



Original Article

Modeling Habitat Potential for Canada Lynx in Michigan

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ABSTRACT In the ruling to list Canada lynx (*Lynx canadensis*) as a federally threatened species, the U.S. Fish and Wildlife Service (USFWS) identified the Great Lakes region as an area that historically contained lynx and, hence, could potentially contribute to population recovery. More recent critical habitat designations by the USFWS only recognize Minnesota, USA as important to recovery in the Great Lakes. Although there is no current evidence of a resident lynx population in the Upper Peninsula (UP) of Michigan, USA, trapping and track records over the past century suggest the region was periodically invaded after lynx population irruptions in Canada. In support of state and federal agency efforts in Michigan to provide and conserve lynx habitat, we quantified habitat potential using a spatially explicit, landscape-level model based on relationships among lynx, their primary prey, snowshoe hare (*Lepus americanus*), and vegetation attributes. Outputs from the model indicated that habitat in the UP supports low hare densities (<0.07–0.75 hares/ha). Corresponding potential lynx densities ranged from 0/100 km² in the southern and northeast UP to 5/100 km² in the central-eastern UP. Model estimates of potential hare density were correlated with winter track-surveys ($R^2 = 0.4$, $P < 0.001$). Current absence of a resident lynx population in Michigan is likely attributed to confounding factors (e.g., habitat, competition, status of source population) but our results indicate that current habitat quality, quantity, and spatial configuration are exerting large-scale negative influences. These results are generally consistent with the USFWS determination that Michigan's UP most likely functions as dispersal habitat. © 2011 The Wildlife Society.

KEY WORDS Canada lynx, geographic information system, habitat, landscape model, *Lepus americanus*, *Lynx canadensis*, Michigan, snowshoe hare.

Canada lynx (*Lynx canadensis*) was listed as a federally threatened species in the contiguous United States following population declines in the southern portion of its geographic range (U.S. Fish and Wildlife Service [USFWS 2000]). Lynx populations in the contiguous United States satisfied the “Distinct Population Segment” (DPS) criteria based on separation from the continental core population by international political boundaries and differences in vegetation types, climate, and ecology. Several regions were identified as potentially important for DPS recovery, including the Great Lakes, but development of conservation and management strategies has been hampered by limited understanding of current and historical population status in each region (McKelvey et al. 2000). Additional recent research in the southern latitudes has increased our understanding of lynx ecology (McDonald 2008), but the long-term outlook of the DPS remains uncertain (Murray et al. 2008).

Lynx occupancy in a region depends on landscape connectivity and habitat quality (Steury and Murray 2004). Landscape connectivity is needed to facilitate emigration from the continental core in northern Canada, as evidenced by interregional gene flow and population synchronies (Schwartz et al. 2002, Rueness et al. 2003, Murray et al. 2008). Habitat quality for carnivore populations is closely linked to prey abundance (Carbone and Gittleman 2002), and the importance of snowshoe hare (*Lepus americanus*) as prey for lynx is well-established (Brand et al. 1976, Ward and Krebs 1985, Squires and Ruggiero 2007). Recovery efforts for lynx in the DPS regions will benefit from assessments of connectivity with source populations in Canada and landscape-level estimates of prey abundance.

The USFWS recently designated critical habitat for lynx based on occupancy and breeding records since 1995 (USFWS 2008). The designation did not include Michigan, USA, where extensive track-surveys during the 1990s in the Upper Peninsula (UP) found no sign of lynx (Beyer et al. 2001). Although concurrent track-surveys in Minnesota, USA yielded a single lynx observation (McKelvey et al.

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2000), recent confirmation of a breeding resident population in northeast Minnesota (Moen et al. 2008) prompted the USFWS to include this area in the final critical habitat designation (USFWS 2008). It is unclear whether the recent lynx population establishment in Minnesota is similarly possible in Michigan; historic trapping records show that lynx periodically dispersed into the UP, yet the last significant influx was in the 1960s (McKelvey et al. 2000). Regardless, the U.S. Forest Service in Michigan incorporates lynx habitat considerations into landscape and project-level planning (S. Sjogren, United States Forest Service, personal communication). Additionally, lynx are state endangered species and, hence, the Michigan Department of Natural Resources and Environment (MDNRE) must consider lynx in their management activities. In the autumn of 2003, a lynx was trapped in the Hiawatha National Forest near St. Ignace—the first verified lynx sighting in Michigan in >20 years. In the winter of 2010, MDNRE confirmed a lynx on Sugar Island, Michigan. Thus, attention by state and federal resource management agencies in Michigan is warranted and an assessment of lynx habitat can help prioritize conservation efforts.

Previous studies have generated maps of lynx habitat by modeling relationships between lynx occurrence and environmental attributes such as annual snowfall (Hoving et al. 2005) and forest cover type (Moen et al. 2008). In both studies, these environmental attributes were assumed to influence prey abundance (i.e., hare density). Our objective was to quantify lynx habitat potential in the UP using documented habitat relationships among vegetation, hare density, and lynx. To our knowledge no landscape-level assessment of snowshoe hare habitat quality or abundance exists for the UP to support lynx conservation efforts.

STUDY AREA

We modeled habitat for the UP of Michigan (approx. 42,600 km²), located in the northern portion of the Great Lakes region. The study area was bounded by Lake Superior to the north, lakes Michigan and Huron to the south, and the state of Wisconsin to the west. Over 80% was forested (Leatherberry and Spencer 1996), and the region occurred within the Laurentian Mixed Forest Province, which represented a transition from broadleaf deciduous to boreal coniferous forests (Dickman and Leefers 2003). The climate was humid continental and influenced by Lake Superior; winters were long and cold with a mean temperature of −11° C, while summers were short and cool with a mean temperature of 18° C (Eichenlaub et al. 1990). Growing season ranged from 130 days to 180 days (Eichenlaub et al. 1990). Snowfall occurred between November and April, with averages between 150 cm across the southern UP and >500 cm along the Keweenaw Peninsula and northern portions of the UP that were subject to lake effect (Eichenlaub et al. 1990).

Human influences after European settlement altered vegetation structure and composition as extensive logging and large-scale fires in the late 19th century resulted in second-growth forest throughout the region (Dickman and Leefers

2003). Forest composition in the UP depends on glacially modified physiographic conditions, resulting in a high diversity of forest types. Hydric lowlands were populated by conifers such as northern white-cedar (*Thuja occidentalis*), balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), and tamarack (*Larix laricina*), with hardwoods including black ash (*Fraxinus nigra*) and red maple (*Acer rubrum*). Mesic uplands were populated by hardwoods such as sugar maple (*A. saccharum*), aspen (*Populus tremuloides*, *P. grandidentata*), birch (*Betula alleghaniensis*, *B. papyrifera*) and beech (*Fagus grandifolia*), with conifers including fir, eastern hemlock (*Tsuga canadensis*), and white spruce (*Picea glauca*). Xeric uplands were populated by conifers such as jack pine (*Pinus banksiana*), red pine (*P. resinosa*), fir, and white pine (*P. strobus*), with hardwoods such as red maple and red oak (*Quercus rubra*).

Primary land uses in the UP were recreation and timber harvesting. Out of the 34,000 km² of forested land, 40% was state and federal land (including 2 national forests) and 18% was owned by timber industry (Leatherberry and Spencer 1996). There were approximately 328,000 residents and >75% of the UP had a population density <4 persons/km² (U.S. Census Bureau 2000).

METHODS

Lynx Habitat Model

Our lynx habitat model was based on previously defined relationships among vegetation, snowshoe hares, and lynx. The model assumed that vegetation attributes could predict hare density, and that hare density could predict lynx density. The importance of horizontal vegetation cover for hare is well-supported in the literature and consistent throughout the species' geographic distribution (Hodges 2000). Hares select vegetation types with thick understory cover typically associated with regenerating conifer forests. Litvaitis et al. (1985) demonstrated a strong association ($r = 0.94$) between estimated hare densities and stem-cover units [$(3 \times \text{coniferous saplings/ha}) + \text{deciduous saplings/ha}$, with saplings defined as <7.6 cm diam] in Maine, USA. The 3-fold weighting of conifers was based on differences in visual obstruction (i.e., horizontal cover) between coniferous and deciduous saplings in the winter (Litvaitis et al. 1985). We used the Litvaitis et al. (1985) regression model to estimate hare density by stem-cover units with the following:

$$N_{\text{hare}} = (4.6 \times 10^{-5} X) - 1.06 \quad (1)$$

where N_{hare} is the hare population density (hares/ha) and X is the stem-cover units (units/ha), with values <23,043 units/ha set to 0.0 hares/ha and values >55,652 units/ha set to 1.5 hares/ha. We used 3 versions of Equation (1) having different slopes, resulting in different maximum hare densities (1.0, 1.5, 2.0) to incorporate uncertainty about hare population potential into our results. A landscape-scale maximum density of 2.0 hares/ha has been observed in northern studies (O'Donoghue et al. 1997).

Carbone and Gittleman (2002) found robust relationships between carnivore density and prey biomass across multiple taxa, and similar relationships have been previously used to model carnivore density in relation to prey density for wolves (*Canis lupus*; Mladenoff and Sickley 1998) and tigers (*Panthera tigris tigris*; Karanth et al. 2004). Recent literature suggests that southern lynx use more diverse prey during winter months than previously thought, yet regardless of geographic location, snowshoe hares constitute >50% of lynx diets (Roth et al. 2007). Carbone and Gittleman (2002) calculated that 10,000 kg/100 km² of prey biomass would support 4.79 lynx/100 km²; we used this relationship to create the following equation relating lynx density to hare density:

$$N_{\text{lynx}} = \frac{N_{\text{hare}}}{(4.79M)^{-1}} \quad (2)$$

where N_{lynx} = lynx population density (lynx/100 km²), N_{hare} = hare population density (hares/ha), and M = average mass of a snowshoe hare. Assuming an average hare mass of 1.5 kg (Grange 1932, O'Donoghue et al. 1997), Equation (2) simplifies to a scale factor of 7.185; therefore, a hare density of 1.0 hare/ha corresponds to 7 lynx/100 km².

Deriving Vegetation, Hare, and Lynx Data Layers

We mapped the UP using the intersection of 4 spatial layers in geographic information systems (GIS): 1) current vegetation, to separate forested from nonforested areas and describe the species composition of the overstory; 2) presettlement vegetation, which indicated potential natural vegetation communities; 3) soils, to provide a context for identifying Daubenmire habitat types (see Coffman et al. 1984, Kotar and Burger 2000); and 4) ecoregions, which defined broad ecological units having similar climate and physiography. Unique patches in the resulting map were termed ecological land units (ELUs). Current vegetation cover types were described by a 30-m land-cover data set derived from Landsat satellite imagery (acquisition dates 1999–2001; Michigan Department of Natural Resources 2001, Donovan 2005). We used the Anderson Level II categories, which had an estimated overall accuracy of 87% (Donovan 2005). Presettlement vegetation was constructed by Comer et al. (1995) using General Land Office surveyor notes recorded between 1816 and 1856. We used the State Soil Geographic database for Michigan (U.S. Department of Agriculture Natural Resources Conservation Service 1994) to portray soils at a coarse resolution (min. mapping unit of approx. 10 km²). The ecoregions layer, developed by Cleland et al. (2005), was used to separate the UP into different climatic and geophysical regions. We processed all spatial layers using ARC/INFO 8.1 in raster format with a 90-m resolution. A more detailed description of the GIS processes used in this study is provided by Linden (2006).

Calculating hare density for ecological land units.—Estimates of stem-cover units and resulting hare densities for the mapped ELUs were derived from fixed-radius forest-plot data collected by the Forest Inventory and Analysis (FIA)

program (U.S. Forest Service 2006). The latest FIA inventory in Michigan's UP (2000–2004) resulted in >4,700 plots (approx. 800 ha/plot). Forest Inventory and Analysis sampling includes individual tree attributes and landscape features that define one or more condition classes (e.g., physiography, land use, stand age). We calculated stem-cover units from plot-level densities of saplings that met the size criteria (<7.6 cm diam), with 3-fold weighting for conifer species.

The exact coordinates of FIA plot locations were mandated confidential by Congress in 2000, precluding simple point overlays with the ELU map; therefore, we matched site descriptors from the FIA plots to those from the spatial data to populate ELUs with estimates of stem-cover units. We used 2-way indicator species analysis (TWINSPAN; Hill 1979) to ordinate FIA plots by species composition of the canopy strata and define groups with similar overstory and understory characteristics. The combination of TWINSPAN group, physiographic class, and ecoregion code was used to assign each FIA plot to an ELU. We omitted plots having characteristics of >1 ELU (representing ecotones), reducing our plot count by approximately 30%. We combined ELUs with <10 FIA plots at a coarser level of ecoregion delineation (e.g., section vs. subsection) to ensure adequate representation from the inventory data for each spatial class. Nonforested ELUs were not represented by FIA plots and we assumed these areas did not provide habitat for hare, with the exception of upland and lowland shrub cover types, which were arbitrarily assigned an intermediate hare density of 0.75 hares/ha; the intermediate density implies these areas could provide hare habitat (e.g., dense thickets of alder and willow) but lack the complete suite of vegetation attributes (e.g., conifer cover) to provide high-quality winter cover. Mean hare density was calculated from the ELU-stratified FIA plots and assigned to each forested ELU. We produced 3 hare-density maps based on different slopes (original, high, and low slope) as applied to the Litvaitis et al. (1985) regression in Equation 1.

Lynx density maps.—The 3 snowshoe hare-density maps were subsequently used to produce corresponding estimates of lynx density at the landscape scale. We used a 100-km² moving window to calculate the average hare density (hares/ha) around each map pixel and then converted that hare density to a lynx density (lynx/100 km²) using the scale factor (7.185).

Model validation.—Model accuracy was assessed with winter track-surveys for furbearers conducted by the MDNRE in 2004 (D. R. Etter and V. T. Frawley, Michigan Department of Natural Resources and Environment, unpublished report). The MDNRE used stratified random sampling to select survey locations on public lands with habitat attributes (e.g., forest vegetation) supporting a high likelihood of American marten (*Martes americana*) presence. The track-surveys consisted of 35 routes totaling 283 km distributed across the UP and were conducted using a standard detection protocol (Zielinski and Kucera 1995). Given that no lynx tracks were detected, we correlated track counts of snowshoe hares to model estimates of potential hare densities as one measure of model predictive capability.

RESULTS

ELU Map and Forest Inventory Data

The ELU stratification by ecoregion resulted in a raster map with 234 classes, consisting of 2 nonforested types and 9 forested types across 21 ecoregions. Over 88% of the forested landscape was classified as an ELU at the finest scale ecoregion level (subsection), with the remaining 12% classified at a coarser level (section or subregion). Subsection ELUs with >20 and >60 FIA plots represented 75% and 50% of the forested landscape, respectively.

Summaries of the FIA plot data, independent of ELU mapping, indicated that 7% (approx. 2,400 km²) of forested land in the UP contained stem-cover unit densities that would support ≥ 1.0 hares/ha according to the Litvaitis et al. (1985) regression; 14% (approx. 4,800 km²) would support ≥ 0.50 hares/ha and 25% (approx. 8,500 km²) would support ≥ 0.10 hares/ha. The only forest type with >10% of FIA plots supporting potential hare densities ≥ 1.0 hares/ha was lowland white cedar (20%); within the ecoregion subsections 212Ra and 212Re (Cleland et al. 2005) of the eastern UP, 38% of FIA plots representing lowland white cedar could support ≥ 1.0 hares/ha.

Lynx and Hare Densities

Maps of potential hare and lynx densities in the UP illustrate the range of potential densities according to 3 versions of the Litvaitis et al. (1985) regression equation (Fig. 1A–C). Modeled hare densities ranged from <0.07 hares/ha to 0.75 hares/ha and lynx densities ranged from 0 lynx/100 km² to 5 lynx/100 km² (Fig. 1). Potential lynx density was highest throughout the eastern UP and on the Keweenaw Peninsula in the north; this trend was consistent for each interpretation of the hare-density relationship (Fig. 1A–C). Median and maximum potential lynx densities ranged from 0.87 lynx/100 km² to 1.80 lynx/100 km² and from 2.67 lynx/100 km² to 5.33 lynx/100 km², respectively, depending on the model run. Areas with relatively higher potential lynx density corresponded to locations of lowland white cedar and lowland shrub ELUs. None of the UP supported hare densities ≥ 1.0 hares/ha at the 100-km² scale, suggesting that the spatial configuration of forest types was too fragmented to provide contiguous habitat at scales required by lynx.

The track-survey data were moderately correlated with the model estimates of potential hare density ($R^2 = 0.40$, $P < 0.001$). Residual variance was constant ($P = 0.34$).

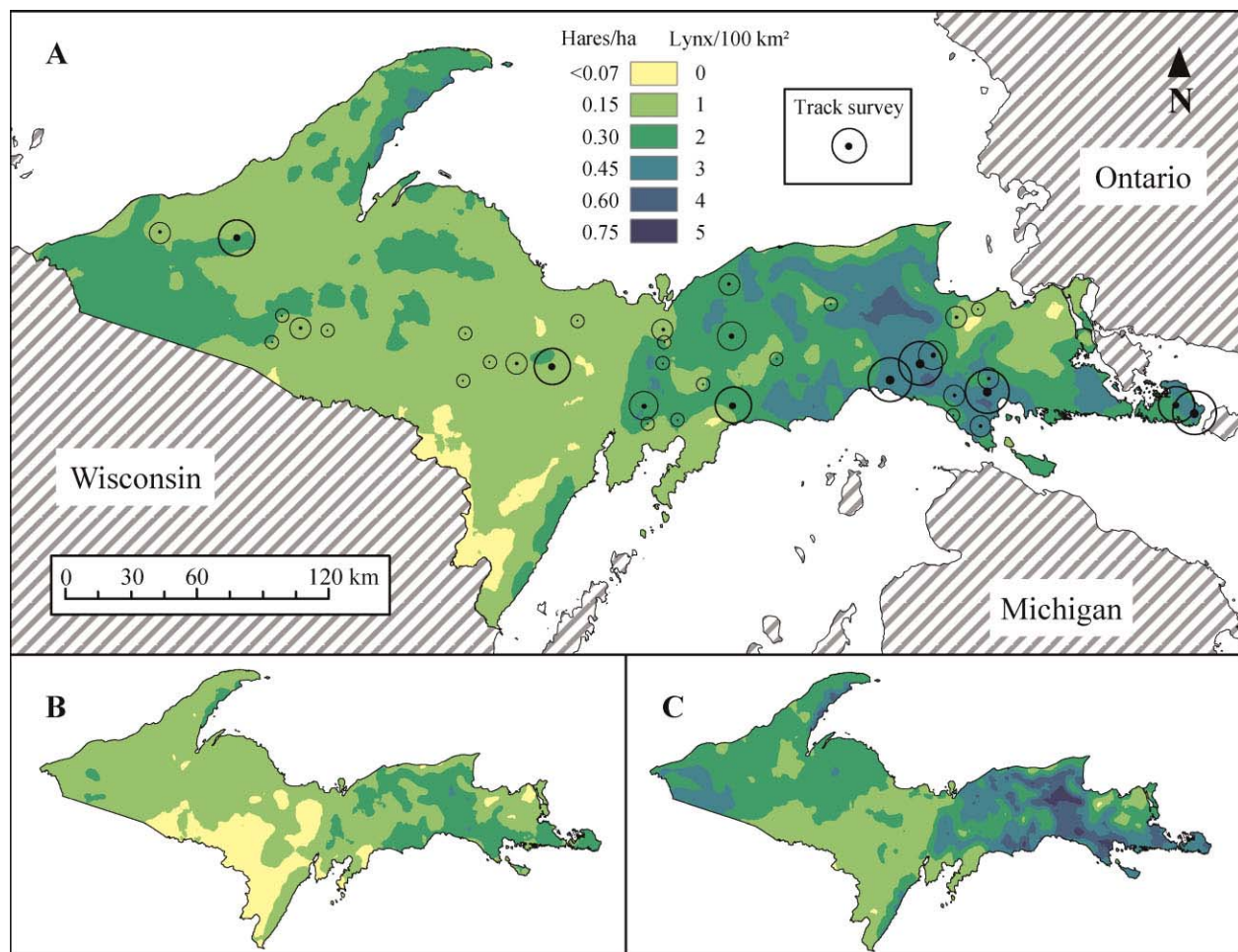


Figure 1. Potential hare densities (hares/ha) and lynx densities (lynx/100 km²) in the Upper Peninsula of Michigan, USA as determined by the lynx habitat model for the original (A), low (B), and high (C) regression slopes predicting hare density from stem-cover units in the Litvaitis et al. (1985) regression. The circled dots represent winter track-surveys conducted in 2004—larger circles correspond with higher counts of hare crossings.

Generally, higher counts of hare tracks were observed in locations predicted to have higher hare densities by the habitat model (Fig. 1). Although the track-surveys do not represent a rigorous field validation, the positive, significant correlation indicates that model outputs are consistent with observations from the field and increases our confidence in the predictive ability of the habitat model.

DISCUSSION

Michigan's natural resource management and regulatory agencies are legally responsible for considering lynx populations and habitat even though lynx rarely occur. When species occurrence data are lacking, theoretical habitat models offer a means to support decision-making, quantify management actions, and document potential impacts (Roloff et al. 2001). Others have demonstrated the utility of theoretical habitat models to support natural resource planning activities (e.g., Kliskey et al. 1999, Dettki et al. 2003, Larson et al. 2004). We offer our results as insights into large-scale habitat potential for lynx in Michigan.

Potential lynx densities in the UP were limited by low estimates of stem-cover units and resulting hare densities across most forest stands. Areas with highest potential lynx density occurred in lowland conifers where cedar was the dominant tree species and stem-cover units supported high hare densities. Although cedar swamps were located throughout most ecoregions of the UP, <18% were estimated to support a hare density >1.0 hares/ha. Cedar swamps with high estimated hare densities were encompassed by 3 ecoregions (212Ra, 212Re, 212Sn; Cleland et al. 2005) characterized by lacustrine deposits of glacial origin where lowland forests grew over poorly drained sands and cedar was historically dominant. Cedar regeneration in the northern Great Lakes has been poor in recent years, likely a result of high white-tailed deer (*Odocoileus virginianus*) numbers and chronic browsing pressure (Rooney et al. 2002). An exception may exist in ecoregion 212Ra, where a severe winter climate maintains the lowest deer densities in the region (<2 deer/km²; MDNRE 2010). The interaction of glacial landforms, climate, and local disturbance history (e.g., low herbivory) has likely contributed to cedar swamps with high densities of saplings not typical of lowland conifer forests in other ecoregions of the UP.

Our model results indicate that potential lynx densities in the UP are lower than those currently found in Maine (9.2–13.0 lynx/100 km²; Vashon et al. 2008) and more typical of northern landscapes during the low phase of the hare-lynx cycle (2.3 lynx/100 km²; O'Donoghue et al. 1997) and western landscapes with relatively stable, low hare densities (2.3 lynx/100 km²; Koehler 1990). While this finding suggests that lynx habitat quality in the UP is relatively poor, it does not necessarily explain the absence of a resident lynx population. Our habitat modeling framework emphasized prey availability as determined by vegetation structure and did not incorporate other factors such as population cycling or interspecific competition, which will invariably affect habitat occupancy for a species. Lynx and hare are famous for their synchronous population fluctuations (Keith

1963), and this cycling will affect colonization and extinction dynamics in a given landscape, especially at low population densities. The presence of coyote and bobcat can potentially reduce hare availability to lynx, even in landscapes with high hare densities (Koehler and Aubry 1994). Hoving et al. (2005) found that lynx occurrence in the northeastern United States was best predicted by annual snowfall and suggested a critical threshold of 270 cm/year, below which the competitive advantage of lynx over other predators is lost; annual snowfall throughout more than half of the northern UP is >270 cm/year (Eichenlaub et al. 1990). Bobcat harvest records from 1985 to 2005 (D. E. Beyer, Jr., Michigan Department of Natural Resources and Environment, unpublished data) illustrate a close agreement with the Hoving et al. (2005) hypothesis—frequency of bobcat harvests decreases above the snowfall threshold (Fig. 2). Competitive exclusion of lynx by bobcats could further reduce habitat potential in the UP.

Another factor that may influence lynx absence in the UP is reduced landscape connectivity with core populations in Canada. Lynx are capable of long-distance dispersals (>1,000 km; Mech 1977, Ward and Krebs 1985), and historical records indicate that lynx commonly immigrated to the UP after population irruptions in Canada (McKelvey et al. 2000). Lynx dispersal will usually result in mortality when high-quality habitat (i.e., high prey abundance) is never found (Poole 1997). Thus, although recent sightings of lynx in the UP indicate that immigration is possible, our results suggest that successful dispersal of lynx from Ontario, Canada could be restricted by poor habitat quality (i.e., low hare densities) in the northeastern UP. An understanding of lynx distribution and movement in the southern range periphery in Ontario would facilitate conservation planning for lynx in the Great Lakes.

MANAGEMENT IMPLICATIONS

Our results indicated that potential lynx densities in the UP are currently limited by forest conditions that cannot support high densities of hare due to a lack of conifer regeneration. We suggest that management of lynx habitat in the UP be addressed at 2 scales. At the scale of individual forest patches, managers should identify those forest types with the potential to support a dense, conifer-dominant understory and implement treatments that facilitate developing these conditions to enhance hare habitat quality. At the landscape scale (i.e., 100 km²), managers should provide a sustainable mosaic of forest structures that offer patches of high hare density, connectivity among high-quality patches, and suitable denning conditions (Koehler and Aubry 1994). We caution that lynx habitat functionality in the Great Lakes region is influenced by numerous factors including interspecific competitors, climate change, and a pervasive anti-predator sentiment in many local communities. As such, managers that are considering lynx habitat improvements should focus on the most northern, least populated portions of the UP. Our habitat maps can help guide that prioritization.

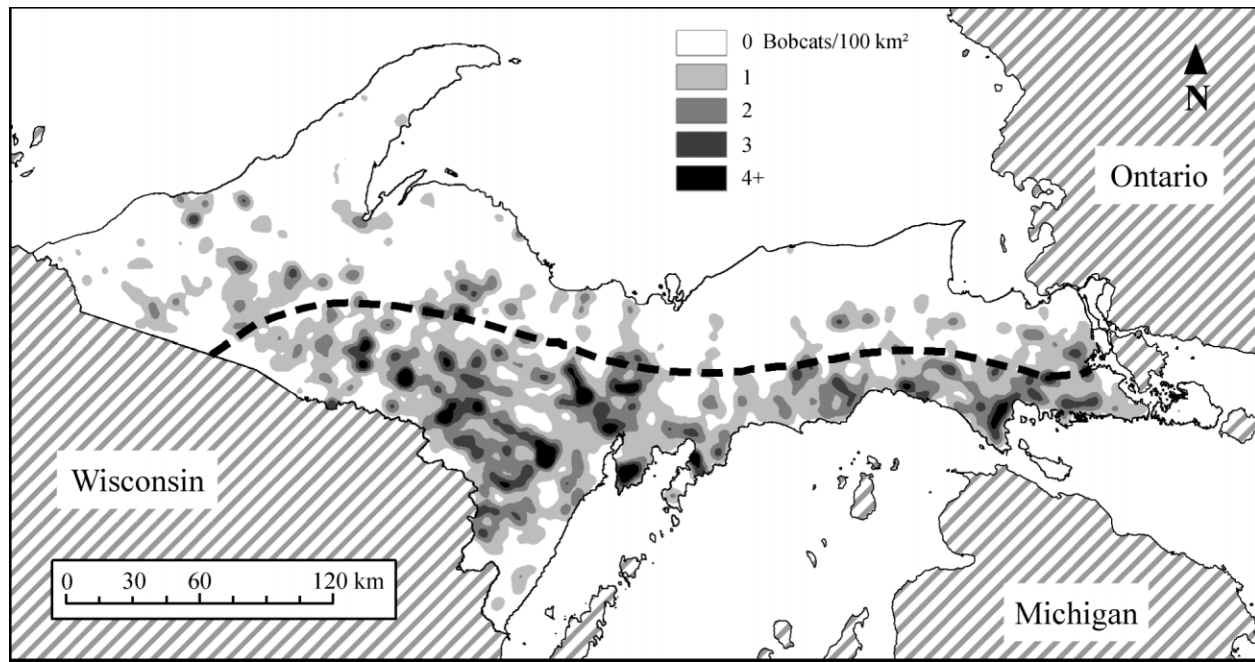


Figure 2. Average annual count of harvested bobcats (animals/100 km²) in the Upper Peninsula of Michigan, USA between 1985 and 2005 (D. E. Beyer, Jr., Michigan Department of Natural Resources, unpublished data). The black dotted line represents a 270-cm annual snowfall isocline (Eichenlaub et al. 1990).

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