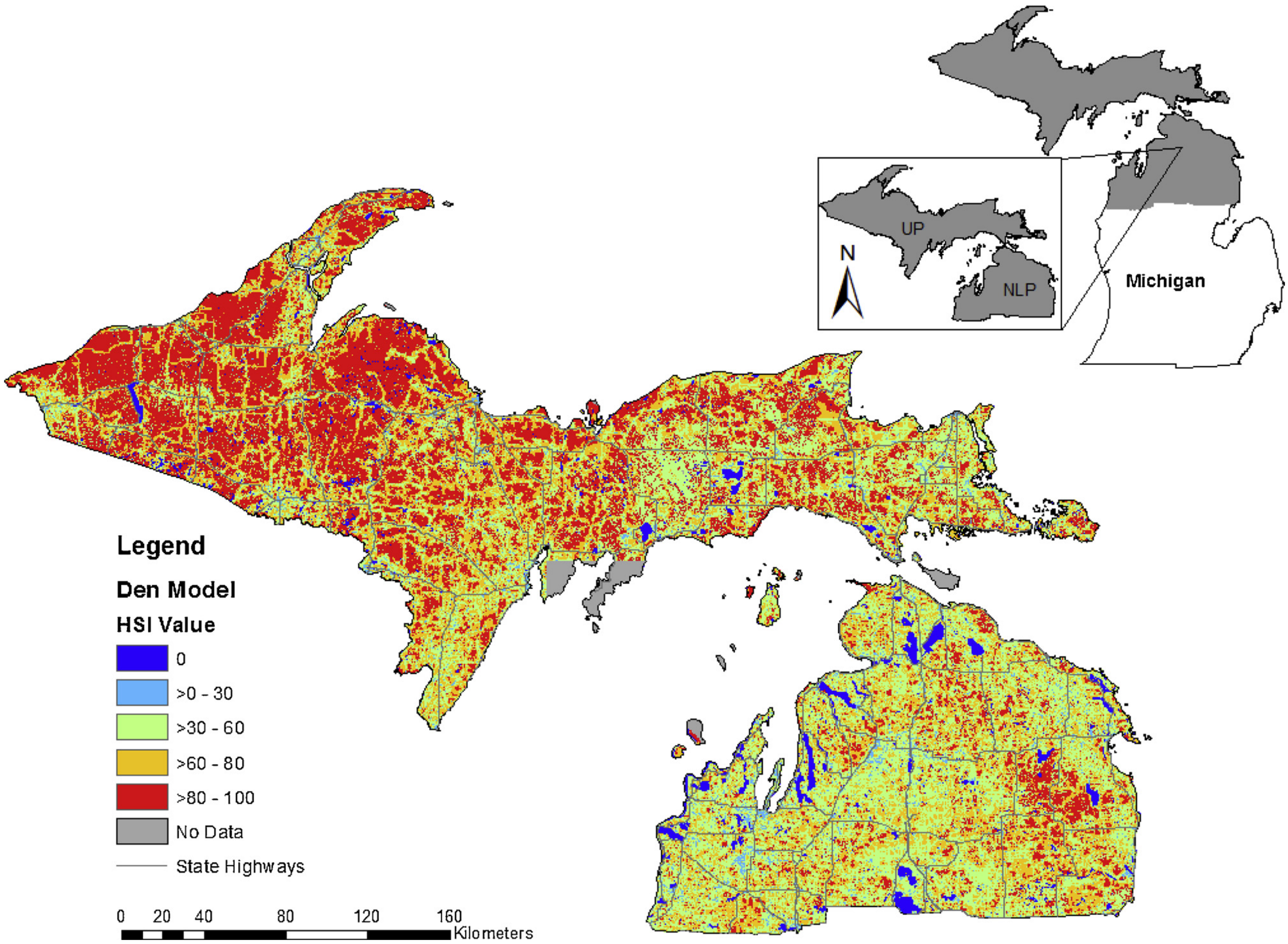

Fig. 1. Gray wolf den habitat suitability raster. Values represent HSI score. Blue (HSI score = 0) areas represent absolute non-habitat while red (HSI score = 80–100) represents best habitat. Full interpretation of HSI scores can be found in Appendix I. Gray areas represent No Data.

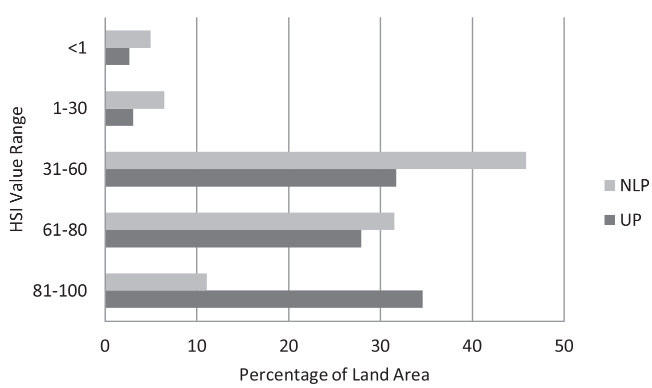

Fig. 2. Proportional comparison of gray wolf den habitat quality (via habitat suitability index values) in the Upper and northern Lower Peninsulas of Michigan.

Table 1
Chi-squared and p-values of "successes" vs. "failures" of known wolf den locations and random points ($\alpha = 0.01$, DF = 1).

	χ2	*p*
Known Dens	10.9	0.0009
Random 1	2.00	0.16
Random 2	0.22	0.64
Random 3	0.89	0.35
Random 4	0.89	0.35
Random 5	3.56	0.06
Random 6	0.89	0.35
Random 7	3.56	0.06
Random 8	0.89	0.35
Random 9	2.00	0.16
Random 10	2.00	0.16

successes of the known den locations are statistically different than expected from random distributions ($\chi2 = 10.9$, $p = 0.0009$, $\alpha = 0.01$, DF = 1), while all random iterations of locations indicate the number of successes do not differ from expected values.

3.3. Landscape connectivity model

Species experts ranked land cover as the most important dispersal corridor variable, followed by road density and topographic position (Appendix C); the prey density variable was dropped due to relatively low expert ranking and lack of reliable prey density data in Michigan. Within the land cover variable, lowland coniferous and lowland deciduous were ranked the most suitable land cover types for dispersal, respectively. Experts ranked a road density range of $\leq 0.38\ km/km^2$ as most suitable for travel. Least suitable were road densities $> 0.53\ km/km^2$, however this was still given a relatively permeable score of 31. Within the topographic position variable, valleys were given the most suitable score for travel.

Modeling efforts suggested high permeability of the landscape for wolves throughout the UP, and much less permeability throughout the NLP, especially west of Interstate 75 which traverses down the center of the peninsula. Approximately 40% of the landscape in the UP was estimated to contain highly suitable habitat (> 80 HSI) for successful

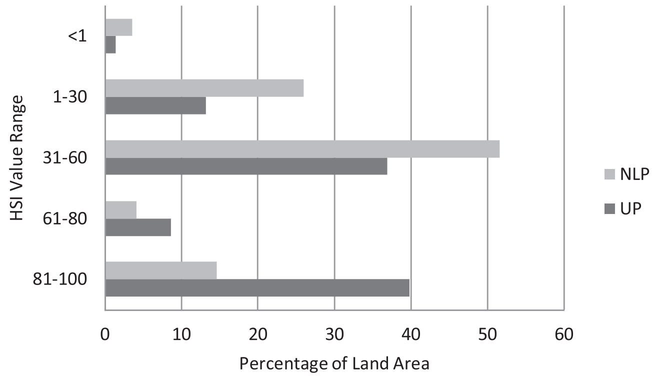

Fig. 3. Proportional comparison of permeable land area for gray wolves (via habitat suitability index values) in the Upper and northern Lower Peninsulas of Michigan.

wolf travel, and another 8.6% of the landscape was estimated to contain habitat of moderate suitability (61–80 HSI) (Fig. 3). The NLP is of much lower quality proportionally, with only approximately 15% of the land area being of optimal permeability and only another 4.6% being moderately suitable. More than 50% of the NLP is of low or marginal quality (31–60 HSI), and approximately 30% is completely unusable (very high energy/mortality) for travel (< 30 HSI).

The route of greatest permeability connecting den habitat in the Ottawa National Forest in the west to habitat in the easternmost block of the Hiawatha National Forest measured 379 km in length (Fig. 4). Forested cover types represented 88% of this path (35% deciduous, 42% coniferous, mixed 11%), and agricultural lands made up < 1%. Additional cover types included small amounts of interspersed water/wetland (9%), paved, barren, and urban land (all < 1% each).

A large corridor was modeled in the NLP connecting den habitat in Wilderness State Park in the northwest to large blocks of den habitat in the largely privately-owned "club country" in the southeastern NLP. The corridor's main route along the northeastern shore of the peninsula (henceforth referred to as the *eastern* branch) is the route of highest suitability, as it contains the most permeable 0.1% of the landscape. This eastern branch contained 72% forested cover type (43% coniferous, 23% deciduous, 6% mixed), 14% water/wetlands, 10% barren/pasture, 2% agriculture, 1% paved and < 1% urban. The minimum width was 3.4 km and maximum width was 10.7 km. While this route contained the highest landscape permeability, it also had greater inter-patch distance than the alternative western route. The alternative branch (western branch) of the corridor identified contained less suitable habitat but was identified by the model as containing the least inter-patch distance. The western branch of the LCP was 125 km in length and contained 74% forested land cover type (44% deciduous, 24% coniferous, 6% mixed), 14% water/wetland, 9% pasture/barren, and < 1% urban, agriculture, and paved. This branch had a minimum width of 293 m, and a maximum width of 7 km.

4. Discussion

Recent studies have shown that resource selection differs significantly during various life events or behavioral states (Abrahms et al., 2017) and as such, resource selection during dispersal for wide-ranging carnivores may vary markedly from daily use and selection within the home range (e.g. Elliot et al., 2014; Zeller et al., 2015). It is therefore important to understand habitat selection and suitability at multiple spatial scales that coincide with various life events for a species such as the gray wolf. Our study is the first to have integrated a

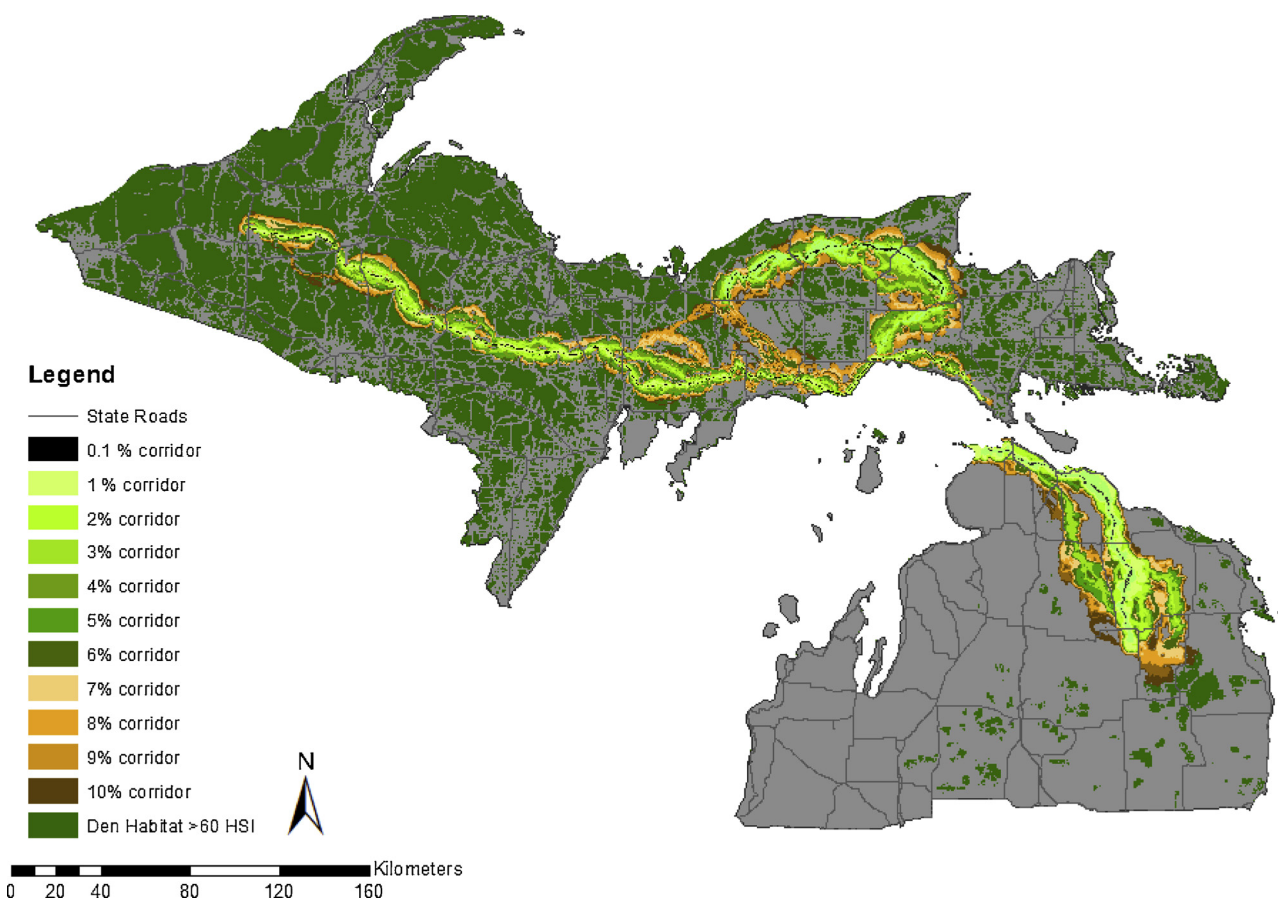

Fig. 4. Combination of models of gray wolf suitable den habitat patches with a habitat suitability index (HSI) of > 60 and least-cost travel paths between them.

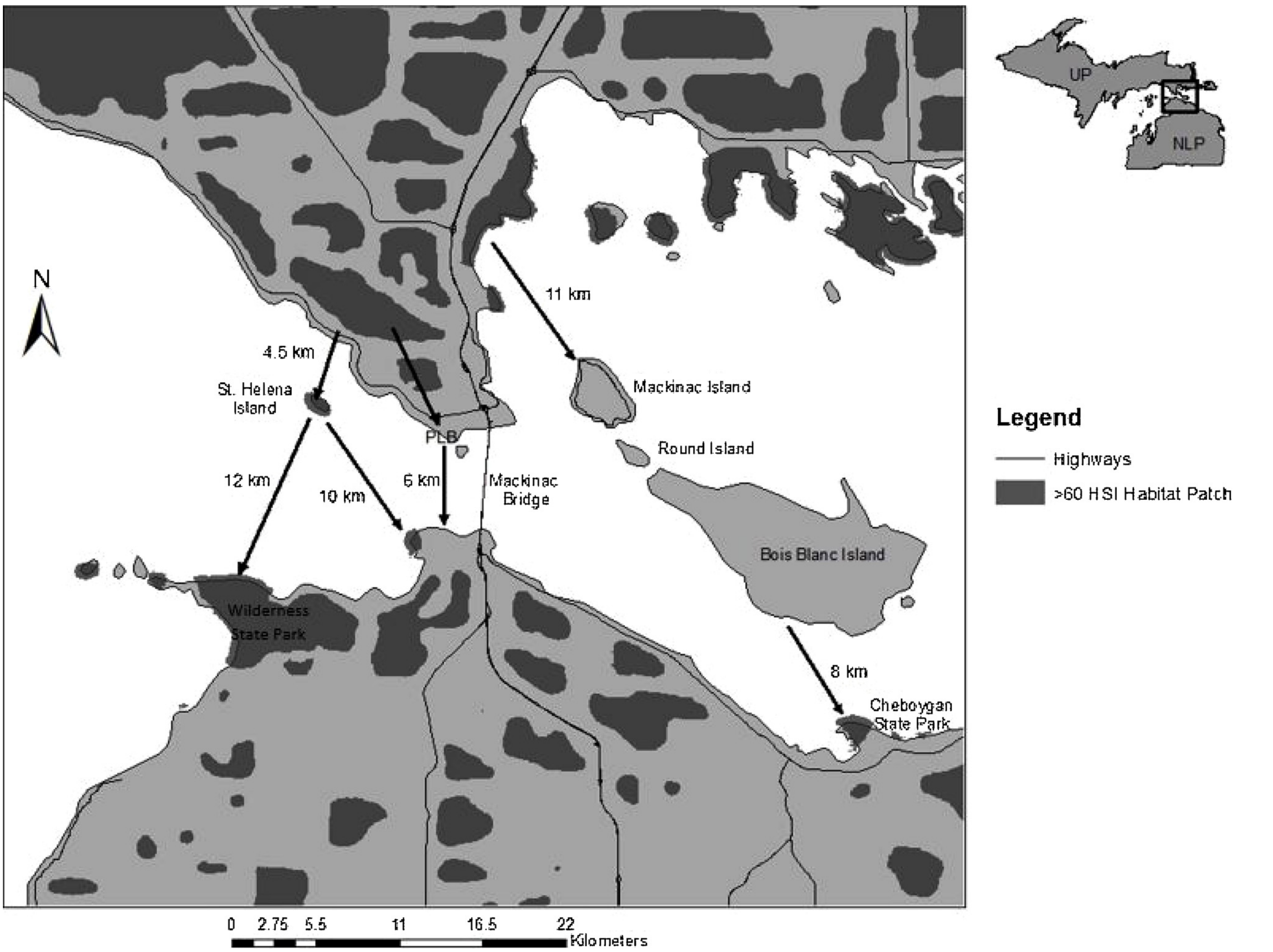

Fig. 5. Speculated routes of gray wolf dispersal from Michigan's Upper Peninsula to the Lower Peninsula. The western-most route to St. Helena Island identifies a path crossing the least distance of unsuitable habitat (~715 m), but greatest total distance on ice (~14.5–16.5 km). The center route identifies a route of greater travel distance in unsuitable habitat (~4.5 km), but the least distance spent on ice (~6 km) on the Straits of Mackinac. The eastern route represents a mix of potential ice (~21 km) and island (~20 km) travel. PLB = Point La Barbe.

multi-scale hierarchical approach to wolf habitat suitability in the Great Lakes.

Previous research conducted at the home range level (Gehring and Potter, 2005) suggested that enough habitat remains in Michigan's NLP to support 50–100 wolves, but the ability to traverse the landscapes between habitat patches to fully use identified suitable habitat was unknown. Our models suggest high quality and quantity of dispersal/range (first-order) and den/rendezvous (third-order; Johnson, 1980) habitat for wolves in Michigan's Upper Peninsula, however quality and quantity of both are greatly reduced in the NLP. Despite our estimates indicating that over 1900 km^2 of high quality den habitat exists in the NLP, permeability between these habitat patches is relatively low which may reduce accessibility to many of these areas for recolonizing wolves. Furthermore, much of the largest, unfragmented den habitat identified in the NLP were largely within private hunt-club land, owned by individuals that may or may not be tolerant of wolves. Given that tolerance of wolves by humans is potentially the most important factor in wolf survival and persistence in human-dominated landscapes (Ballard et al., 1987; Fuller, 1989; Mech, 1989; Wydeven et al., 2001, Treves and Bruskotter, 2014), land ownership may be a significant issue in the recolonization of breeding populations of wolves in the NLP.

Nevertheless, notably large patches of den/rendezvous site habitat on public lands were also identified in the northernmost areas of the NLP, such as in Wilderness State Park in the northwest and the Pidgeon River State Park in the northeast, which may support small populations of breeding wolves without the need to traverse significant portions of the landscape of the Lower Peninsula. Additionally, modeling efforts identified potential dispersal corridors that, while in an overall less permeable landscape than the UP, still represented habitat fairly amenable to dispersing wolves, with greater than 70% forest cover and little to no urban areas. Thus, lower connectivity between den patches may impede, but not necessarily totally prevent, the successful return and endurance of established wolf populations to the NLP.

4.1. Dispersal from UP source populations

Further confounding the potential for recolonization is the likelihood that the input of new individuals into NLP populations may be perpetually low, although field documentation and public reports indicate occasional dispersers arriving from the UP. For example, in 2004 a radio-collared female wolf originally from the UP was accidentally trapped and killed in Presque Isle County (Michigan Department of Natural Resources, 2008) and in 2015 a gray wolf was detected via trail camera on the Little Traverse Bay Band of Odawa Indians (LTBBOI) reservation, and confirmed by genetic testing of scat (LTBBOI *unpublished data*). Both of these confirmed detections were relatively near to the Straits of Mackinac (or "Straits"; narrow channel of water connecting Lakes Michigan and Huron) where wolves have been documented dispersing across ice in winter during full ice-over (Williams, 2003). We theorize that the Straits area would be the most likely area

Table A1
Biological interpretation of attribute ranks, and ultimately, habitat suitability indices (HSI) for den habitat and travel corridor attribute classes, adapted from Beier et al. (2007).

HSI Score	Biological Interpretation
100	Best den possible den habitat; highest likelihood of pup survival. Best habitat for travel; highest survival and least energy cost.
80	Lowest score typically associated with consistently successful dens and pup survival. Sub-optimal permeability for travel; moderate survival and energy cost.
60	Lowest score associated with consistent use for denning and rearing (but may not be consistently successful in terms of pup production and survival). Lowest score associated with consistent use for dispersal/travel; high energy costs and frequent mortality.
30	Lowest value associated with occasional use for denning and travel. High risk of mortality.
< 30	All values less than 30 typically avoided for den site selection and travel. Very high mortality risk and energy cost (travel).
0	Absolute non-habitat.

Table B1
Den habitat variable weights* and attribute class ranks† as summarized from species expert surveys.

Variable/Attribute Class	Weight (%) / Rank
Distance to Water	30%
0-50 m	82
51-80 m	86
81-100m	78
101-200m	64
> 200m	40
Distance to Roads	29%
0-500 m	28
501-1000m	59
1001-2000m	75
> 2000m	87
Landcover	22%
Agriculture	11
Barren	23
Upland Deciduous	68
Upland Coniferous	74
Lowland Deciduous	59
Lowland Coniferous	63
Mixed Forest	78
Non-Forested Wetland	12
Urban	1
Water	0
Roads/Paved	2
Soil Type (Percent Sand)	19%
Non-sand	30
1-25% sand	39
25-50% sand	58
50-75% sand	71
75-100% sand	73

* Weights for habitat variables are a percentage of 100 and therefore must sum to a total of 100%. Attribute classes within each variable are ranked 0–100 following the biological interpretations in Appendix I but are not a percentage and therefore do not need to sum to 100.

for wolf dispersal across ice, as even in milder winters the Straits tend to obtain > 80% ice-over (NOAA-GRERL, 2018: https://www.glerl.noaa.gov/data/ice/historicalAnim/). Moreover, ice-breaking regimes that keep the Straits open for shipping channels typically pause from late January through mid- to late-March (Miller, 2017), allowing up to 6–8 weeks annually of potential dispersal across the Straits. Indeed, wolves can and do disperse relatively long distances across ice (Peterson, 1977; Hutt, 2003; Linnell et al., 2005), and as such, successful dispersal across the Straits would be bolstered by the persistence of on-land "refuge" habitat near dispersal and arrival points.

Therefore, we saw an opportunity to use our model to identify potential dispersal routes across the Straits, using a combination of ice travel and patches of habitat suitable for dispersal as "stepping stones" through relatively unsuitable or high-risk landscape. Theoretically, a dispersing wolf would choose between traversing greater distances of ice, or spend more time traversing through unsuitable habitat on land. Our model indicates that a suitable travel corridor in the UP terminates in the Hiawatha National Forest northwest of Point La Barbe, (see Fig. 4). This particular area near the Mackinac Bridge represents the shortest water/ice distance between the UP and the NLP (6 km), however there is a considerable distance of unsuitable habitat between the small patch of suitable habitat just north of Point La Barbe (PLB) and the habitat that terminates in the Hiawatha National Forest (Fig. 5). Crossing near the Mackinac Bridge would therefore represent the least amount of time spent on ice but ultimately navigating through approximately 4.5 km of unsuitable habitat and high human activity (due to cities near the bridge) on land.

Another speculative route would again involve dispersing from the Hiawatha National Forest to the large habitat patch northwest of Point La Barbe, but traveling approximately 4.5 km on ice to St. Helena Island, then dispersing another ˜10 km on ice if it entered the NLP at the habitat patch at McGulpin Point, or 12 km if it entered in the larger habitat patch within Wilderness State Park. This potential route would reduce time spent traversing in unsuitable habitat on land (715 m) but

Table C1
Landscape permeability variable weights* and attribute ranks†, summarized from species expert surveys. Grouping of road densities adapted from Mladenoff et al.'s (1995) probability classes of wolf occurrence.

Variable/Attribute Class	Weight (%) / Rank
Road Density (km/km2)	39%
0 - 0.38	92
0.39 - 0.45	76
0.46 - 0.53	58
0.53 - > 1.5	31
Landcover	43%
Agriculture	30
Barren	33
Upland Deciduous	81
Upland Coniferous	83
Lowland Deciduous	84
Lowland Coniferous	88
Mixed Forest	82
Non-Forested Wetland	44
Urban	6
Water	6
Roads/Paved	16
Topographic Position	18%
Valley	81
Ridgetop	68
Slope	62
Flat	69

* Weights for habitat variables are a percentage of 100 and therefore must sum to a total of 100%. Attribute classes within each variable are ranked 0–100 following the biological interpretations in Appendix I but are not a percentage and therefore do not need to sum to 100.

would increase the travel distances on ice to potentially 17 km. A final speculative route would be a mix of ice and island travel, beginning in the UP at the habitat patch on the eastern edge of the minor peninsula, crossing approximately 11 km of ice to Mackinac Island, another ˜2 km combined ice travel to Round Island and Bois Blanc Islands, and finally 8 km ice travel to Cheboygan State Park on the mainland of the NLP. Our models did not include Round and Bois Blanc Islands due to lack of data, however these islands are heavily forested, with very few roads or developed areas, making them likely to be suitable for wolf travel. Mackinac Island has a high level of human activity during snow-less seasons, however is very sparsely populated during winter months and could likely be easily traversed by wolves at that time.

4.2. Conclusions

While previous studies of wolf habitat suitability in the Great Lakes region have shown adequate habitat availability at the home range level, our study used a multi-scale modeling approach and revealed that other levels of critical habitat may be lacking in Michigan's NLP. Individuals need to be capable of moving through the landscape beyond their natal areas to find resources and unoccupied habitat, as well as maintain genetic flow between groups (Hanski and Gilpin, 1997; Young and Clarke, 2000). For the wide-ranging gray wolf, landscape habitat suitability beyond home range needs to be assessed as well as micro-scale habitat such as denning and birthing grounds. A large portion of den habitat in the NLP was identified on private hunt-club property, potentially making conservation and management challenging. The lower permeability of the NLP landscape, combined with low input levels from founding wolf populations in the UP may lead to isolated populations and thus genetic inbreeding issues (Shaffer, 1978; Gilpin and Soule, 1986; Walker and Craighead, 1997). Low population numbers and high human presence in the NLP may also confound establishment of resident wolf populations as conflict with humans (and thus high mortality) is probable. Inclusion of first- and third-order habitat suitability provided a more comprehensive assessment of wolf habitat suitability and recolonization potential in the NLP, indicating that areal estimates of available second-order habitat alone may potentially overestimate the number of wolves the NLP could support.

Our results suggest that gray wolves may benefit from increased connectivity of habitat patches in Michigan's NLP to fully use identified suitable habitat. Because road density plays an important role in landscape connectivity (permeability model), minimizing road effects within our identified dispersal corridors may be a conservation option (Saunders and Hobbs, 1991). In addition, land managers can use our identified potential routes of dispersal between the NLP and UP to target monitoring activities to key patches, and if being used, provide added protections to enhance recolonizing the NLP. Given our finding that NLP landscape has adequate but more disconnected suitable habitat to support dispersing individuals and breeding packs, determining the effects of potentially increased mortality and energy expenditure while dispersing on recolonization potential is an important aspect requiring additional research and conservation measures.

Hierarchical habitat modeling can provide a more complete picture of landscape habitat suitability and often have stronger inference abilities than a single level alone (Johnson et al., 2004; DeCesare et al., 2012; McGarigal et al., 2016; Zeller et al., 2017). Our modeling technique using GIS and expert opinion presents a unique opportunity for other locales and other highly-mobile species to be modeled relatively quickly and inexpensively. Applying our hierarchical approach integrates habitat selection theory as well as an assessment of spatial structure that provides a habitat framework to assess how population demographics may be influenced to better guide regional conservation planning.

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Appendix A

Table A1

Appendix B

Table B1

Appendix C

Table C1

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