

Wolves in the Lower Peninsula of Michigan: habitat
modeling, evaluation of connectivity, and capacity
estimation

By

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Abstract

Gray wolf populations have been rebounding in the Great Lakes region, after being nearly extirpated from the conterminous United States. Breeding populations of wolves have established in the Upper Peninsula of Michigan but have not yet become widely established in the Lower Peninsula (LP) of Michigan, despite several sightings of wolves in the LP since 2004. The objective of this analysis was to determine the quantity of potential habitat for wolves in the LP using wolf occurrence data obtained by radio telemetry, Maxent software, and ArcGIS software. The habitat model was evaluated to determine if the potential habitat could support a viable population. A species distribution model (SDM) was created in Maxent and analyzed in ArcGIS to estimate the amount of potential habitat for wolves in the LP. Connectivity of potential habitat was evaluated by looking at least cost paths, corridors, and potential dispersal land. I found that there is 2,674-3,246 km² of potential habitat in the LP, which could support 52-63 wolves. This is below the minimum of 100 necessary to sustain a viable population. All habitat patches at least 50 km² in size are in the northern LP, but are not connected by land suitable for dispersal. Thus, although there are habitat patches of sufficient size in lower Michigan, it is likely that packs of wolves that may inhabit these patches will remain relatively isolated and have difficulties dispersing throughout lower Michigan. It is unlikely that they will be able to inhabit or disperse through the southern LP without land management geared towards creating larger unfragmented habitat patches and suitable dispersal corridors. This analysis highlights the need for land management geared towards wolves in order to allow them to continue to recover their former range in the United States.

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Introduction:

The gray wolf (*Canis lupus*) was nearly extirpated from the United States by the 1900s, with the exception of a small part of Minnesota and Isle Royale, Michigan (U.S. Fish and Wildlife Service, 2010). Wolf bounties and employment of state trappers incentivized the removal of this species throughout the country. Thanks to legal protection and changing public attitudes, wolves have been slowly recovering in the United States (US), however their range is still a tiny fraction of what it once was (Figure 1). There are now over 4,100 wolves across Minnesota, Wisconsin, and Michigan (US Fish and Wildlife Service, 2010). The recovery of the Great Lakes subpopulation has led some to believe that wolves no longer need to be listed as an endangered species under the federal Endangered Species Act (ESA), as evidenced by a complicated history of listings and delistings under the ESA. However wolves are only found in a small fraction of their former range throughout the US and the existing subpopulations are widely dispersed, suggesting the full recovery of the gray wolf throughout the US, in a general sense, has yet to occur. Habitat loss and a growing human population throughout the US point to a need for increased efforts for planning for wolf conservation to allow for its continued recovery.

The Lower Peninsula (LP) of Michigan is the last major region of the Great Lakes area with potential habitat where breeding populations of wolves have not yet become widely established. Wolves have been sighted in the LP since 2004, with sightings confirmed in Presque Isle, Emmett, and Cheboygan counties (Figure 2) (Michigan Department of Natural Resources, 2010), and wolf reproduction documented in 2010 (D. Beyer, MDNRE, pers. comm.).

I wanted to determine the location of potential habitat for wolves in the LP using a different modeling method, more environmental variables, and with actual wolf occurrence data obtained by telemetry, to obtain a potentially more accurate model that considers the adaptability of wolves. I also wanted to evaluate the connectivity of that potential habitat to see what difficulties dispersing wolves may face. I also wanted to assess the quantity of potential habitat in order to estimate the number of wolves the potential habitat would be able to support, to determine if the LP could support a viable population of wolves. The LP seemed to be a likely target for doing an analysis of wolf recovery and conservation planning, since wolf sightings there have been becoming more common. Geospatial mapping of potential wolf habitat (habitat modeling) and likely dispersal routes between habitat patches is a useful tool in guiding management decisions that impact the wolf, such as determining where to site conservation preserves or development projects.

Figure 1: Historical range, range at time of listing, and current range of the gray wolf in the United States (U.S. Fish and Wildlife Service, 2010).

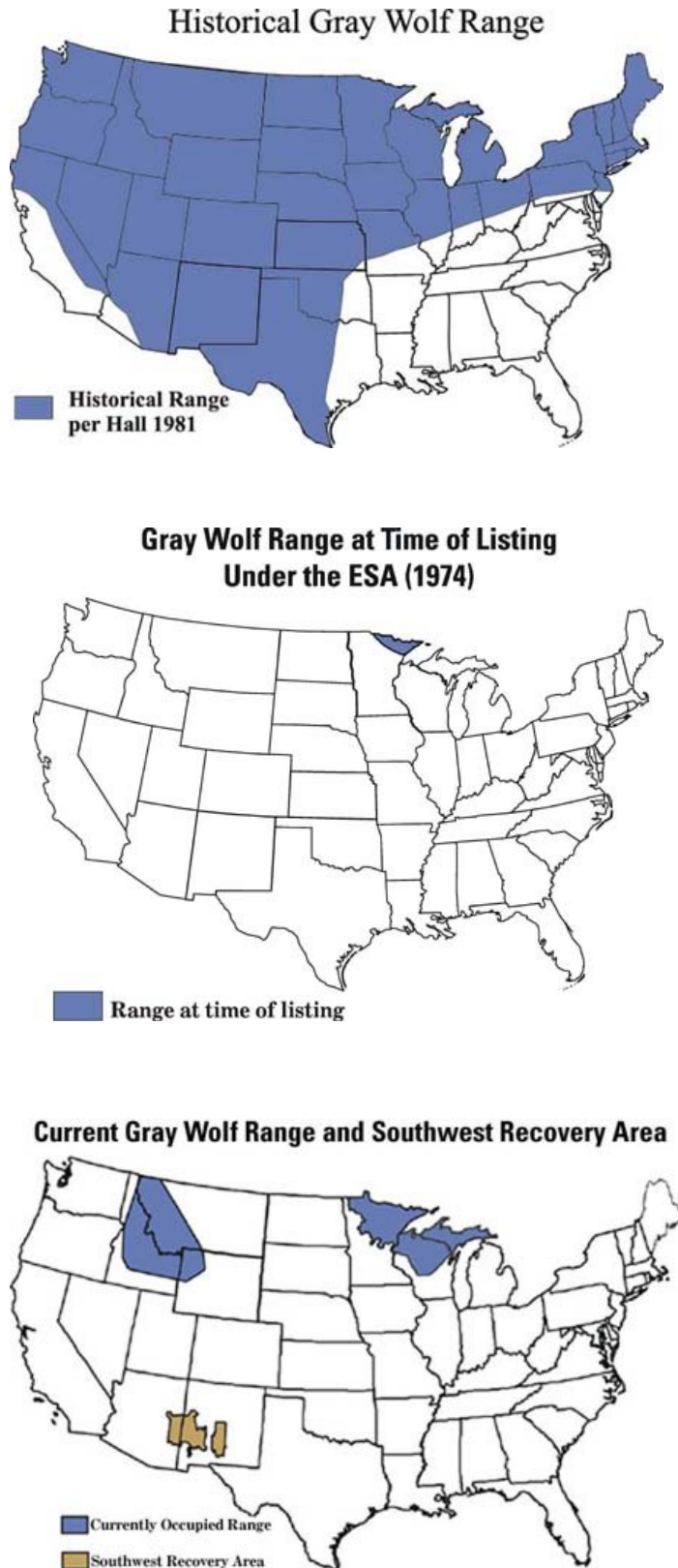
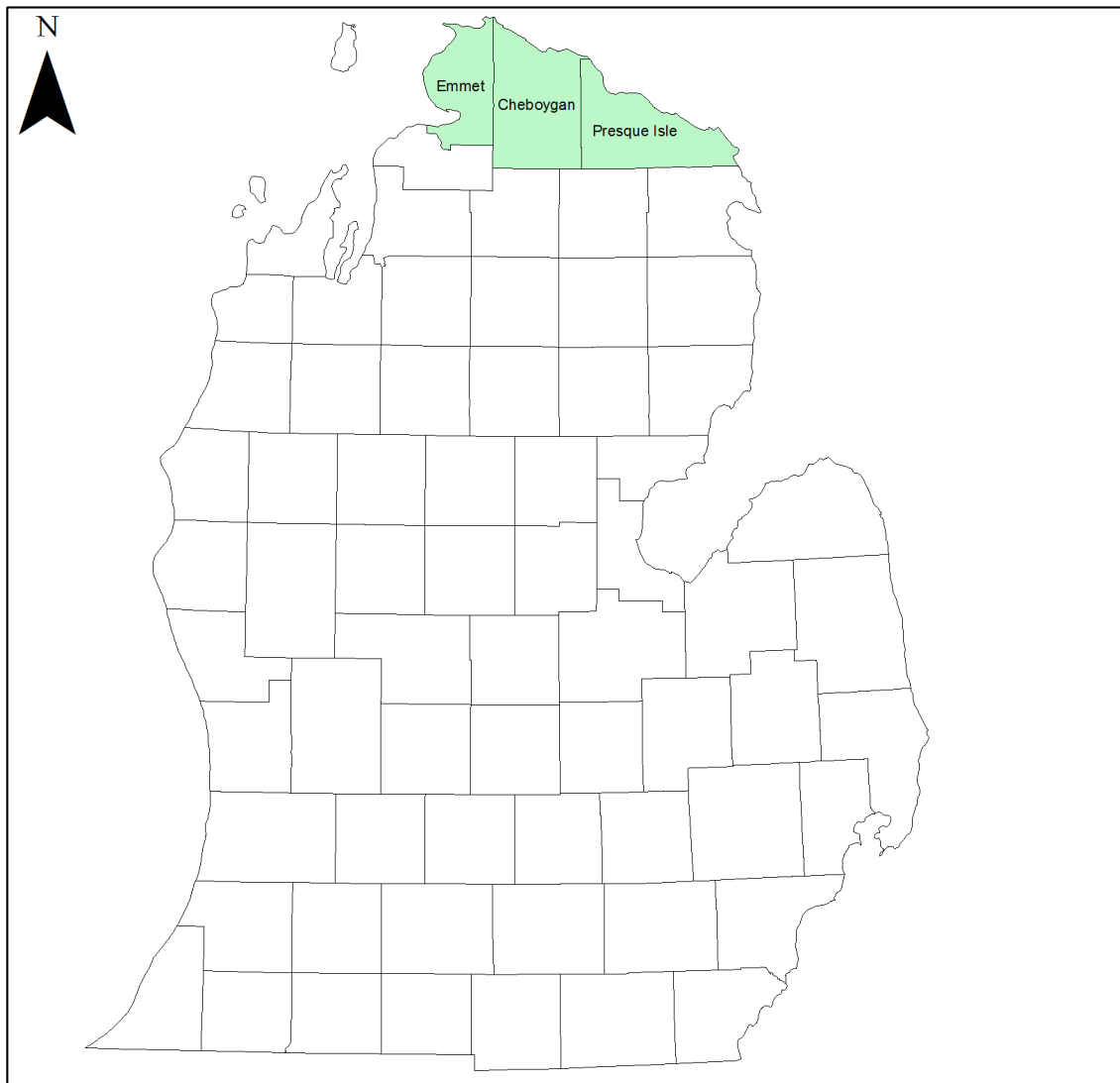


Figure 2: Counties with confirmed wolf sightings since 2004.

Counties with confirmed wolf sightings since 2004



0 30 60 120 Kilometers

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Projection: NAD 1983 UTM Zone 16N

Wolf habitat modeling

Mladenoff et al. (1995) found that road density was the most significant variable in a logistic regression model predicting where wolves will occur in Wisconsin. He found that wolves were unlikely to inhabit areas with road density greater than 0.7 km/km². Gehring and Potter (2005) used this road density model to quantify potential wolf habitat in the northern lower peninsula (NLP) of Michigan, and found that 2,198-4,231 km² of favorable habitat existed in the NLP, which they estimated would support a population of 40-105 wolves. Potvin (2003) also completed a habitat model for the LP that included deer density as a predictor variable.

These analyses have been useful, however Mech (2006) found that 60% of wolf pack territories formed in Wisconsin during 1993-2004 were in locations that Mladenoff's model had predicted to be less than 50% suitable, including 22% in suitabilities of 0-9%. Mech suggested this model failed to consider the adaptability of wolves. A model that includes more predictor variables and uses actual wolf occurrence data may be more accurate in predicting actual wolf habitat.

Objective

The objective of this analysis was to determine the quantity of potential habitat for wolves in the LP. My modeling approach differed from Mladenoff's in that it included additional variables and used actual wolf occurrence data. I compared the results of my study with the prior analyses and determined the significance of other environmental variables in predicting wolf occurrence. I also evaluated the connectivity of potential habitat and estimated

the capacity of wolves that the potential habitat could support. These factors were evaluated to determine if the wolves in the LP could establish a viable population and serve as a source population for dispersers to more southern states.

Factors influencing wolf habitat

Harrison and Chapin (1998) defined core wolf habitat in the northern US as areas with less than four humans per km², and defined dispersal land as areas with ten humans or less per km². Wolves were found to generally not persist in areas where road densities exceeded 0.58 km/km² (Thiel, 1985, Jensen et al, 1986, Harrison and Chapin, 1998) but may persist in areas with road densities as high as 0.73 km/km² if these areas are adjacent to habitat with less human access. Acceptable human density can vary based upon the road density in an area (Carroll et al, 2003). Wolves were found to most often occur in forests with at least some coniferous stands and they avoided agricultural land (Conway, 1996). Forest cover appears important, perhaps by reducing the level of contact with humans (Boitani, 2003). Mladenoff et al. (1995) found that most pack areas were located within some type of forest. Treves (2009) found that dispersing wolves selected wildland areas and avoided exposed habitats and areas modified by humans, including pastures, hayfields, row crops, roads, houses, and farms. The most highly selected areas were similar to habitats selected by wolf packs. Elevation and slope may be significant; wolves are coursing predators that avoid steep terrain (Pacquet et al., 1996). Precipitation is associated with ecosystem productivity and may thus be a surrogate for prey availability (Larsen and Ripple, 2006). Mladenoff et al. (1995) found that public land

ownership had a strong association with wolf habitat, as did Houts (2000) for the northern Rocky Mountain region. The probability of wolf occupation in upper Michigan was positively correlated with deer density (Potvin et al., 2005).

Numerous studies have evaluated the potential for gray wolves to return to areas they formerly inhabited, based on Geographic Information System (GIS) habitat modeling. Beerman (2009) performed such an analysis in Pennsylvania that included human density, road density, and land use classifications. Belongie (2008) created a habitat suitability model to assess wolf pack ranges in the western UP and used population density, road density, prey density, and land use/land cover as the predictor variables. Carroll et al. (2003) used vegetation, brightness, greenness, and wetness from satellite data, topography, climate, and human impact variables to predict wolf distribution in the US Southern Rocky Mountain (SRM) region. Glenz et al. (2001) used percentage urban areas, inhabitant density, percentage arable lands, minimum of altitude, percentage northwest exposure, and a wild ungulate diversity index as predictors of wolf habitat suitability in Switzerland. Jedrzejewski et al. (2004) used percent forest cover, forest fragmentation, river length, length of roads, length of railways, number of villages, number of towns, number of domestic animals killed by wolves, and the shortest straight-line distance to the eastern border of Poland (as proxy of distance to continuous range of wolves) as predictors associated with wolf distribution and abundance in Poland. Harrison and Chapin (1998) included land use/land cover, human density, and road density for predicting potential wolf habitat in eastern North America. Massolo and Meriggi (1998) included 58 variables and found that anthropic variables, total forest cover, wild prey availability, altitude, and snow

cover were significantly different among their four classes of wolf presence in northern Italy. Larsen and Ripple (2006) modeled gray wolf habitat in the Pacific Northwest using prey availability, road density, human density, percentage forest cover, percentage public land, and annual precipitation. Oakleaf et al. (2006) used Bailey's ecoregions, road density, human density, protection status, land ownership, slope, elevation, land cover, ungulate density, cattle density, and sheep density to construct wolf habitat models for recolonizing wolves in the northern Rocky Mountains.

For my analysis, I chose variables that were included most often in the prior studies, that I determined to be relevant in Michigan, and that I thought would contribute unique information to the habitat model. I chose land cover/land use, human density, road density, land ownership, slope, elevation, and precipitation. Some analyses have included brightness, greenness, and wetness indices as they are correlated to ecological factors such as net primary productivity (Carroll et al. 2003), but these variables were not included here since precipitation was included as a surrogate for productivity. Human presence variables other than road or human density such as the number of villages or towns, distance to nearest city, percentage urban areas, etc. were considered to be redundant and thus were not included. Since prey data were not readily available and deer were assumed to be well distributed and abundant in lower Michigan (Michigan DNRE, 2010), this variable was not included.

History of wolves in Michigan

Wolves were essentially eradicated throughout Michigan by 1960 (Michigan DNRE, 2010). The wolf was first given full legal protection in Michigan by the state in 1965. In 1967, the wolf was protected on federal lands by the Endangered Species Preservation Act of 1966. In 1974, the wolf was protected federally when it was listed as an endangered species under the Endangered Species Act of 1973. In 1974 a wolf recovery program was started in Michigan and in 1990 the first documented reproduction of gray wolves on the mainland of Michigan since 1954 occurred. The population has been increasing since 1991, with about 580 wolves in the UP counted in late winter 2008-2009 (US Fish and Wildlife Service, 2010).

In 2003, the federal government reclassified wolves to threatened in the eastern distinct population segment (which includes Michigan). In 2005, federal court enjoined and vacated the reclassification and wolves were returned to their federally endangered status. In 2007, the federal government delisted wolves in the Western Great Lakes distinct population segment (DPS). In 2008 a court ruling placed Western Great Lakes wolves back under ESA protection, but in 2009 there was a final rule to delist the Western Great Lakes DPS. Later in 2009 ESA protection was restored for Western Great Lakes wolves, which was still in effect at the time of this analysis (US Fish and Wildlife Service, 2010).

Wolf biology

Wolves are habitat generalists and use all types of habitats in the northern hemisphere with the exception of rain forests and deserts (Mech, 1970). In the United States the historical range covered most of the country except part of California, Arizona, and the southeastern US.

The gray wolf did not occupy the southeastern US due to the red wolf (*Canis rufus*) occupying this region (US Fish and Wildlife Service, 2010). Ungulates (large cloven-hoofed mammals) are the primary prey of wolves, but they also eat snowshoe hare (*Lepus americanus*), beaver (*Castor canadensis*), and other small prey to supplement their diet (DeGiudice et al. 2009). Wolves are pack animals with an average winter pack size of 4.6-4.9 wolves in Michigan from 2003-2007 (Michigan Wolf Management Plan, 2008). Generally, only the dominant (alpha) male and female of each pack breed (Mech, 1970).

Average wolf territory sizes in the UP have ranged from 56-331 km² (Huntzinger et al. 2005). Dispersers can travel hundreds of kilometers; metapopulations tend to occupy very large areas. In a study of wolves that dispersed from the UP of Michigan to other states, the average distance between the source and destination points was 216 km (Michigan Wolf Management Plan, 2008). The farthest documented dispersal by a Michigan wolf was 756 km; the wolf was killed in Missouri in 2001 and likely crossed major highways and agricultural land. Wolves can disperse across ice; they have crossed 24 km of ice to colonize Isle Royale (Mech, 1966). The Straits of Mackinac separated the LP from the UP and is 6.5 km in width at the narrowest point.

Study Area

This study was conducted within the boundary of the state of Michigan. The state has an area of 151,548 km², excluding Great Lakes waters (State of Michigan, 1990). The state had a total population of 9,938,480 on April 1, 2000 (US Census Bureau, 2000). Michigan is the only

state that consists of two peninsulas; the Great Lakes of Huron, Ontario, Michigan, Erie, and Superior surround the state (Figure 3). The LP has a higher density of agricultural and urban land and human population than the UP; the northern LP had 1 farm/13 km² whereas the UP had 1 farm/49km² (Beyer et al. 2006).

Figure 3: Great Lakes region (GLIN, 2010).



Materials and methods:

Data

Maxent was chosen as the probability distribution modeling method, as it has been found to be higher-performing (higher Area Under the Curve, or AUC) than generalized linear models (GLM) and other species distribution predicting methods and can use presence-only data (Elith and Graham, 2006). Maxent is a machine-learning probability distribution modeling software that estimates distributions by finding the distribution of maximum entropy with the constraint that the expected value of each predictor (or environmental) variable in the estimated distribution matches its empirical average (Phillips et al. 2006). It is a maximum-likelihood method that generates a probability distribution over pixels in the grid. The idea of maximum entropy is to ensure that the estimated distribution satisfies any known constraints based on the ranges of the environmental variables associated with the occurrence data, and subject to the constraints the distribution should be most spread out (maximum entropy). The pixels of the study area comprise the space on which the Maxent probability distribution is defined, pixels with known species occurrence records comprise the sample points, and the features are the environmental variables (Phillips et al. 2006). The probabilities Maxent generates must sum to 1 over the whole grid. Maxent combines data from environmental variables and occurrence points and creates its own random 'background' points. It then outputs a species distribution model (SDM) with accompanying statistics and graphics.

Species occurrence points were provided by the Michigan Department of Natural Resources and Environment (DNRE). The DNRE obtained the points from radio telemetry,

observed by aircraft (Cessna 182s) at a median frequency of every 2 days from 1998-2008. A cartographic boundary file of Michigan with county boundaries was downloaded from the U.S Census Bureau (U.S. Census Bureau, 2010). Land cover, road data, a Digital Elevation Model (DEM), and Gap Analysis Program (GAP) land stewardship data were downloaded from the Michigan Geographic Data Library website (Michigan Center for Geographic Information, 2010). For human density, census data at the block group level were downloaded from the Duke Libraries website (Duke Libraries, 2010). Precipitation data were downloaded from the PRISM (Parameter-elevation Regressions on Independent Slopes Model) climate group website (PRISM, 2010).

The road layer that was downloaded was the “Michigan Geographic Framework all roads” layer, which consists of all roads in the Michigan Geographic Framework, as of 2003. Roads passable only by a 4-wheel drive vehicle (classes A65 and A7-A9) were excluded from the analysis, as was done by Mladenoff et al (1995). Road density was calculated using the line density tool to obtain a density for roads in km/km^2 . Land cover data downloaded was GAP land cover data derived from LANDSAT Thematic Mapper (TM) imagery. Imagery from 1997-2001 was used to identify land cover classes. There were 35 land cover classes in this layer, which were reclassified to only 9 categories based on significance of the classes to wolves, similar to the classification in Mladenoff et al. (1995) (Table 1). The DEM was at a 90-meter resolution with units measured in meters. Slope was calculated as percent rise using the slope tool in ArcGIS. A land ownership variable was calculated by using the GAP land stewardship layer’s variable for land category (which indicates public land) and merging with the counties

layer to set any non-public land to null. Human density in humans/km² was obtained by dividing the humans/mi² variable by 2.59. Precipitation data downloaded were the 30-year (1971-2000) average annual precipitation for the United States.

All analyses were conducted in ArcGIS 9.3. Environmental variables that were not already in raster format were converted to raster with a 1000 x 1000 meter raster cell size so that each pixel would represent 1 km², for ease of data interpretation, area calculations and compatibility with Maxent software. Data layers were projected to NAD 1983 UTM Zone 16N projection. The extent was set to the extent of the state of Michigan (the county boundaries layer).

Table 1: Land use reclassifications used for land cover/land use data layer in ArcGIS.

<p>Urban:</p> <ul style="list-style-type: none"> low intensity urban high intensity urban airports roads/paved parks/golf courses
<p>Agriculture:</p> <ul style="list-style-type: none"> not vegetated farmland row crops forage crops/non-tilled herbaceous orchards/vineyards/nurseries
<p>Deciduous forest:</p> <ul style="list-style-type: none"> northern hardwood association oak association aspen association other upland deciduous mixed upland deciduous lowland deciduous forest
<p>Coniferous forest:</p> <ul style="list-style-type: none"> pinus other upland conifers mixed upland conifers lowland coniferous forest
<p>Mixed forest:</p> <ul style="list-style-type: none"> upland mixed forest lowland mixed forest
<p>Water</p>
<p>Wetlands:</p> <ul style="list-style-type: none"> floating aquatic mixed non-forest wetland emergent wetland
<p>Shrubs/herbaceous:</p> <ul style="list-style-type: none"> herbaceous openland upland shrub/low density trees lowland shrub
<p>Non-vegetated:</p> <ul style="list-style-type: none"> sand/soil exposed rock mud flats other bare/sparsely vegetated

Maxent analysis

The seven aforementioned environmental variables were uploaded to Maxent 3.3.1, along with the wolf occurrence data. The model was run and accompanying model statistics were obtained: an analysis of omission/commission that shows how the model performed in accurately predicting wolf presence with suggested thresholds for model tuning, a response curve of each environmental variable that shows probability of wolf occurrence for different values of each variable, a table of variable contributions that shows how much each variable contributed to explaining wolf presence, and a jackknife analysis of variable importance that shows how important each variable is in explaining wolf presence when used by itself, and how much the model is affected when each variable is left out. Maxent output its SDM into a data layer in ascii format; the ascii layer was converted to a raster format using ArcGIS toolbox and was displayed in ArcGIS. The con tool was used to mask out land that would be unlikely to be wolf habitat based on the Maxent-suggested threshold value of 0.458 that maximizes the sum of training sensitivity plus specificity.

Least cost paths/corridors

A cost surface was created using a weighting scheme similar to what was used by Beerman (2009) (Table 2). I chose these values to be consistent with another analysis, and I thought the range of values would be enough to show differences between the value classes without resulting in a cost surface with values that were too large to work with. Only road density, human density, and land cover/land use were included in the cost surface, which was

created using the reclassify tool in ArcGIS. Forest was considered the least costly (least resistance) through which to pass (cost=0), while developed areas and water were considered the most costly (cost=10). Agriculture, shrubby or herbaceous land, and bare land were considered intermediate in cost (cost=5). Road densities of 0-0.58 km/km² were classified as least costly (cost=1), while the densest areas were classified as a cost of 15. Finally, human densities between 0-4 were considered least costly (cost=1), while the areas with highest human population density were assigned the highest cost (cost=15). These three layers were multiplied together to obtain the final cost surface, with values ranging from 1-2,250. This cost surface was used to create a corridor between the largest patch (patch 4) and an isolated patch that was the patch that was farthest from patch 4 that was at least 50 km² in size (patch 10). Corridors are useful in that they identify the range of accumulative costs between the two source patches and thus identify a swath of pixels that represent the best route, rather than just a single-pixel-wide path as in a least cost path. However, they are CPU intensive, so it would have been time prohibitive to choose this method to look at potential routes for wolves between all patches. Least cost paths between patch 4 and all the other patches were created, and flow direction and stream order tools were used to show which of these paths would be most heavily used. The single output map algebra tool was used with the equation “Int(Exp2(backlink_raster) / 2)” to create the flow direction raster (converts the cost backlink raster to a flow direction raster), and Shreve stream orders were assigned to the least cost path line segments. These hydrology tools are useful to label each least cost path segment with a value representing how much traffic it might get. With stream orders, a higher stream order

means that there is more water flowing through it because it has more tributaries; here a higher least cost path line segment value means that it is more likely that a wolf would use it due to its lower-cost terrain.

Table 2: Cost surface classifications	
Land cover	Cost
Forest (all types)	0
Agriculture, herbaceous, shrub, bare/sparsely vegetated	5
Urban, roads, airports, parks/golf courses, water, wetlands	10
Human density (humans/km ²)	
0	0
0-4	1
4-10	5
10-25,251	15
Road density (km/km ²)	
0	0
0-0.58	1
0.58-0.73	5
0.73-15.499	15

Habitat patches/connectivity

Habitat patches were created using the region group tool on the predicted wolf habitat layer using the 0.458 threshold from Maxent. Area of potential habitat was summed for all habitat patches, and also with only habitat patches larger than 50 km², based on what is known about minimum territory size for wolves. Dispersal land was defined as pixels with road densities less than 0.73 km/km² and human densities less than 10 humans/km² (Harrison and Chapin, 1998). Any land that did not meet these two requirements was set to null for the

potential dispersal land layer. Habitat patches were considered to be connected to each other if there was dispersal land between them.

Area of potential habitat/wolf capacity estimation

The area of total potential habitat and area of potential habitat in only the 50-km² or larger patches were calculated using the pixel count in the respective attribute tables and were converted to square kilometers (which, in this case, was the same as the pixel count since each pixel was 1,000 m² or 1 km²). Potential wolf capacity was calculated using the algorithm used in Gehring and Potter (2005):

$$N = \{AW / [M(1+i)]\} / (1-D)$$

N = estimated number of wolves

A = area of potential habitat (3,246 km² for all habitat patches, 2,674 km² for only 50km² or larger patches)

W=mean midwinter pack size (4.1)

M = mean midwinter territory size (179 km²)

i = proportion of saturated habitat in interstitial areas (0.37)

D = proportion of dispersers (0.15)

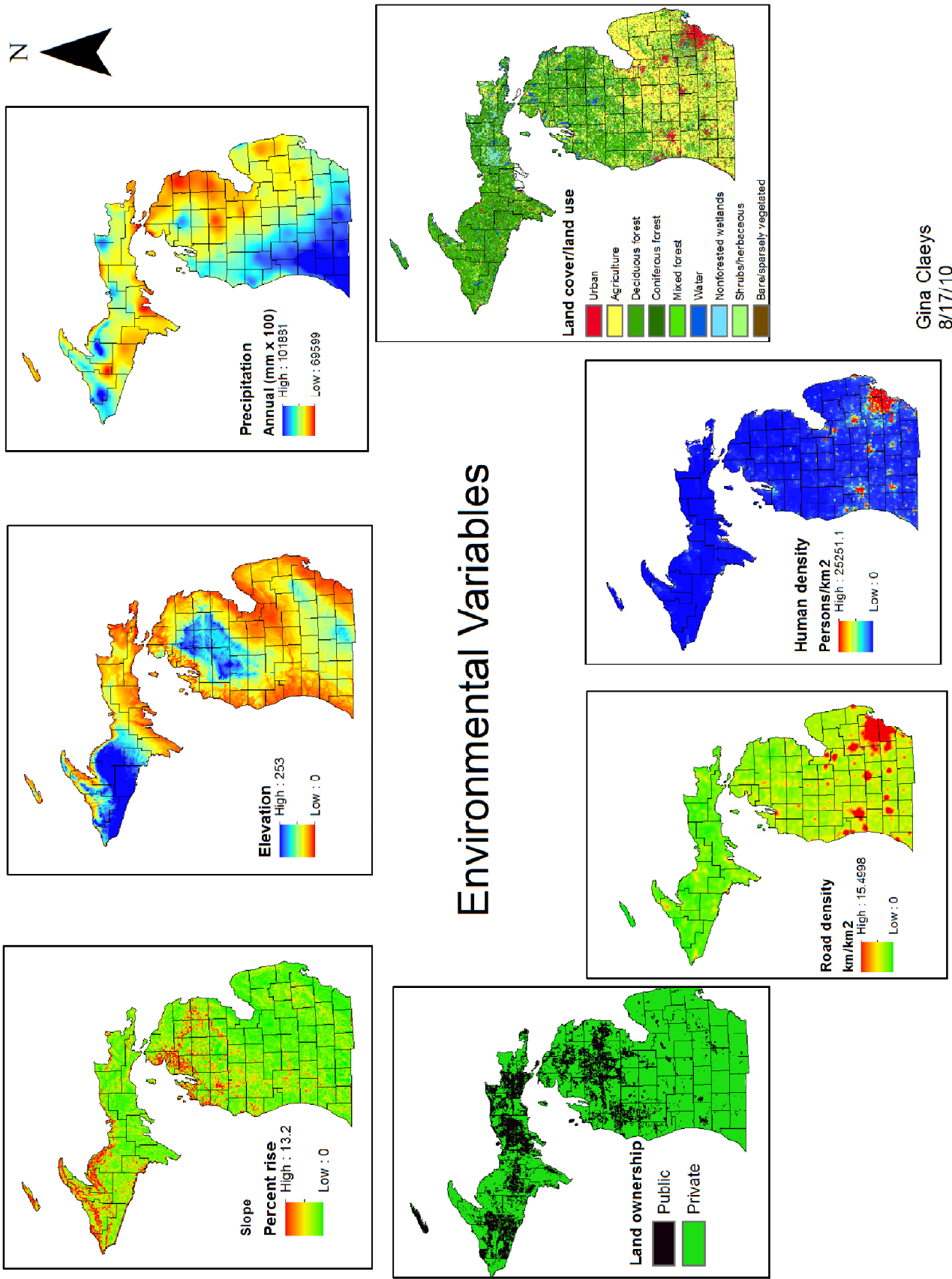
The only value that was different was the area of potential habitat; the values for mean midwinter pack size (4.1), mean midwinter territory size (179 km²), proportion of saturated habitat in interstitial areas (0.37), and proportion of dispersers (0.15) were kept the same as what was used in their analysis. This value is an estimate of the number of wolves that could potentially be supported in the LP. The algorithm was calculated using the total area of potential habitat (a larger estimate) and using only the 50-km² or larger patch area (a smaller estimate) to obtain a range of values.

Results:

Environmental Variables:

All distributions of environmental variables were displayed in ArcGIS (Figure 4). Slope is relatively low overall throughout Michigan, with some high-slope areas in the northwestern part of the LP and in the northwestern UP. Slopes ranged from 0-13.2 percent rise. Elevation ranges from 571-1,979 feet (174-603 meters) with the highest-elevation areas in the north-central part of the LP and the northwestern portion of the UP. Precipitation is highest in the southwestern part of the LP and gradually increases towards the northeast. Values range from 27.4-40.1 inches average annual precipitation over the 30-year period (1971-2000). Land ownership is primarily private in the southern part of the LP. Most of the UP and large portions of the northern LP are public (state parks, national forests, federal land, etc.). Road density ranged from 0-15.5 km/km², with the highest densities in southern parts of the LP near Detroit, Grand Rapids, and Saginaw. Human densities ranged from 0-25,251 persons/km² with a distribution similar to the road density distribution. Land cover is primarily forest in the northern LP and UP, with mostly agriculture and urban areas in the southern portion of the LP.

Figure 4: Environmental variables.



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Projection: NAD 1983 UTM Zone 16N

Maxent results

Road density explains 69% of the variability of the model and human density contributes 25%, while the other variables each contribute from 0-3.2% each (Table 3). The AUC for the model generated by Maxent has a value of 0.903, which is considered an excellent model for predicting the wolf presences contained in the test sample (wolf occurrences) (Figure 5). The variable that increases the fit of the model the most when used by itself is human density, meaning that it is the most useful variable when used by itself, while the variable that decreases the fit of the model most when it is omitted is road density, which means that it has the most information not present in other variables (Figure 6).

Table 3: Maxent output: analysis of variable significance showing relative predictive power of each environmental variable in determining wolf presence.

Variable	Percent contribution
Road density	69
Human density	25.4
Elevation	3.2
Precipitation	1.3
Land cover/land use	1
Slope	0.3
Land ownership	0

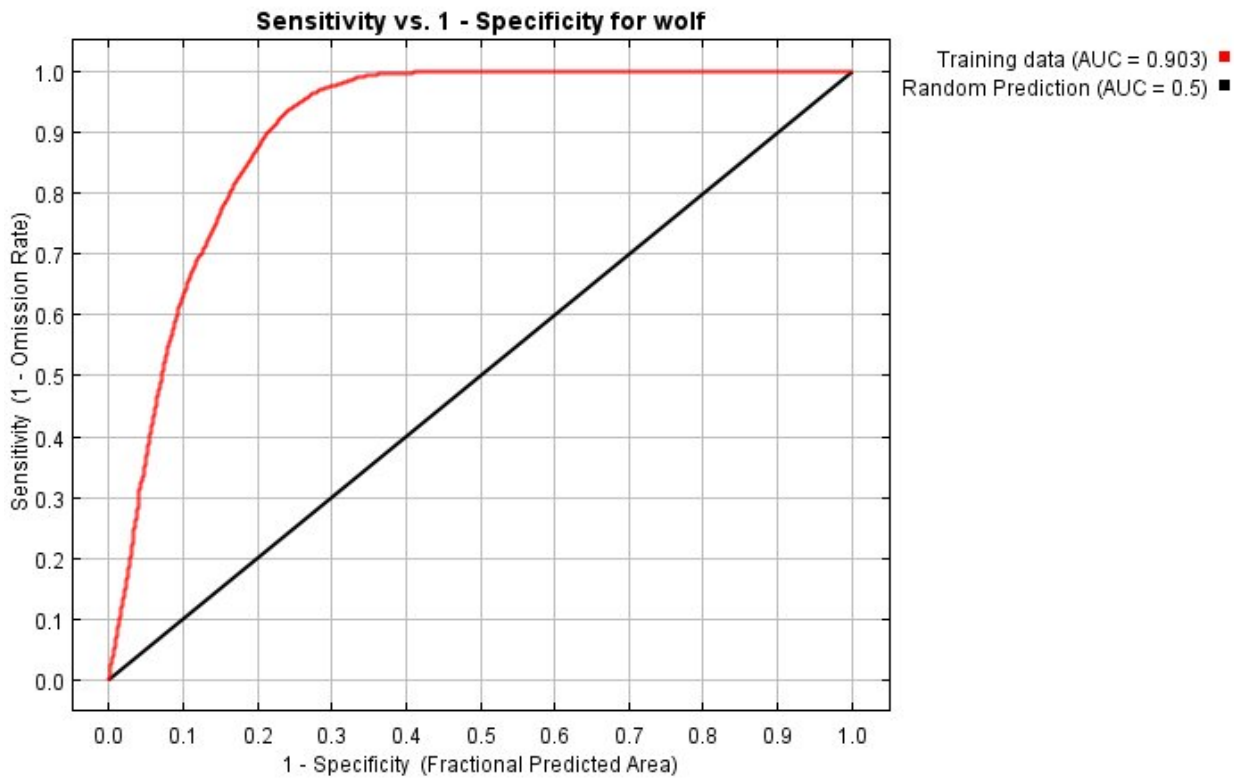


Figure 5: Maxent output: analysis of omission/commission showing how well the model accurately predicted wolf presence; the AUC of 0.903 means that the model is an excellent predictor of wolf presence.

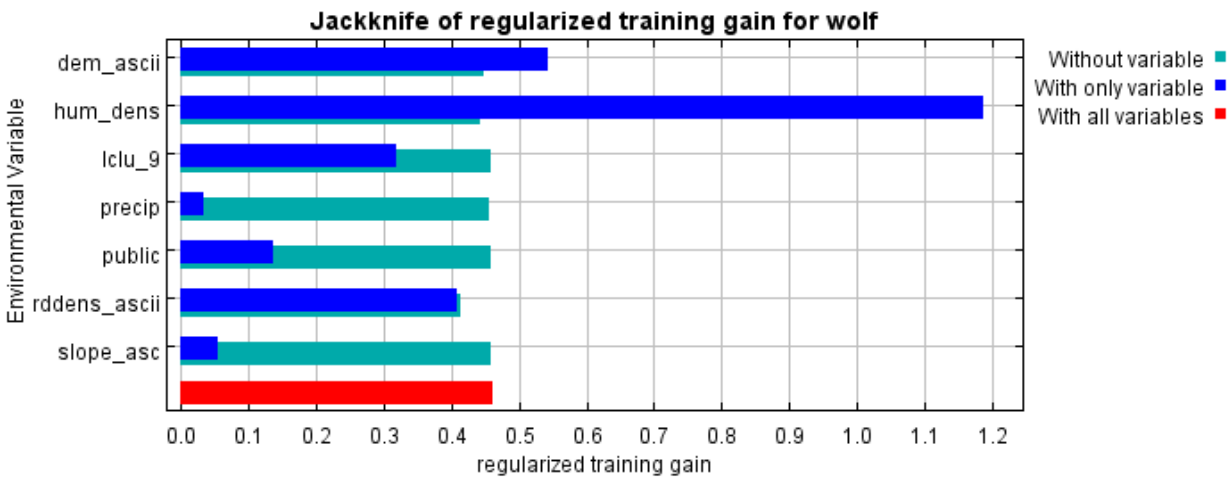


Figure 6: Maxent output: jackknife analysis of variables showing how important each variable is in explaining wolf presence when used by itself (cobalt blue), and how the model is affected when each variable is left out (aqua).

Species Distribution Model (SDM) and habitat patches

Most land in lower Michigan has a low probability of wolf occurrence, with some areas of high probability of occurrence in the northern LP (Figure 7). When masking out pixels with less than a 0.458 probability of occurrence, there are 115 potential habitat patches in the LP (Figure 8). Potential habitat totals 3,246 km² when considering all potential habitat, and only 2,674 km² when considering only potential habitat that is in a cluster of size 50 km² or larger. There were 10 potential habitat patches of at least size 50 km² that wolves could use for territory in the LP (Figure 9). However, one of the patches is an island, Beaver Island, located 30 miles off the coast in Lake Michigan.

Least cost paths and corridor analyses

The least cost paths that would be of highest use of the wolves are the ones coming from the largest patch (patch 4) to patch 7, patch 7 to patch 9, and from patch 4 to patch 2 (Figure 9). The least cost paths to some of the other patches often appear to use the closer patches as a stepping stone, such as the least cost path to patch 3 (uses patch 2 as a stepping stone), to patch 9 (uses 7), to patch 8 (uses 9), to patch 6 (uses 8), and to patch 10 (uses 9). The lowest-cost portion of the corridor between patches 4 and 10 is a fairly direct route between the two patches (Figure 10).

Dispersal land/connectivity analysis

Using the prior definition of land suitable for dispersal, none of the patches are connected to each other by dispersal land (Figure 11). However, patches 6 and 8 are in close proximity to each other so they may be functionally considered one large patch.

Capacity Estimation

The LP would be able to support 52-63 wolves, depending on which habitat patch layer was used (all patches, or only patches 50 km² or larger).

Figure 7: Maxent Species Distribution Model.

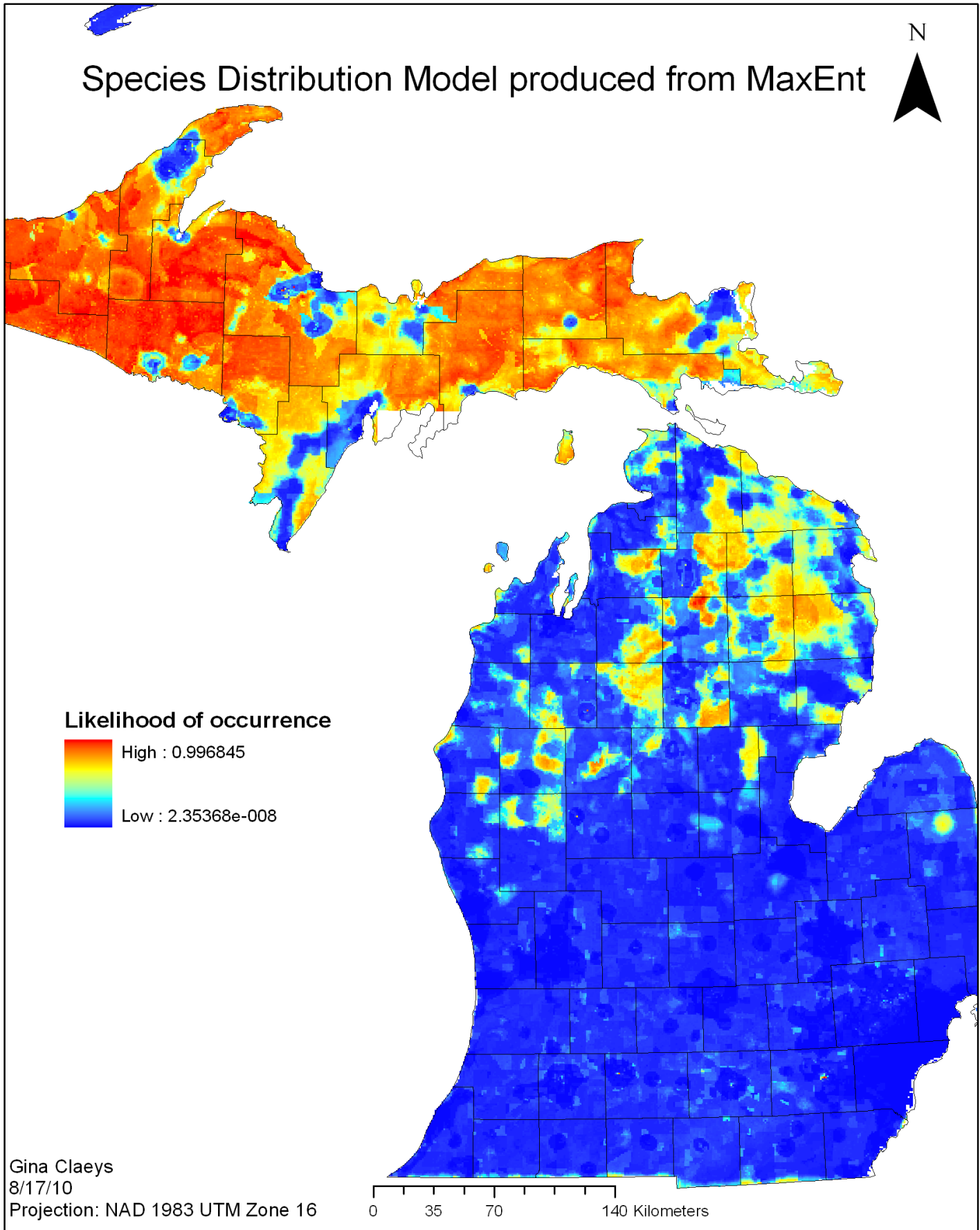


Figure 8: Potential wolf habitat using threshold from MaxEnt.

Predicted wolf habitat using MaxEnt threshold

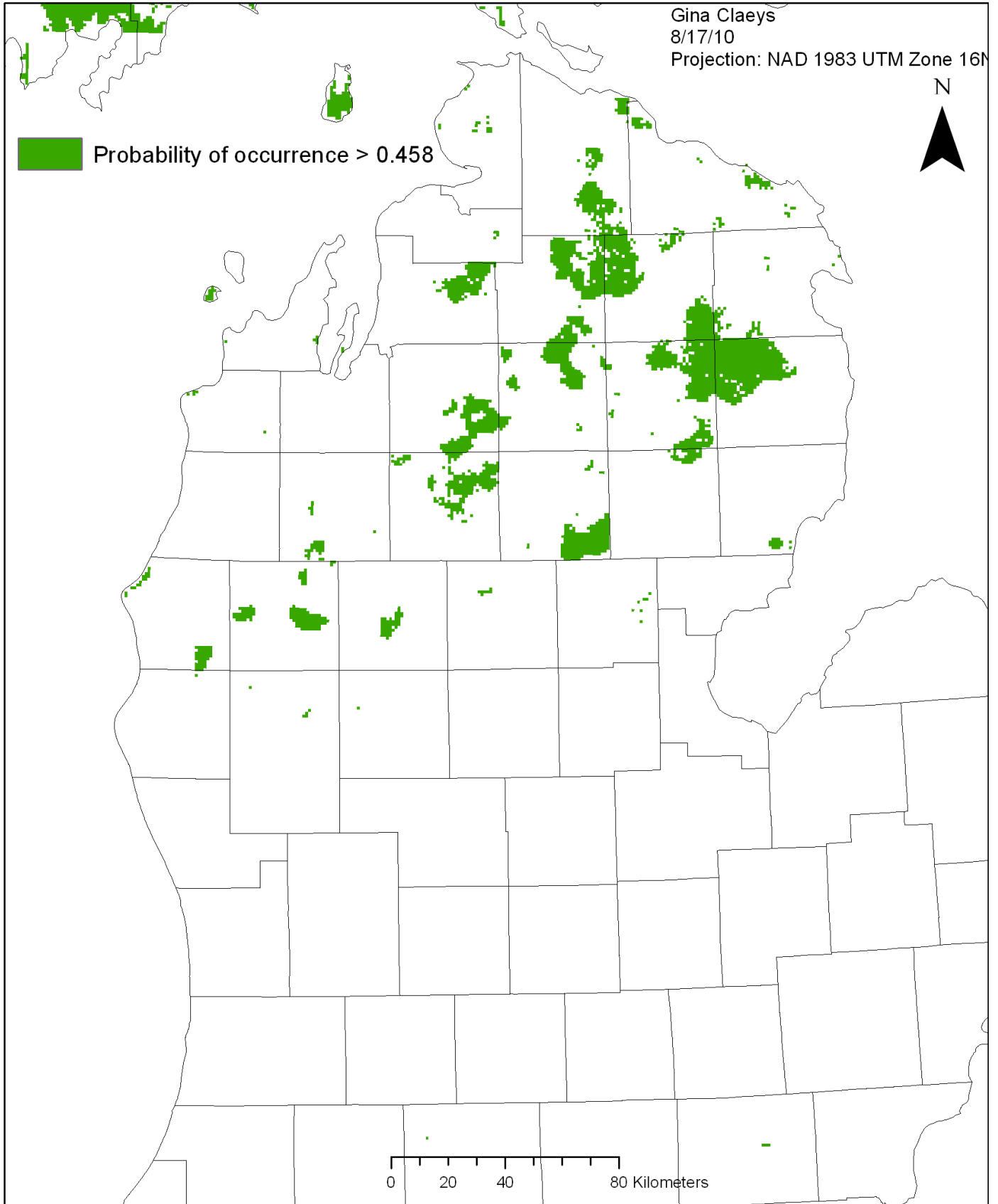


Figure 9: Least cost paths between patch 4 and other patches.

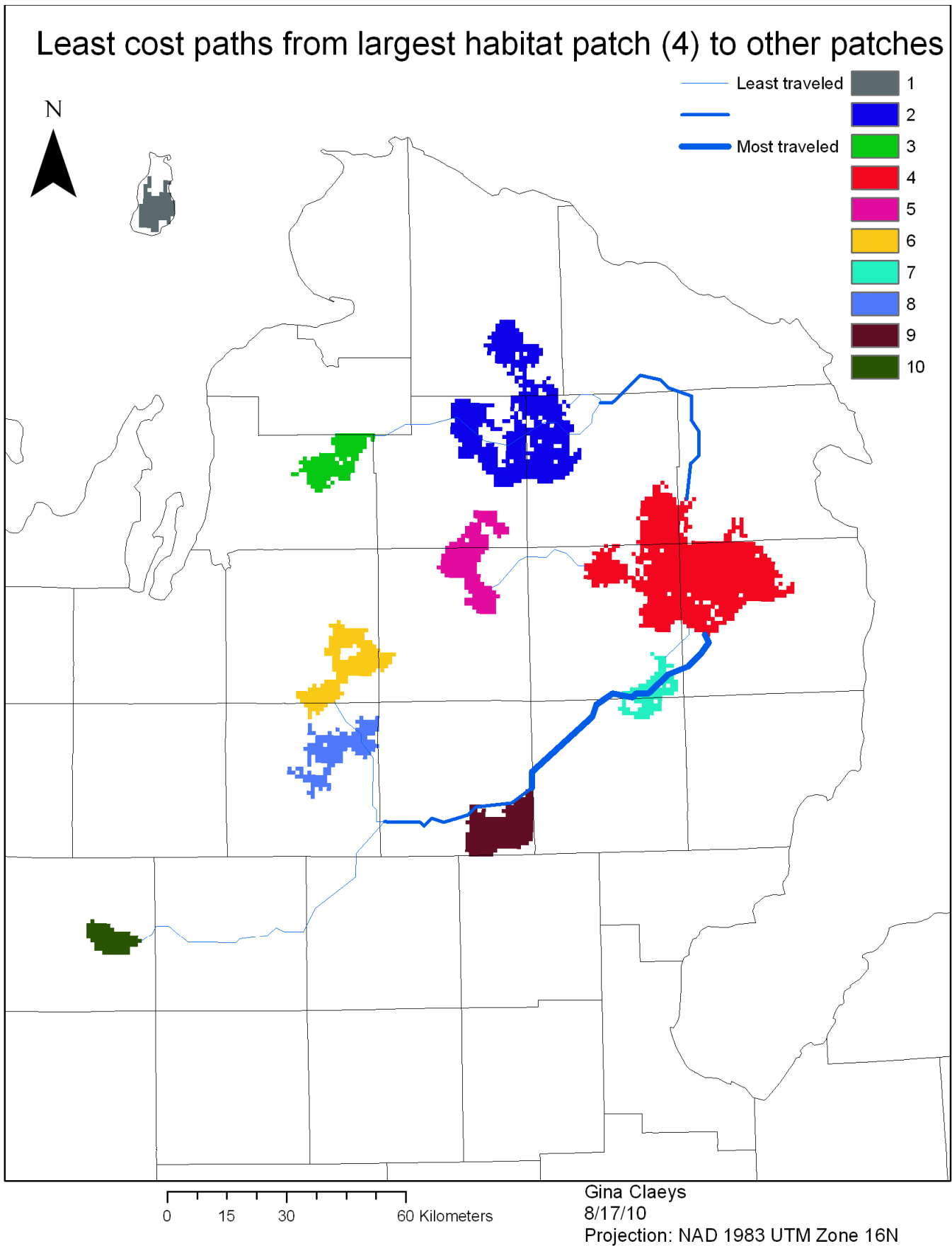


Figure 10: Corridor between patches 4 and 10.

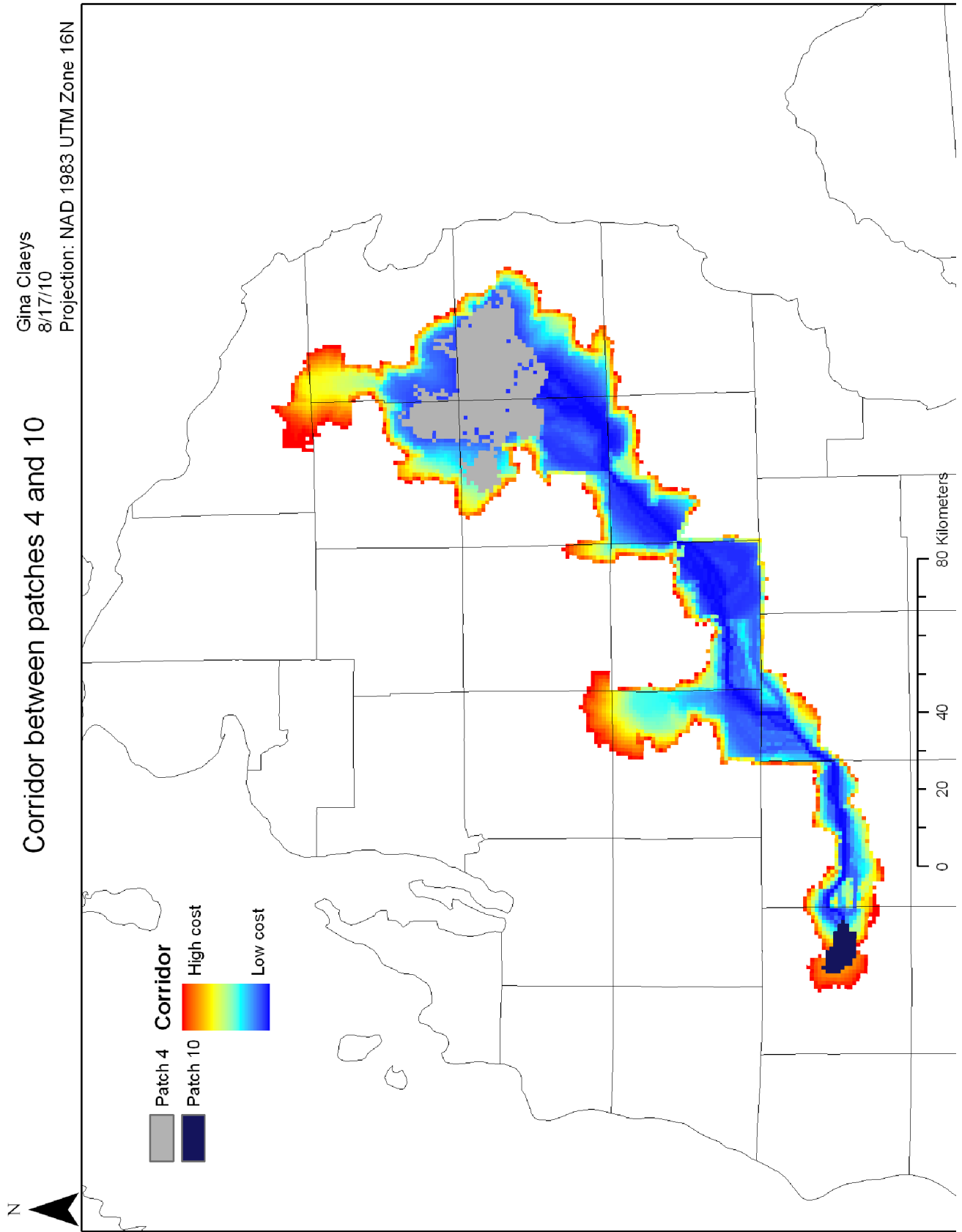
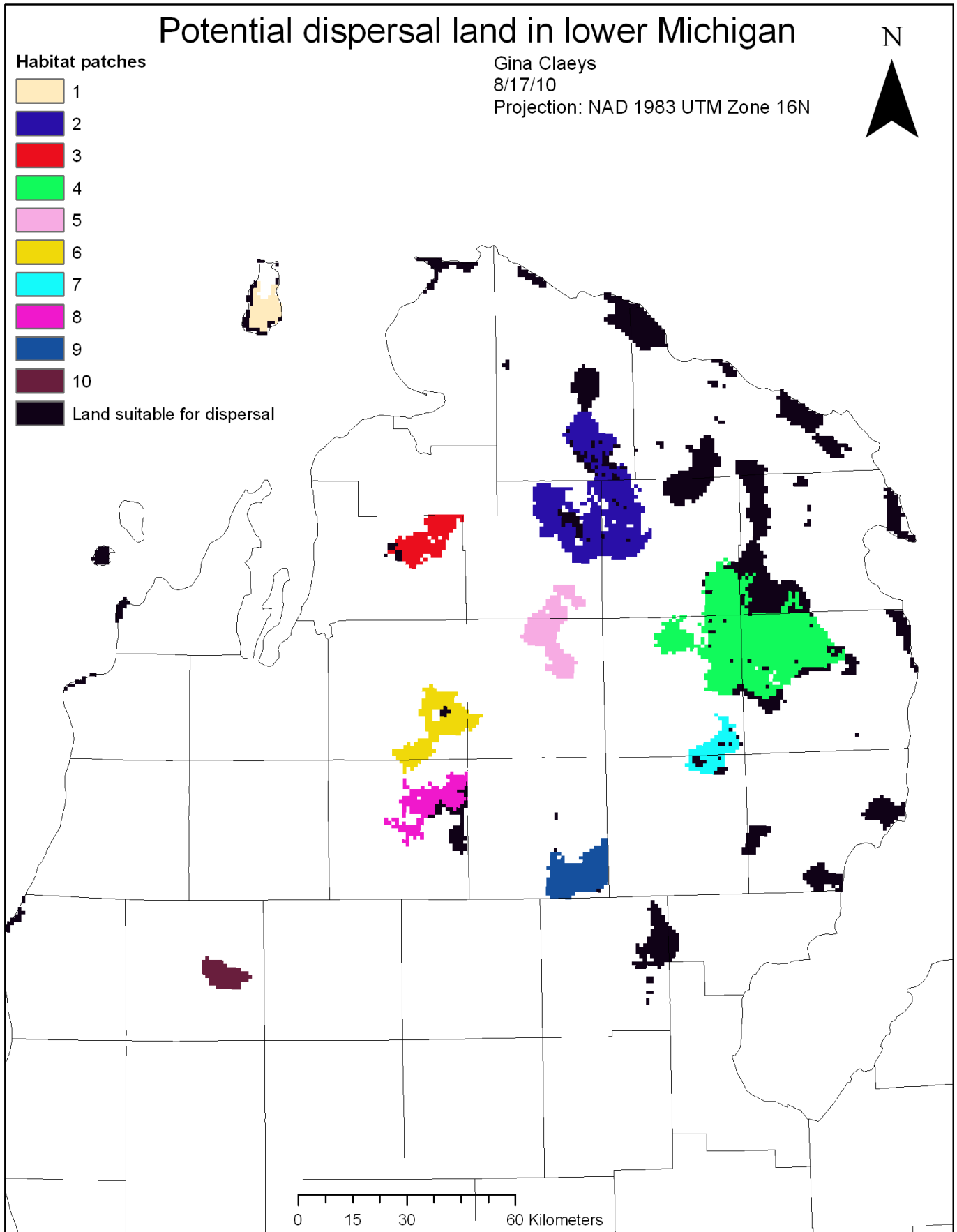


Figure 11: Potential dispersal land in lower Michigan.



Discussion:

These results show that there is enough suitable habitat to support a breeding population of wolves in the LP, since there are numerous habitat patches large enough to support a wolf home range. Since most of the potential habitat is located in the northeastern portion of the LP, this would be the best and most likely location for an initial colonizing pack. It is most likely that movement between patches would be between 4 and 7, 7 and 9, and 4 and 2. Dispersal between patch 4 and the farthest patch, 10, would most likely be a fairly direct route between the two patches.

However, since none of the 50-km² patches are connected by acceptable dispersal land, it seems unlikely that wolves will be able to move between patches significantly without some sort of further action. The variables used to define acceptable dispersal land were only road density and human density, which are both indicators of human presence. Further details of the local conditions in the area of each habitat patch are necessary to be able to assess the likelihood of wolf dispersal between patches. Blanco et al. (2005) found that highways did not appear to be a barrier to wolf movements, but that multiple obstacles together (such as roads, railways, disturbed habitat, etc.) may act synergistically and act as more of a barrier to wolves. Further analyses should be done on a smaller spatial scale surrounding each potential habitat patch to be able to make a more definitive assessment, taking into account the landscape and the types of roads surrounding and crossing through each patch. This information is obtainable, as there is research on wolf mortality based on different types of roads, and the road GIS layer has information on classes of roads (width, surface type, etc). Kohn et al. (2009)

found that the type of road, traffic volume, and regularity of road use all influence the likelihood of wolf crossings and the use of roads by wolves. Based on what was discussed previously about wolves, they are capable of crossing through much unfavorable habitat, but there are many factors, known and unknown, that influence wolf dispersal (including individual differences between wolves) and it should not be assumed that all wolves will willingly cross through any amount of unfavorable habitat.

It is unknown if there is suitable habitat to the south of Michigan, in Ohio, Indiana, and beyond. Some wolves may certainly disperse through southern Michigan in a southward-bound dispersal, but as discussed previously it is unknown how many wolves may actually do so. A regional, multi-state analysis will need to be conducted to determine if wolves will be able to spread further south throughout their former range. Ice conditions would have allowed wolves to cross the Straits of Mackinac (separating the LP from the UP) every winter since 1990 (Beyer et al, 2009), so dispersal is certainly possible to and from the UP. Wolves are unlikely to cross over the ice of the Great Lakes to Wisconsin or Ontario, due to wind and water movement that make large bodies of water such as the Great Lakes unlikely to completely freeze over for any significant amount of time (GLIN, 2010).

The Gehring and Potter (2005) paper estimated that the LP could support 40-105 wolves, depending on which potential habitat estimate was used (total or using only the larger patches). The estimate from this analysis of 52-63 wolves falls within that range, thus it seems that these two different methods of habitat modeling resulted in similar estimates of the

potential number of wolves that the LP could support. The wider range of potential wolves that the Gehring and Potter analysis obtained could have been due to using fewer environmental variables making the model less precise, or may be characteristic of using a different modeling method, although the habitat models were similar spatially, with most potential habitat in the northeastern region of the LP, with some smaller patches in the north-central region. The fact that I used actual occurrence points in my model may have helped to improve the precision of my estimate, although Maxent could have underestimated the area of potential habitat. Further analyses could be done using more or different environmental variables, such as Normalized Difference Vegetation Index (NDVI) instead of precipitation to estimate net primary productivity as did Carroll et al (2003). Assigning a wider range of cost values for the cost surface could have increased the accuracy of the least cost path and corridor analyses, as would consulting a wolf expert to get a more realistic picture of the likelihood of wolves crossing different types of land or road densities. And again, performing the analyses at a smaller spatial scale would give more accurate and useful information.

Since all the wolf occurrence points occur in the UP and the LP is more fragmented and less forested than the UP, the probability distribution modeled by Maxent may not be directly applicable. With all the environmental variables included in the analysis, it should have captured all this variation, but there may have been a variable excluded (such as patch metrics including shape, edge/core area ratio, etc.) that may differ significantly between the UP and LP that, due to its exclusion, could bias the interpretation of the results. However, since this

model was shown to be an excellent predictor of wolf occurrence based on the AUC value of 0.903, it should be a strong predictor of wolf occurrence.

These results provide further support what has been shown before: that wolves do not need any one particular type of habitat, as human presence variables are the most significant in predicting where they will occur. The fact that road density and human density together contributed 94% to the model suggests that as long as wolves are in areas with low human presence they can persist; they do not need any particular type of habitat, topography, or land ownership. Thus, land management geared towards wolf recovery does not need to be pristine, publicly-owned conifer habitat, it just needs to be away from people and roads so there will not be conflicts that may jeopardize their survival. Mechanisms to reduce illegal killing of wolves are also needed, such as improved investigation into violations, more severe penalties for violations, and a more efficient system for reporting violations (Michigan Wolf Management Plan, 2008). Since prey density was not included as one of the variables here, the model will not be accurate if the assumption of sufficient prey in lower Michigan is not met.

Given the dispersal capabilities of wolves and their known locations in upper Michigan, Ontario, and Wisconsin, there will be plenty of source populations for wolves in the LP. The available land in the LP is certainly enough for packs to establish territories. There is enough habitat to support about 12-15 packs based on the average midwinter pack size of 4.1 in Michigan. Based on the USFWS Recovery Plan for the Eastern Timber Wolf (1992), a viable wolf population consists of at least 100 wolves in a region if the new population of wolves is within

100 miles of the large Minnesota population, or 200 wolves if the new population of wolves was more than 100 miles away from the large source population. The UP population is considered a viable population since it consists of over 100 wolves and is within 100 miles of the Minnesota population. Since our estimate of 52-63 wolves for the LP is below the minimum of 100 wolves, lower Michigan is unlikely to support a viable wolf population. It probably would not be a large enough population to act as a source for dispersers through southern Michigan to states south of Michigan. If more suitable habitat is created for wolves throughout the LP, it may sustain a population of at least 100 and become a viable population at some point in the future.

In order to create land suitable for wolf dispersal throughout lower Michigan, active land management needs to be pursued to allow for areas without dense human presence. Unfragmented areas with connecting corridors with low road densities and low human development need to be created and maintained via conservation easements on private land or via creating or adding to protected areas. These areas might be agricultural areas where land owners have non-lethal methods to keep wolves away from their livestock (or do not own livestock), or might be herbaceous/shrubby areas with low tree density, just as long as there is space for wolves to avoid contact with people.

Since agricultural areas are much more dense in the LP than they are in the UP, it will be difficult to avoid conflict with wolves in areas with livestock. There will always be livestock depredations as livestock are easy prey for wolves, but based on past experience depredation

problems are usually due to a few individual wolves and are best managed at a small spatial scale (Michigan Wolf Management Plan, 2008). There are various nonlethal methods to minimize these conflicts, such as using barrier fencing for livestock, using sirens, flagging, or livestock-guarding animals (Beyer et al. 2006). If dispersal land is managed for throughout lower Michigan, then dispersal to states south of Michigan will be possible so that wolves may continue to recolonize their former range throughout the United States.

Conclusion

Based on the SDM created using Maxent software, there is enough potential habitat in the LP of Michigan to maintain 52-63 wolves, below the minimum of 100 for a viable population. Habitat patches in the LP are not connected by dispersal land, thus active land management is needed to create corridors between these potential habitat patches and throughout lower Michigan to allow dispersal to other regions. Wolves are unlikely to inhabit the southern portion of the LP, but may disperse through this area if there is suitable habitat to the south of Michigan.

In order to maintain a population of gray wolves in Michigan, unfragmented habitat patches with low human or road presence need to be maintained, as well as dispersal corridors. Avoidance of sprawl would be helpful to maintain areas with low development and low road density. These actions, in combination with education about wolves and continued federal protection, will help to ensure that wolves can continue to recover their former range and will help restore connectivity of the Great Lakes subpopulation of wolves to other wolf populations.

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