Factors influencing snowshoe hare (*Lepus americanus*) in Michigan

By

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ABSTRACT

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The goal of my thesis was to identify the climatic and vegetation factors that influence snowshoe hare occupancy in Michigan. My objectives were to: 1) quantify snowshoe hare occupancy as related to climate change and 2) quantify the relationships between patch-level snowshoe hare occupancy and land cover change over time, current land cover, habitat structure, and mesocarnivore presence. In Chapter 1, I determined the most efficient transect configurations for winter track surveys and found that transects 150m in length with 100 or 75m spacing, or 125m in length with 75m spacing provided reliable estimates of hare occupancy. In Chapter 2, I researched climatic variables that are potentially linked to snowshoe hare population performance and assessed whether those factors affected the localized extinction of snowshoe hares. I found that localized extinction was influenced by maximum temperature from May 15 – January 19; as temperature increased the likelihood of localized extinction increased. I also found that the total number of days with measurable snow on the ground affected localized extinction; as number of days with snow on the ground decreased the likelihood of localized extinction increased. In Chapter 3, I evaluated whether land cover change over time, current land cover, and habitat factors affected snowshoe hare occupancy and habitat use. I found that land cover change over time did not affect hare occupancy. Rather, a current land cover covariate (the ratio between forest and open edge) and the habitat covariates of visual obstruction at 1.0-1.5m above snow level and stem density were important; all 3 parameters were positive but only the transect-level covariates were significant.
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INTRODUCTION

Culturally, snowshoe hares (Lepus americanus) are part of the hunting heritage in Michigan. In the 1970s over 100,000 individuals hunted hares each year, but this number declined to just under 20,000 in 2007 (Frawley 2008). Small-game hunter surveys indicate that snowshoe hare harvest and presumably abundance have consistently declined statewide over the past few decades (Frawley 2008). In addition to being culturally important in Michigan, snowshoe hares are also an important component of predator-prey communities, particularly at northern latitudes. Hares are known prey for numerous mesocarnivores and raptors, including Canada lynx (Lynx canadensis), red fox (Vulpes vulpes), American marten (Martes americana), fisher (Martes pennanti), coyote (Canis latrans), bobcat (Lynx rufus), red-tailed hawk (Buteo jamaicensis), and great horned owl (Bubo virginianus) (Carreker 1985). In some ecosystems (e.g. boreal forests of Canada and Alaska) predator population dynamics closely correlate with hare populations, underscoring the importance of hares to ecosystem function (Brand et al. 1976). The importance of lagomorphs to community function is not limited to hare-lynx systems. For example, generalist predators (e.g. coyotes) have lower predation rates on white-tailed deer when snowshoe hares exist in high abundance (Patterson and Messier 2000, Hurley and Garton 2011).

Snowshoe hares can be used as an indicator of climate change. The hare population in Michigan is at the southernmost boundary of the species range in the Lake States region (Figure 1.1). With a warming and drying climate, the range will likely shift northward because of reduced duration of snow cover and depth (Buehler and Keith 1982). Mechanisms causing this
range shift are not understood. Plausible hypotheses relate to direct effects on population vital rates and indirect effects on individual life history strategies (Bardsen et al. 2011). For example, molting at the proper time is essential for hare survival. This topic has drawn an increase of attention lately with researchers studying molting times and causes of snowshoe hares (Mills et al. 2013, Zimova et al. 2014).

A coarse, broad-scale habitat assessment corresponding to the late 1990s and early 2000s indicated that hare habitat quality in the Upper Peninsula of Michigan ranged from poor to marginal with only small, isolated areas of higher quality habitat (Linden et al. 2011). Snowshoe hares occupy continuous forested areas with a dense understory (>60% visual obstruction) that provides food, safety from predators and thermal cover. Hare survival rate is lower in areas with sparse horizontal cover (Litvaitis et al. 1985, Hodges 2000, Berg et al. 2012).

For my study on Michigan snowshoe hares, I used stakeholders to identify potential study sites. The use of individuals familiar with local history and ecology to supplement research and management is common and often referred to as local ecological knowledge (or traditional ecological knowledge if the stakeholders are indigenous to the area). Use of local ecological knowledge has increased since 1980, with 421 papers being published between 1980 and 2004. Of these papers, over half used interviews as the process for generating local ecological knowledge (Brook and McLachlan 2008). Gilchrist et al. (2005) found that local ecological knowledge was valuable to complement empirical data. Traditional ecological knowledge has proven reliable compared to more western science based approaches for generating information and can be used in conjunction with biological assessments (e.g. resource selection functions; Jacqmain et al. 2007, Polfus et al. 2014). Using stakeholders to
supplement traditional scientific approaches is also the basis for citizen science research and projects (Dickinson et al. 2010). The data stakeholders generate in these studies has proven reliable (Jordan et al. 2012). From each stakeholder I requested a relatively low level of local knowledge; stakeholders were asked for when and where they saw snowshoe hares, not specifics such as the exact day, sex, or abundance. As a testament to the repeatability of data generated from stakeholder interviews, independently interviewed stakeholders in my study provided the same exact locations.

Given that: 1) snowshoe hare harvest and presumably abundance have declined throughout Michigan, 2) hares are important in many predator-prey communities, 3) hares are a potential indicator of climate change, and 4) Michigan contains low quality and fragmented habitats, this research was designed to study factors influencing snowshoe hare occupancy in Michigan. My thesis consists of 2 distinct questions: 1) what is the optimal snow-tracking configuration for effectively and efficiently sampling a snowshoe hare population and 2) what factors are driving snowshoe hare localized extinctions, current occupancy, and habitat use in Michigan?

In Chapter 1 I describe the experimental design I implemented, with assistance from the Michigan Department of Natural Resources – Wildlife Division, and results of a captive hare study that I used to determine the optimal transect configuration for snow-tracking surveys. I implemented the captive hare study at 2 locations in the Upper Peninsula of Michigan by building ~6.1ha enclosures to control hare densities, trapping and radio-collaring hares near the enclosure and releasing them inside, and implemented snow track surveys as I manipulated hare densities. I simulated different transect configurations by varying transect length and
spacing. The optimal transect configuration was based on accuracy (needed to correctly designate the site as occupied >90% of the time) and efficiency (minimize the distance traversed by a surveyor).

In chapter 2, I assessed the effects of climate change on the extinction probability (over time ranging from 1955 to 2012) of snowshoe hares across Michigan. I compiled historically occupied sites using stakeholder interviews and surveyed a subset of those sites (using the optimal transect configuration from Chapter 1) to determine current occupancy status. I reviewed the published literature on snowshoe hares and identified 7 climate variables that other researchers denoted as important to snowshoe hare demographics. I used a logistic regression to determine which of the 7 climate variables were affecting localized snowshoe hare extinction in Michigan.

In Chapter 3, I evaluated how land cover and habitat factors influenced snowshoe hare occupancy and small-scale habitat use. I conducted 2 separate analyses: 1) the influence of historical land cover change on site level occupancy and 2) the effects of current land cover and habitat structure on site level occupancy and transect level use. Land cover covariates were mapped from aerial photography ranging from 1977 to 2012. I calculated the net change of land cover variables and used a logistic regression to determine which variables were significantly affecting snowshoe hare localized occupancy over time. Current land cover (mapped photography) and habitat variables (collected on transects) were modeled using the 2-level occupancy model in the package “Unmarked” in R to determine which variables were significantly influencing snowshoe hare occupancy and habitat use in Michigan. Additionally, I provide management recommendations based on the relationships between stem densities
and visual obstruction for 3 different forest types (conifer dominated, deciduous dominated, and mixed).
LITERATURE CITED
LITERATURE CITED


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CHAPTER 1

RELIABILITY OF WINTER TRACK COUNTS FOR QUANTIFYING SNOWSHOE HARE OCCUPANCY

ABSTRACT

I determined the optimum transect length and spacing for quantifying snowshoe hare (*Lepus americanus*) occupancy in a fixed area from snow track surveys. I also evaluated the utility of the most reliable and efficient designs for indexing hare density. I constructed enclosures (~6.1ha) at 2 locations in the Upper Peninsula of Michigan, USA, and populated the enclosures with radio-collared hares. Hare densities ranged from 0.2 – 1.5 hares/ha in the enclosures, comparable to low and high densities recorded at the southern extent of snowshoe hare range. I conducted snow track surveys along 9 transects spaced 25m apart in the enclosures 12-65 hours after a snowfall and mapped the location of every track that intersected a transect. After standardizing the track maps by time since last snowfall, I simulated different transect lengths and spacings and evaluated if hares were documented on the resultant transect segments. I deemed transect configurations reliable if >90% of the 10,000 simulations correctly denoted the site as occupied. Of the 28 possible transect configurations, only 10 combinations provided reliable estimates of hare occupancy. I refined the 10 reliable configurations based on efficiency, where efficiency was based on the distance traversed by a surveyor. I recommend using transects that are 150m in length with 100 or 75m spacing, or 125m in length with 75m spacing to reliably and efficiently survey a fixed area for snowshoe hares. Each of these 3 configurations was non-linearly related to the range of snowshoe hare densities evaluated in the study.
Key Words

*Lepus americanus*, Michigan, occupancy, snowshoe hare, snow track surveys, survey methodology, transect configuration

1.1. INTRODUCTION

Snowshoe hares (*Lepus americanus*) are vulnerable to climate change (Buehler and Keith 1982, Hoving et al. 2013, Mills et al. 2013), thus interest in documenting occupancy and abundance across large areas has increased. With models projecting warmer and drier climates during the 21st century for many parts of the world (IPCC 2013), knowing how to efficiently sample populations of vulnerable species is critical to documenting range shifts and implementing conservation activities. Efficient sampling of wildlife populations across large spatial extents relies on methods that can be quickly implemented during a single site visit and produce reliable results.

Selection of appropriate survey techniques in any wildlife study depends on the spatial and temporal extents of the research question(s), logistics of data collection, and the study system (organism and environment). For members of the genus *Lepus*, common techniques for documenting occupancy, abundance, and habitat use include live trapping (often used with mark-recapture), visual detection surveys along transects, fecal pellet counts, and snow track surveys (Marcström et al. 1989, Koehler 1990, Litvaitis et al. 1985, Shimizu and Shimano 2010, Lu 2011); combining these techniques may be appropriate depending on survey objectives (e.g., Roy et al. 2010). Some techniques are proven reliable, like using live trapping and fecal pellet counts to index hare abundance (e.g., Litvaitis et al. 1985, Hartman 2009), but these techniques
generally require multiple visits to the same location and are labor intensive. Fecal pellet counts can also be difficult to interpret in areas where multiple members of the Leporidae co-exist.

Snow track surveys are another proven technique for estimating hare habitat use and abundance (e.g., Marcström et al. 1989, Shimizu and Shimano 2010). Arguably, snow track surveys are better suited for larger areas than live trapping or fecal pellet counts, particularly in remote and difficult to traverse (like swamps) areas. The primary benefit of snow track surveys is that they can produce reliable results with a single site visit (Brocke 1975, Conroy et al. 1979, Thompson et al. 1989), however transect dimensions and configurations are inconsistent among studies so information on the most efficient design is lacking. To date, studies on snowshoe hare have used varying transect dimensions including a single 70m transect per study site (Roy et al. 2010), 2 – 1km transects spaced >1km apart (Thompson et al. 1989) and multiple transects spaced 50m apart (Conroy et al. 1979), with little guidance on efficacy of the various designs.

I sought a reliable and efficient survey methodology to estimate snowshoe hare occupancy. I sought a technique that could be: 1) used to reliably assess localized extinction, 2) implemented across a large spatial extent, 3) conducted with a single site visit, and 4) implemented with minimal equipment and survey time. Given the available techniques for estimating snowshoe hare occupancy and abundance, snow track surveys satisfied these criteria. My objective was to determine the optimum (i.e., most reliable and efficient) transect length and spacing for quantifying snowshoe hare occupancy from snow track surveys. Secondarily, I also evaluated the utility of the most reliable and efficient designs for indexing
hare abundance. I used a known number of radio-collared hares in ~6.1ha enclosures to evaluate a variety of transect lengths and spacings.

1.2. STUDY AREA

I conducted this study at 2 locations in the Upper Peninsula of Michigan: the Cusino State Wildlife Research Area (hereafter referred to as Cusino; 46°20′54″N 86°28′13″W) in Alger County, and on tribal land in Chippewa County near the town of Kinross (hereafter referred to as Kinross; 46°16′52″N 84°34′36″W). Cusino and Kinross are located >300 km north of the southern edge of hare range in Michigan (Fig. 1.1), and both locations were known to historically support snowshoe hares. Both locations have low topographic relief yet high landform complexity because of glacial activity (Bailey 1995). On average, Cusino received 7.0cm of precipitation monthly from December to March, resulting in snow depths that ranged between 60 and 120cm yearly (NOAA Weather Station Id MI205690; data from 2000-2009). Average minimum temperatures during winter at Cusino averaged -10°C (NOAA Weather Station Id MI205690; 2000-2009). Average monthly precipitation in Kinross from December through March was 5.7cm, resulting in 40 to 85 cm of snow yearly (NOAA Weather Station Id MI207190; data from 2000-2009). Minimum average temperature during December through March averaged -11°C at Kinross. Vegetation at the study sites included overstory alder (*Alnus* spp.), black spruce (*Picea glauca*), white cedar (*Thuja occidentalis*), and hemlock (*Tsuga canadensis*) in low-lying areas and balsam fir (*Abies balsamifera*), pine (*Pinus* spp.), maple (*Acer* spp.), birch (*Betula* spp.), and aspen (*Populus* spp.) on drier areas.
1.3. METHODS

I constructed ~6.1ha enclosures at Cusino and Kinross using 2.4m high chicken wire supported by posts at approximately 2.4m spacing. I selected ~6.1ha for the enclosure based on the amount of suitable habitat available at Cusino, the logistics of fence building, and to encompass the average home range of a snowshoe hare (Keith 1990). Depressions along the bottom of the fence were filled with woody debris. After >30cm of snow accumulation, the bottom of the fence was impervious to hare movements. My goal was to control snowshoe hare numbers (i.e., prevent escape or immigration) during the winter sample period. I ensured that the pen was unoccupied prior to the start of the study by repeatedly walking the enclosure and looking for tracks.

I used wooden box traps to live-trap snowshoe hares in habitats <32 and <5km from the enclosures at Cusino and Kinross, respectively. Traps were baited with fresh alfalfa and apples, set in and under suitable cover, and checked daily. Each captured hare was sexed, weighed, and for those >900g fitted with a 20g radio collar (with mortality sensor; Advanced Telemetry Systems, Isanti, MN). Radio-collared hares were subsequently released at a random location in the enclosure. The maximum hare density within an enclosure (1.5 hares/ha) corresponded to the maximum density documented in the southern portion of snowshoe hare range (Hodges 2000). After hares were released into the enclosure, I allowed them to acclimate for a minimum of 7 days before track sampling occurred.

At the beginning of each track sampling event, the observer confirmed that the released hares were in the enclosure (via the radio signals) and alive (via the mortality sensors). I conducted the track surveys along 9 north-south transects, spaced 25m apart and from the
fence edge, that ranged in length from 212 to 256m (Fig. 1.2A). I established transects by using a meter tape and hanging a labeled flag every 10m to facilitate mapping track locations. Track surveys were initiated >12hrs after a snowfall event that was substantive enough to cover old tracks (Brocke 1975). Observers (1 or 2) would walk transects 12-65 hours after a snowfall event and record the location where every hare track crossed a transect (Fig. 1.2B). All 9 transects were surveyed in a single day (usually within 4 hours).

After ≥1 track survey at a specific hare density, I removed hare(s) from the enclosure and the track survey(s) was repeated. For hares that were re-captured inside the pen, I removed radio collars and returned them to their capture origin. Sampling and hare removals continued when snow conditions permitted and until I could no longer ensure population closure (based on radio-collar and track evidence along the perimeter of the pen). I replicated this study in 2012 and 2013 at Cusino and in 2014 at Kinross, but starting hare densities varied at each location. All trapping and animal handling procedures were conducted by the Michigan Department of Natural Resources – Wildlife Division or Sault Ste. Marie Tribe of Chippewa Indians following internal animal use and care guidelines that were consistent with the American Society of Mammalogists Animal Care and Use Guidelines (Sikes et al. 2011).

1.3.1. Data Analysis

To help control for track accumulation based solely on time since the last snowfall, I standardized the number of tracks from each survey to a 12-hour period. For example, if a survey occurred 16 hours after snowfall and there were 40 tracks, the total number of tracks was randomly reduced by 25% to 30 tracks (i.e. 40 * (12 hours/16 hours) = 30 tracks). Once the track maps from all surveys were standardized to 12 hours (Fig. 1.2B), I subsampled the 212-
256m full transects into segments that were 10, 25, 50, 75, 100, 125, and 150m long. To subsample the data, I generated random locations along each transect and then created the appropriate transect segment from that random location (Figs. 1.2C,D). I then determined if any snowshoe hare tracks occurred on that resulting segment (Fig. 1.2E). A track on any segment indicated that the site was occupied (i.e., at least 1 track was documented on at least 1 transect).

I also simulated different transect spacing of 25, 50, 75, and 100m by removing transects from the analysis, creating 28 total transect configurations. For example, at a 25m spacing, all 9 transects were used (Fig. 1.2E), but at 100m spacing, only the 1st, 5th, and 9th transects were used (Fig. 1.2F). I simulated changes in spacing because I was interested in the number of transects that were needed to accurately sample a fixed area. The combination of transect length and distance traversed between transects ultimately defined sampling efficiency. I iterated each combination of transect length and spacing 10,000 times. I also tallied the number of occupied transects as a potential index to density. Analyses were performed in the statistical software R v. 3.1.0 (R Core Team 2014).

In the study, optimal transect configuration had 2 components: efficiency and reliability. I defined a configuration as reliable if occupancy status was correctly designated for >90% of the 10,000 iterations. I quantified efficiency based on the distance a surveyor would traverse as defined by transect length and spacing. Longer transects are less efficient to survey than shorter transects, and tightly spaced transects less efficient than further spaced transects (because more transects are needed to survey a fixed area). Given the parameters of the study,
10m transects spaced 100m apart would theoretically be the most efficient study design if accuracy was >90%.

**1.4. RESULTS**

I conducted track surveys at hare densities ranging from 1.5 hares/ha (9 in the enclosure) to 0.2 hares/ha (1 in the enclosure; Table 1.1). Starting hare densities varied at each enclosure because of annual variations in snow conditions, timing of the enclosure being completed, and availability of field technicians to run the study. I generally completed ≥2 surveys at each hare density, except for 0.5 hares/ha (Table 1.1). All surveys, except for the 5 surveys at 0.2 hares/ha (a single male), were conducted with hares from both sexes in the pen.

The shortest transect (10m) was generally inaccurate (i.e., ≤90% correct designation of occupancy) regardless of hare density, except for 25m spacing at 1.5 hares/ha (Fig. 1.3A). Generally, as spacing increased the shorter transects became more inaccurate, particularly at low hare densities (Figs. 1.3D,E). At high hare densities (1.5 to 1.2 hares/ha) several transect configurations satisfied the accuracy criterion (Figs. 1.3A,B), hence the decision on which configuration to use depended on length and spacing. At higher hare densities 50m transects spaced 100m apart was the most efficient configuration for estimating site occupancy (Figs. 1.3A,B). The more relevant question, particularly for surveys at the southern edge of hare distribution, is how to optimally sample at low hare densities. At 0.2 hares/ha, transects ≥75m long were required to satisfy the accuracy criterion (Fig. 1.3E). The most efficient design was a 150m long transect at 100m spacing (Fig. 1.3E). This configuration requires surveyors to traverse 1,150m to accurately survey ~6.1ha (Table 1.2).
Although my ability to rigorously evaluate the relationship between hare density and the number of occupied transects was limited to a low number of transects at wide spacing (n=3), my data suggest that counts of occupied transects correlate with hare density when a broad range of hare densities is evaluated (Fig. 1.4). This pattern was consistent for the 3 most efficient transect configurations and warrants further evaluation (Fig. 1.4). At low hare densities typical of the southern range (i.e., 0.2 to 0.5 hares/ha), counts of occupied transects were not consistently correlated with density (Fig. 1.4).

1.5. DISCUSSION

Given recent attention to snowshoe hares as a species vulnerable to climate change (Hoving et al. 2013, Mills et al. 2013), interest in accurate and efficient survey techniques that can be implemented across large areas has increased (Fortin et al. 2005). Results from the snow track surveys and associated data simulations offer guidance to researchers on how to optimize survey methodologies for quantifying snowshoe hare site occupancy. Given the ~6.1ha survey area and a 12-65-hour survey window following a snow event, I recommend 3 transect designs as being most efficient for sampling hares at low densities that include 150m length with 100 or 75m spacing, and 125m length with 75m spacing (Table 1.2). I based my estimate of efficiency on the total distance traveled by a surveyor (Table 1.2), but caution that selection of a specific configuration should also be based on the spatial pattern of potential habitats. If potential habitats are large and blocky (e.g., expansive coniferous swamps), the 150m long with 100m spacing is the most efficient design. However, if habitats are patchy or narrow (e.g., riparian zones) a configuration based on shorter transects may be more desirable to help ensure that survey effort is concentrated in areas that likely support hares. My recommendation that
multiple transect configurations are suitable for quantifying occupancy is consistent with others that evaluated hare survey techniques. For example, Hodges and Mills (2008) found that multiple designs were effective for fecal pellet surveys.

MacKenzie et al. (2006:7) noted that proper inference from sampling animal populations depends on 2 critical components: the ability to capture spatial variation and detectability. Spatial variation is important because in large scale monitoring programs, like those needed to identify range shifts in widely distributed species, investigators cannot survey entire areas (MacKenzie et al. 2006). Instead, rigorous experimental designs based on accurate and efficient sampling are required (Fortin et al. 2005). For snowshoe hares, I found that snow tracking could produce reliable data on occupancy and could be efficiently implemented across large areas if snow and ice conditions were favorable (see Burt 2014: Chapters 2,3).

Like other techniques used to measure hare occupancy, abundance, and habitat use, snow track surveys also have limitations. Although Hartman (1960) found that snow track indices for hares in southern Ontario were relatively consistent between early and late winter, the number of tracks encountered on transects can be affected by the hare population cycle, weather, predators, and social interactions (Thompson et al. 1989). For example, during the low phase of the population cycle snowshoe hares may only occupy prime habitats (Keith and Windberg 1978). Conroy et al. (1979) found that distance to lowland coniferous-hardwood habitats and habitat interspersion were the 2 most important vegetation factors determining snowshoe hare activity (and hence track deposition) in Michigan. I contend that variability in track deposition resulting from population and environmental factors supports the use of
lengthy transects to increase the likelihood of encountering a localized movement and likely
limits the population response variable of interest to site occupancy.

Although I did not incorporate the effects of short-term weather on the track survey
results, I encourage researchers implementing track surveys to document the weather between
the end of snowfall and the start of the track survey. The surveys were conducted during
periods of low wind and without precipitation so that deposited tracks were not obscured.

Snowshoe hare movements during winter in the Laurentian Mountains of Quebec was
positively influenced by lack of wind, overcast skies, and warmer temperatures (Bider 1961),
consistent with research from Minnesota where hares remained close to forms (e.g., in or
under hollow logs and under fallen trees) during inclement weather (i.e., high winds, rain,
snowstorms; Aldous 1937). Hartman (1960) also found that hares reduced movements during
rain, and further hypothesized that hare movements were inversely correlated with the
abundance of suitable food.

For single species monitoring, the most commonly used state variable of interest is
abundance or population size (MacKenzie et al. 2006:6). Hence, monitoring programs that
accurately quantify occupancy across large spatial extents (to assist with documenting range
shifts) while simultaneously estimating or indexing abundance are desirable. Limited data from
my study suggests that hare densities and the results of track surveys are positively related,
though the relationship appears to be non-linear and only applicable to a broad range of hare
densities (Fig. 1.4). If transects are spaced far enough apart (75 to 100m in my study) in a fixed
area, the number of occupied transects should theoretically relate to the number of hares using
that area. Although further research is needed to verify whether the observed relationship

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between occupied transect counts and hare density is robust, I caution that such an approach should be viewed as an index to abundance and not used to estimate density, primarily because I likely double-count individual hares during snow transect surveys that are based on a grid design.

1.6. ACKNOWLEDGEMENTS

I am thankful for the assistance of MDNR-Wildlife Division employees J. Belman, D. Beyer, D. Brown, J. Lukowski, K. Sitar, K. Swanson, T. Swearingen, and C. VanHorn for their assistance with fence construction and/or data collection at the Cusino Wildlife Research Area. Also, thanks to S. Beyer from MDNR for helping me manage the social and political aspects of the project. In addition, thanks to R. Aikens and B. Sillet of the Sault Ste. Marie Tribe of Chippewa for their help in fence construction at Cusino, the replication of the research at Kinross, and their commitment as a partner to this research project. Funding for this project was provided by the Michigan Department of Natural Resources – Wildlife Division through the Michigan Federal Aid in Wildlife Restoration program grant F13AF01268 in cooperation with the U.S. Fish and Wildlife Service, Wildlife and Sport Fish Restoration Program and Safari Club International Michigan Involvement Committee.
APPENDIX
Table 1.1. Snowshoe hare densities, track survey efforts, location of surveys, and year(s) that surveys were completed in ~6.1ha enclosures, Upper Peninsula of Michigan, USA.

<table>
<thead>
<tr>
<th>Hare Density (hares/ha)</th>
<th>Number of Surveys</th>
<th>Location</th>
<th>Year completed</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.5</td>
<td>2</td>
<td>Cusino</td>
<td>2012</td>
</tr>
<tr>
<td>1.2</td>
<td>4</td>
<td>Cusino</td>
<td>2012, 2013</td>
</tr>
<tr>
<td>0.8</td>
<td>2</td>
<td>Cusino</td>
<td>2013</td>
</tr>
<tr>
<td>0.5</td>
<td>1</td>
<td>Cusino</td>
<td>2013</td>
</tr>
<tr>
<td>0.2</td>
<td>5</td>
<td>Kinross</td>
<td>2014</td>
</tr>
</tbody>
</table>
Table 1.2. Transect dimensions, the number of transects in a ~6.1ha study site, and distance traversed during snow track surveys for snowshoe hares. Table includes the 10 combinations of transect length and spacing that produced ≥90% accuracy for estimating site occupancy. The Efficiency is determined by the total distance walked for a complete survey.

<table>
<thead>
<tr>
<th>Transect Dimensions</th>
<th>Length</th>
<th>Spacing</th>
<th>Number of Transects</th>
<th>Distance Traversed (m)$^a$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>75</td>
<td>25</td>
<td>33</td>
<td>3275</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>25</td>
<td>25</td>
<td>3100</td>
</tr>
<tr>
<td></td>
<td>125</td>
<td>25</td>
<td>20</td>
<td>2975</td>
</tr>
<tr>
<td></td>
<td>150</td>
<td>25</td>
<td>17</td>
<td>2950</td>
</tr>
<tr>
<td></td>
<td>100</td>
<td>50</td>
<td>13</td>
<td>1900</td>
</tr>
<tr>
<td></td>
<td>125</td>
<td>50</td>
<td>10</td>
<td>1700</td>
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<tr>
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<td>150</td>
<td>50</td>
<td>9</td>
<td>1750</td>
</tr>
<tr>
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<td>7</td>
<td>1325</td>
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<tr>
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<td>150</td>
<td>75</td>
<td>6</td>
<td>1275</td>
</tr>
<tr>
<td></td>
<td>150</td>
<td>100</td>
<td>5</td>
<td>1150</td>
</tr>
</tbody>
</table>

$^a$ \[((\text{Length} + \text{Spacing}) \times \text{Number of Transects} - 1) + \text{Length}\)
Figure 1.1. The geographic range of snowshoe hares (diagonal striping), with Michigan outlined in bold black (map inset), and the locations of Cusino and Kinross hare enclosures, Upper Peninsula of Michigan, winters of 2012-2014. The geographic range of hares was adapted from the International Union for Conservation of Nature (www.iucnredlist.org/technical-documents/spatial-data#mammals).
Figure 1.2. Schematic of how snowshoe hare tracks in enclosures were subsampled including (A) the outline of the enclosures (black) with 9 transects spaced 25m apart (gray), (B) snowshoe hare tracks during 1 survey as black circles, (C) random locations generated on each transect to denote the start of transect segments for 1 iteration as black 4-pointed stars, (D) transect segments of 25m on each transect as black lines originating from the black 4-pointed stars, (E) snowshoe hare tracks that intercepted transect segments, and (F) example of the results of 1 iteration with 100m spacing.
Figure 1.3. Proportion of 10,000 iterations that a site was correctly deemed as occupied for all transect configurations at hare densities of (A) 1.5, (B) 1.2, (C) 0.8, (D) 0.5, and (E) 0.2 hares/ha. The 90% accuracy threshold is designated by the black horizontal line.
Figure 1.4. The average number of transects occupied at each of the 5 hare densities for the 3 most efficient transect configurations: 125 m length x 75 m spacing, 150 m length x 75 m spacing, and 150 m length x 100 m spacing.
LITERATURE CITED


CHAPTER 2

CLIMATIC FACTORS INFLUENCING THE DISTRIBUTION OF SNOWSHOE HARES

ABSTRACT

I aimed to: (1) compare the effects of different climate factors on snowshoe hare (*Lepus americanus*) localized extinction probability in Michigan, USA; (2) inform recently published vulnerability assessments; (3) identify the most influential climate variables affecting snowshoe hare distribution; and (4) provide insights into population-level mechanisms causing localized extinctions. I implemented track surveys at historically occupied sites that were identified by interviewing snowshoe hare hunters and wildlife biologists. I identified climate variables that potentially described population demographics of snowshoe hares. I modeled the likelihood that a localized (approximately 7.5 ha) snowshoe hare population went extinct from year of last known occupancy. I created a candidate model set from all possible combinations of uncorrelated climate variables and used Akaike Information Criterion to rank the models and 95% confidence internals to estimate parameter significance. The top-ranking model for describing localized snowshoe hare extinction in Michigan was based on the maximum temperature from May 15 – January 19. As maximum temperature increased the likelihood of localized extinction increased. The 2nd ranking model was based on total number of days with measurable snow on the ground. As the number of days with snow on the ground decreased, the likelihood for localized extinction increased. I found that the current distribution of snowshoe hares at the southern edge of the range shifted northward by ~45 km over the last 20 years. Average climate conditions over time were correlated with localized extinction of
snowshoe hare in Michigan. Warmer temperatures and fewer days with snow on the ground were correlated with a northward shift of snowshoe hare distribution. Population mechanisms potentially linked to the localized effects of these climate variables include reduced litter sizes and increased predation. Interactions with additional factors (e.g., habitat quality, predator-prey relationships) will likely exacerbate this northward shift in snowshoe hare distribution.

**Key Words**

Climate change, geographical range, *Lepus americanus*, logistic model, Michigan, snowshoe hare, snow track surveys, species distribution

### 2.1 INTRODUCTION

Climatic factors are often thought to limit species ranges and these limits shift with changes in climate (Araújo and Rozenfeld 2014). Models project warmer and drier climates during the 21st century for many parts of the world (IPCC 2013). Warmer and drier climates negatively affect species that are uniquely adapted to snowy or cold environments (Thomas et al. 2004, IPCC 2007, Pereira et al. 2010), such as American marten (*Martes americana*), American pika (*Ochotona princeps*), Arctic lemming (*Dicrostonyx torquatus*), Canada lynx (*Lynx Canadensis*), fisher (*Martes pennanti*), moose (*Alces alces*), and snowshoe hare (*Lepus americanus*). For example, Wasserman et al. (2012) predicted that by 2080, climate change would reduce American marten habitat connectivity by over 50% in the Rocky Mountains, USA, resulting in decreased genetic diversity and a constantly declining population. Similarly, American marten and lynx populations in the northern Appalachian and Acadian Ecoregion (eastern USA) are expected to decline 40% and 59%, respectively, by 2055 because of climate change (Carroll 2007). Carroll (2007) posits that the additive effects of logging and trapping will
exacerbate vulnerability for these species (Carroll 2007). The population of Arctic lemmings in northern Russia has declined since the Last Glacial Maximum and future climate is projected to further reduce the population, eliminate genetic diversity, and cause local extinctions (Prost et al. 2010).

The process of localized extinction and colonization is often a precursor to range contraction or expansion, respectively. For winter-adapted species, localized extinction caused by warming or drying climates can be difficult to document because the effects are potentially confounded by other stressors like changes in food abundance, competitors, or mismatched timing with host species (Cahill et al. 2013). Some species (e.g. moose) exhibit direct behavioral responses (e.g., changes in foraging) to changing climatic conditions that ultimately can be linked to population-level processes (van Beest et al. 2012). Generally, evidence is sparse for direct relationships between species distributions or population performance and climate change (Cahill et al. 2013). For most species, climate affects are inferred from the spatial distribution of occupied and unoccupied sites over time.

Snowshoe hares are adapted to environments with abundant snowfall and prolonged winters and hence populations are sensitive to climate change (Mills et al. 2013). Michigan is at the southernmost boundary for the range of snowshoe hare in the Lake States region, North America (Fig. 2.1). Buehler and Keith (1982) noted that hare populations in the Lake States region will likely shift northward in response to a warming and drying climate because of reduced duration of snow cover and depth. The population-level mechanisms causing this potential range shift are not understood. Plausible hypotheses relate to direct effects on population vital rates and indirect effects on individual life history strategies (Bardsen et al.}
For example, some have suggested that hare productivity is lower during years with warmer summers, falls, and winters (Meslow and Keith 1971, Kielland et al. 2010; Table 2.1); others have indicated that survival is lower during winters with more snow-free days (Kielland et al. 2010, Mills et al. 2013; Table 2.1). Most support to date exists for the survival hypothesis as it relates to higher predation rates (Hone et al. 2011).

During various phases of the 10-year population cycle at southern latitudes, mortality of snowshoe hares from predation can be >90% (Hodges 2000). Concealment is recognized as a leading evolutionary force that influences pelage coloration among mammals (Caro 2005); molting at the proper time is critical to the survival of individual hares (Mills et al. 2013). Molt initiation dates for hares in Maine and Montana (USA) began in late September and early April, and research to date indicates that onset of the fall molt exhibits low plasticity (Severaid 1945, Mills et al. 2013, Zimova et al. 2014). Climate data suggest that the number of days with snow on the ground throughout much of the southern distribution of hare range has decreased by up to 25 days from 1972-2004 (Choi et al. 2010). By the end of the 21st century, duration of snow cover throughout the entire range of snowshoe hares is expected to significantly decrease (Brown and Mote 2009). Hence, the number of days with snow on the ground is likely an important determinant of localized extinction for snowshoe hares.

I compared the effects of different climate factors on snowshoe hare distribution in Michigan, USA. I modeled how changes in climatic variables influenced localized (7.5 ha) extinction probability at sites throughout the state. My results have relevance to recently published vulnerability assessments (e.g., Hoving et al. 2013) and provide indirect insights into
potential population-level mechanisms causing localized extinctions that ultimately lead to changes in broad-scale distribution of snowshoe hares.

2.2 STUDY AREA

My study occurred in the Upper and northern Lower Peninsulas of Michigan on publically owned lands during the winter of 2013 (Fig. 2.1). This spatial extent corresponds to the known historic distribution of snowshoe hares in Michigan (Fig. 2.1). My study consists of three broad regions: 1) western Upper Peninsula, 2) eastern Upper Peninsula, and 3) northern Lower Peninsula. Landforms of the western Upper Peninsula consist of glacial moraines, lake plains, outwash channels and plains, and glacially scoured bedrock ridges (Albert 1995). Primary vegetation types include northern hardwoods, aspen (*Populus* spp.), pine (*Pinus* spp.), and conifer swamps (Albert 1995). The western Upper Peninsula experiences the most extreme winters and shortest growing seasons of the three regions I studied (Albert 1995). Monthly average temperatures ranged from -10°C to 17°C, with average annual precipitation of 90 cm, including 435 cm of snowfall (NOAA 2012).

Landforms of the eastern Upper Peninsula consist mostly of flat lake plain with areas of exposed bedrock (Albert 1995). Vegetation types include northern hardwoods, upland conifers (white pine (*P. strobus*), red pine (*P. resinoso*), jack pine (*P. banksiana*)), hardwood-conifer swamps, rich conifer swamps, and northern wet meadows (Albert 1995). Monthly average temperatures vary from -10°C to 18°C with average annual precipitation of 80 cm, including 194 cm of snowfall (NOAA 2012).

Landforms in the northern Lower Peninsula (NLP) consist of large, sandy outwash plains and large glacial moraines (Albert 1995). The climate of coastal areas in the NLP is moderated...
by Lakes Huron and Michigan resulting in warmer and cooler temperatures in winter and summer, respectively. Interior areas are subjected to more extreme temperature fluctuations. Forest types include northern hardwoods, aspen, oak (Quercus spp.), pine, and lowland conifer (Albert 1995). Monthly average temperatures range from -8°C in January to 20°C in July, with average annual precipitation of 90 cm, including 169 cm of snowfall (NOAA 2012).

2.3. METHODS

2.3.1. Site Selection

I interviewed 45 individuals that had knowledge of historical snowshoe hare locations in Michigan. Interviewees included Michigan Department of Natural Resources employees, hare hunters, and tribal members. I identified potential interviewees by contacting various hunting clubs, attending sportsperson coalition meetings, talking with colleagues, and by individuals providing contact information for hare hunters they personally knew. Each interviewee was asked to map locations that were unequivocally occupied by snowshoe hares sometime in the past. Unequivocal evidence included tracks, harvested hares, or observed hares. Each interviewee was asked to estimate the year of last confirmed occupancy within 5 yrs. I also checked museum records (e.g. VertNet or MaNIS) for historical snowshoe hare collection locations, but opted not to use these records because the locational error was generally large (i.e. >1km). Islands of Michigan (e.g. Drummond Island or North Manitou Island) were not added to the list of potential study locations. I compiled potential study sites from the interviews and selected a subset of locations that encompassed broad spatial (throughout hare range in Michigan; Fig. 2.1) and temporal (1955-2010; Fig. 2.2) domains. The 7.5 ha study sites were separated by >1.6 km (mean = 10.2 km, SE = 0.7). My interview protocol was reviewed
and approved by the Human Research Protection Program, Institutional Review Board, at Michigan State University (IRB# x11-805).

2.3.2. Field Sampling

Winter track counts along transects are commonly used to document snowshoe hare occupancy and habitat use (Brocke 1975, Conroy et al. 1979, Thompson et al. 1989). However, transect dimensions and configurations are inconsistent among studies. I evaluated the effects of transect number (2-9), length (10-150m), and spacing (25-125m) on my ability to accurately portray site occupancy using a known number of telemetered snowshoe hares in a 6 ha enclosure during the winters of 2012 and 2013. Prior to releasing telemetered hares, I surveyed the enclosure to ensure that no hares were present. I demarcated 9 transects, spaced 25 m apart, ranging in total length from 225-250 m. Track surveys were conducted 12-65 hours after fresh snowfall. Track locations along transects were mapped to the nearest 5m and random sub-sampling of transect lengths and spacing was used to identify the most efficient transect configuration, where efficiency was defined as the highest probability of correctly denoting site-level occupancy. I replicated transect sampling at densities ranging from 0.2 to 1.5 hares/ha. These densities represented low to high snowshoe hare densities recorded at the southern edge of hare range (Hodges 2000). Snowshoe hare trapping and radio-collaring were conducted by the Michigan Department of Natural Resources – Wildlife Division following internal animal use and care guidelines that were consistent with the American Society of Mammalogists Animal Care and Use Guidelines (Sikes et al. 2011).

I implemented the most efficient transect methodology from the enclosure study at a subset of locations selected from the interview process (Fig. 2.1). Sampling for snowshoe hares
occurred on a single day and was completed 12-72 hours after fresh snowfall to allow for track accumulation. If a track was detected on ≥1 transect at a site, then the site was designated as occupied. Sites without tracks were deemed unoccupied and presumed to have experienced localized extinction since the time of last known occupancy.

2.3.3. Climate Covariates

A priori, I conducted a review of scientific publications that evaluated how climate affected snowshoe hare population demographics. I identified 4 precipitation and 3 temperature variables (Table 2.1). I note that most of the observed climate effects on hares were indirect, often based on speculation as to the physiological mechanism(s) causing the observed population response. The precipitation variables included mean snow depth (SD) in an annual snow season (approximately November through April), total number of days with measurable snow on the ground (DSOG), total number of days with a snowfall event (DSE), and total spring precipitation from March 20 – June 20 (spring precipitation; Table 2.1). Temperature variables included mean minimum temperature from February 4 – April 24 (minimum winter temperature), mean maximum temperature from May 15 – January 19 (maximum temperature), and mean winter temperature from December 21 to March 19 (mean winter temperature; Table 2.1).

I compiled climate covariates for each snowshoe hare survey site from the closest National Oceanic and Atmospheric Administration (NOAA) weather station that had archived data for all 7 variables dating back to the year of last known hare occupancy (http://www.ncdc.noaa.gov/; Fig. 2.2). I used 35 weather stations and evaluated multiple approaches for summarizing climate data across time (e.g., year-to-year variation, total
difference, and deviance) and, based on model weight of evidence, found that average values calculated from the year of last known occupancy to 2012 were most useful in portraying hare extinction probability. I note that although climate data from some sites came from the same weather station, times of last known occupancy often varied among those sites so the average climate conditions often differed.

2.3.4. Data Analysis

I analyzed all combinations of climate covariates for colinearity using Pearson’s correlation coefficient (Sokal and Rohlf 2011); covariates were considered correlated if $r \geq |0.15|$ and $p \leq 0.05$. I modeled the likelihood that a localized (approximately 7.5 ha) snowshoe hare population went extinct from year of last known occupancy using logistic regression. I included a random effect for each weather station to account for autocorrelation among sites that used the same weather station data. I created a candidate set of models ($n=9$; Table 2.2) from all possible combinations (additive terms) of uncorrelated climate variables. Models were ranked based on Akaike Information Criterion (AIC) and parameter estimates were deemed significant if the 95% confidence intervals did not overlap 0 (Burnham and Anderson 2002, Nakagawa and Cuthill 2007).

2.4. RESULTS

My interviews resulted in 386 potential study sites with year of last known hare occupancy ranging from 1955 to 2010; climate data were compiled for 134 of those sites (Fig. 2.1). Most climate variables were correlated except for spring precipitation and DSoG and spring precipitation and SD. Regardless of the climate variable I documented a broad range of minimum and maximum values and considerable variation in measurements across sites (Table
These results typify the temperature and precipitation variation often found at small scales in Michigan that are caused by a combination of lake effect, topography, and prevailing direction of weather fronts.

From the captive hare study, I found that reliable (i.e., occupancy probability correctly designated >95% of the time) estimates of hare occupancy were obtained by surveying 9 – 125m long transects spaced 75m apart. After implementing this transect configuration on the 134 sites spread throughout Michigan, I found that hare populations experienced localized extinction on 52 sites (39%) statewide. In the northern Lower Peninsula 36 of 74 sites (~49%) were unoccupied during 2013. Only 16 out of 60 (~27%) sites were unoccupied in the Upper Peninsula. My results indicate almost a two-fold increase in localized extinction probability from north to south in Michigan.

All candidate models for describing the localized extinction of snowshoe hares received some support (i.e., \( \omega_i \geq 0.01 \)), but a clear top-ranking model emerged based on weight of evidence (Table 2.2). My top-ranking model accounted for 52% weight of evidence and was based on maximum temperature (Table 2.2). As maximum temperature increased the likelihood of localized extinction significantly increased (\( \beta = 0.043, 95\% \text{ CI} = 0.014 – 0.073; \text{Table 2.2} \)). The next ranked model (\( \Delta AIC = 2.6 \)) accounted for 15% weight of evidence and was based on DSoG (Table 2.2). The DSoG indicated that as the number of days with snow on the ground decreased, the likelihood for localized extinction significantly increased (\( \beta = -0.026, 95\% \text{ CI} = -0.026 – -0.004; \text{Table 2.3} \)). All other models received minimal support (i.e., \( \omega_i \leq 0.11 \)) and only one additional significant covariate was identified (SD). As SD decreased, the likelihood for localized snow hare extinction increased (\( \beta = -0.004, 95\% \text{ CI} = -0.0078 - -0.0003; \text{Table 2.3} \)).
Mean maximum temperature from time of last known hare occupancy across the study sites ranged from 13 to 17°C and corresponded to a 3-fold increase in localized extinction probability (Fig. 2.3A). Average days with snow on the ground in the study ranged from 60 to 140; sites with fewer DSoG were >3 times more likely to go extinct (Fig. 2.3B). Average snow depths in the study ranged from 100 to 600mm; hares occupying sites with greater snow depth were ~1.5 times less likely to go extinct (Fig. 2.3C). Because these three climate covariates were correlated and significant in my models, my results suggest that maximum temperature, DSoG, and SD have an integrated effect on localized extinction probabilities for snowshoe hares.

2.5. DISCUSSION

I sampled a broad spatial and temporal domain throughout the range of snowshoe hares in Michigan and found that climate variables were significantly correlated to localized extinction probability. My findings substantiate assessments that hares are vulnerable to climate change (Hoving et al. 2013; Mills et al. 2013). I demonstrated a greater proportion of extinct sites closer to the southern range periphery, but also found extinct sites in more centrally located areas suggesting that factors other than climate are also affecting localized snowshoe hare extinctions. Sites with warmer temperatures from summer to early winter, fewer days with snow on the ground, and shallower snow depths were more likely to go extinct. Population mechanisms potentially linked to localized hare extinction include reduced litter sizes from higher temperatures (Meslow and Keith, 1971), increased predation from fewer days with snow on the ground (Kielland et al. 2010, Mills et al. 2013), and less food availability during periods of low snow depths (Bider 1961, Meslow and Keith 1971, Conroy et al. 1979).
My results are consistent with other studies that have explored climate-related mechanisms associated with population declines in other species. For example Lee et al. (2000) found that warmer weather and wetter winters resulted in fewer reindeer (*Rangifer tarandus*) calves in northern Finland and Norway. Higher total rainfall in spring was correlated with a smaller proportion of wild pig (*Sus scrofa scrofa* L.) females to breed the following season (Sabrina et al. 2009). While deep snows impose higher energetic costs to hares (Hodges et al. 2006), similar to findings observed for Alpine red deer (*Cervus elaphus* sp.; Schmidt 1993, Rivrud et al. 2010) and moose (Dussault et al. 2005), my results indicate that deeper snows may benefit snowshoe hares by increasing the availability of browse on portions of plants that were not available during the summer or early winter (Bider 1961, Meslow and Keith 1971, Conroy et al. 1979).

Although my results suggest that multiple climatic factors influence snowshoe hare extinction probability, these factors likely interact with predator-prey relationships, vegetation structure, spatial arrangement of habitats, and food availability. Predators are the primary cause of mortality for snowshoe hares and early winter is a time of increased predation from mammalian predators (Hodges 2000). With a changing climate that results in fewer days with snow on the ground, coupled with a relatively fixed timing of the fall molt in hares (Mills et al. 2013), the camouflage advantages of white pelage are negated. Increased predation pressure resulting from compromised camouflage can also have negative indirect effects on hare body condition and fecundity (Hodges et al. 1999). Increased predation pressure, indirect effects of predation on fitness, and decreased litter sizes associated with warmer maximum temperatures likely interact to favor localized extinction of hares.
Climate can also potentially affect snowshoe hares indirectly through climate induced changes to forest communities. Increasing temperatures in northern latitudes are expected to change forest composition from needle-leaved (e.g. *Abies* spp., *Betula* spp., *Picea* spp., *Pinus banksiana*, and *Populus* spp.) to broad-leaved (e.g. *Fagus* spp., *Picea* spp., and *Quercus* spp.) landscapes and decrease forest productivity and total biomass (Prentice et al. 1991, Prentice et al. 1993, Lenihan et al. 2003, Duveneck et al. 2014). The potential loss of conifer dominated forests to deciduous forests could negatively impact hares because conifers are 3 times more important to hares (Litvaitis et al. 1985). A meta-analysis found that the range limits of 99 species have moved northwards by 6.1 km per decade on average and forests in northern Michigan may experience conditions similar to those about 2° south causing reduced species regeneration success (Reed and Desanker 1992, Parmesan and Yohe 2003). Correspondingly, this northward transition of critical hare habitat components may also result in a northern shift in hare distribution. A changing climate may also fragment habitats (Root et al. 2003). Hare habitat in the Upper Peninsula of Michigan is already considered fragmented (Linden et al. 2010) and climate change may exacerbate those negative effects on hare populations.

Most of the Upper Peninsula of Michigan is estimated as poor to marginal snowshoe hare habitat (Linden et al. 2010). Snowshoe hare populations tend to thrive in continuously forested areas with dense understories (>60% visual obstruction) that provide food, safety from predators, and thermal cover (Litvaitis et al. 1985). Hare survival rates are lower in areas with sparse horizontal cover (Litvaitis et al. 1985). Sparse understory cover further exacerbates higher predation pressures resulting from fewer days with snow on the ground. Additionally, lower mean snow depths can restrict access to forage during critical winter months (Bider 1961,
Meslow and Keith 1971, Conroy et al. 1979). Although food availability does not appear to limit hares during winter (Conroy et al. 1979, Carreker 1985), low levels of understory cover coupled with decreased snow depths potentially concentrates hares and restricts access to high quality forage. The effective browse height for snowshoe hares is about 46 cm and browsing efficiency is maximized when snow depths increase throughout the winter making new browse available (Bider 1961).

My results indicate that future climate change will move the southern edge of snowshoe hare range northward. Abundant and diverse predators and poor habitat conditions will likely exacerbate this change. In Michigan, I found that the current distribution of snowshoe hares at the southern edge of the range shifted northward by ~45 km over the last 20 years. An important unanswered question is whether management focused on reducing predator numbers or improving hare habitat quality and connectivity can help reduce the negative impacts of climate change. The loss of snowshoe hares from Michigan would have important ecological and cultural ramifications and hence developing and testing strategies for conserving this species during periods of rapid climate change are needed.

2.6. ACKNOWLEDGEMENTS

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sportsperson coalition meetings and S. Beyer for helping me manage the social and political aspects of the project. Funding for this project was provided by the Michigan Department of Natural Resources – Wildlife Division through the Michigan Federal Aid in Wildlife Restoration program grant F13AF01268 in cooperation with the U.S. Fish and Wildlife Service, Wildlife and Sport Fish Restoration Program and Safari Club International Michigan Involvement Committee.
APPENDIX
Table 2.1. Climate covariates identified from the literature review, associated citation, and observed relationship to snowshoe hare population demographics.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Publication(s)</th>
<th>Importance to hares</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean snow depth (SD)</td>
<td>Bider 1961, Meslow and Keith 1971, Conroy 1979, Hodges et al. 2006, Kielland et al. 2010</td>
<td>Increased snow depth creates different browse availability and increased energetic costs</td>
</tr>
<tr>
<td>Total number of days with measureable snow on the ground (DSoG)</td>
<td>Kielland et al. 2010, Mills et al. 2013</td>
<td>Incorrect pelage coloration for crypsis with lack of snow on the ground during winter months, presumably decreasing survival</td>
</tr>
<tr>
<td>Total number of days with a snowfall event</td>
<td>Kielland et al. 2010, Meslow and Keith 1971</td>
<td>Decreased juvenile and adult survival with more snowfall</td>
</tr>
<tr>
<td>Total spring precipitation (March 20 – June 20)</td>
<td>Kielland et al. 2010</td>
<td>Duration of decline phase associated with increased spring precipitation</td>
</tr>
<tr>
<td>Mean minimum temperature (February 4 – April 24)</td>
<td>Meslow and Keith 1971</td>
<td>Warmer minimum temperatures during this time period, the greater the adult survival</td>
</tr>
<tr>
<td>Mean maximum temperature (May 15 – January 19)</td>
<td>Meslow and Keith 1971</td>
<td>Colder temperatures during this period were associated with larger litter sizes in subsequent breeding seasons</td>
</tr>
<tr>
<td>Mean winter temperature (December 21 – March 19)</td>
<td>Kielland et al. 2010</td>
<td>Warmer temperatures during this time period associated with the decline phase of the snowshoe hare cycle</td>
</tr>
</tbody>
</table>
Table 2.2. Candidate model set for estimating the likelihood of a localized snowshoe hare population going extinct in Michigan. LL = log-likelihood, ΔAIC = difference in AIC value from top-ranking model, k = model parameters, ω_i – Akaike weight of evidence.

<table>
<thead>
<tr>
<th>Candidate Model</th>
<th>LL</th>
<th>ΔAIC</th>
<th>K</th>
<th>ω_i</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum temperature</td>
<td>-85.23</td>
<td>0.0</td>
<td>3</td>
<td>0.52</td>
</tr>
<tr>
<td>Days snow on ground (DSoG)</td>
<td>-86.51</td>
<td>2.6</td>
<td>3</td>
<td>0.15</td>
</tr>
<tr>
<td>DSoG + Spring precipitation</td>
<td>-85.80</td>
<td>3.1</td>
<td>4</td>
<td>0.11</td>
</tr>
<tr>
<td>Snow Depth (SD)</td>
<td>-87.04</td>
<td>3.6</td>
<td>3</td>
<td>0.09</td>
</tr>
<tr>
<td>SD + Spring precipitation</td>
<td>-86.59</td>
<td>4.7</td>
<td>4</td>
<td>0.05</td>
</tr>
<tr>
<td>Days snowfall event (DSE)</td>
<td>-88.10</td>
<td>5.7</td>
<td>3</td>
<td>0.03</td>
</tr>
<tr>
<td>Mean winter temperature</td>
<td>-88.34</td>
<td>6.2</td>
<td>3</td>
<td>0.02</td>
</tr>
<tr>
<td>Spring precipitation</td>
<td>-88.42</td>
<td>6.4</td>
<td>3</td>
<td>0.02</td>
</tr>
<tr>
<td>Minimum winter temperature</td>
<td>-89.10</td>
<td>7.7</td>
<td>3</td>
<td>0.01</td>
</tr>
</tbody>
</table>

Maximum temperature = mean maximum temperature between May 15 and January 19; Days snow on ground = Total number of days with measurable snow on the ground in an annual snow season (approximately November through April); Spring precipitation = total spring precipitation from March 20 thru June 20; Snow depth = Mean snow depth in an annual snow season; Days snowfall event = Total number of days with a snowfall event in an annual snow season; Mean winter temperature = Mean winter temperature from December 21 thru March 19; Minimum winter temperature = Mean minimum temperature from February 4 thru April 24.
Table 2.3. Means (SE) and ranges of climate covariates used for estimating the likelihood of a localized snowshoe hare population going extinct in Michigan.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean</th>
<th>SE</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean snow depth (SD; mm)</td>
<td>234.40</td>
<td>9.55</td>
<td>107 - 562</td>
</tr>
<tr>
<td>Total number of days with measureable snow on the ground (DSoG)</td>
<td>108.26</td>
<td>1.59</td>
<td>61 - 145</td>
</tr>
<tr>
<td>Total number of days with a snowfall event</td>
<td>49.81</td>
<td>1.52</td>
<td>20 - 90</td>
</tr>
<tr>
<td>Total spring precipitation (March 20 – June 20; mm)</td>
<td>221.80</td>
<td>29.69</td>
<td>150.1 - 310.3</td>
</tr>
<tr>
<td>Mean minimum temperature (February 4 – April 24; °C)</td>
<td>-6.24</td>
<td>0.14</td>
<td>-9.8 - -2.7</td>
</tr>
<tr>
<td>Mean maximum temperature (May 15 – January 19; °C)</td>
<td>14.96</td>
<td>0.12</td>
<td>12.6 – 17.6</td>
</tr>
<tr>
<td>Mean winter temperature (December 21 – March 19; °C)</td>
<td>-5.52</td>
<td>0.14</td>
<td>-9.2 - -1.4</td>
</tr>
</tbody>
</table>
Figure 2.1. Location and occupancy status of snowshoe hare survey sites throughout the northern Lower and Upper Peninsulas of Michigan, USA, winter 2013. The geographic range of snowshoe hares and Michigan are portrayed in the map inset. The geographic range was derived from the International Union for Conservation of Nature (www.iucnredlist.org/technical-documents/spatial-data#mammals).
Figure 2.2. Number of study sites and year (5-year groupings through 2010) of last confirmed snowshoe hare occupancy in the northern Lower and Upper Peninsulas of Michigan, USA.
Figure 2.3. Localized snowshoe hare extinction probability and (a) mean maximum temperature during May 15 – January 19, (b) number of days with snow on the ground, and (c) mean snow depth in Michigan, USA and the 95% confidence intervals. The points along the x-axes represent the values of each study site.
LITERATURE CITED
LITERATURE CITED


CHAPTER 3

LAND COVER AND VEGETATION FACTORS INFLUENCING SNOWSHOE HARE OCCUPANCY IN MICHIGAN

ABSTRACT

Snowshoe hares (*Lepus americanus*) depend on dense forest vegetation for concealment, escape, and thermal cover. To quantify how surrounding land cover and finer scale vegetation factors influenced snowshoe hare occupancy and habitat use in Michigan, I conducted line-transect track surveys in 117 historically occupied (i.e. 1955-2010) sites during winter 2012-2013. I found that 62% of the sites were still occupied. I created an 812m buffer around my survey transects (~332 ha), compiled historical data from aerial photographs from 1978 to 2012, and computed net change over time for 5 land cover covariates. I evaluated 17 candidate models of various covariate combinations of land cover change over time. All land cover change models had AIC weight >0.01 and ≤12 (ΔAIC <4.0) and none of the parameters estimates were significant, indicating that land cover change over time was having a negligible effect on current occupancy status for hares. I subsequently hypothesized that in forest-dominated landscapes, current land cover and vegetation structure were more important determinants of hare occupancy because this species is short-lived, highly mobile, and evolved in disturbance-prone environments. I analyzed 2012 land cover covariates in combination with transect-level covariates of woody stem densities and visual obstruction. I analyzed 41 models using a 2-level occupancy model in the package “Unmarked”. My top-ranking model (AIC weight=0.51) for predicting snowshoe hare occupancy and use included a land cover covariate (the ratio between forest and open edge) and the transect-level covariates of visual obstruction...
at 1.0-1.5m above snow level and total stem density; all 3 parameters were positive and only
the transect-level covariates were significant. My results indicated that historical land cover
changes were not related to current site-level occupancy of snowshoe hares. Rather, the
preponderance of current forest relative to open areas was the most influential land cover
variable on occupancy. At a fine scale, woody stem density and visual obstruction were
important determinants of snowshoe hare habitat use.

**Key Words**
Forest patch sizes, visual obstruction, land cover, *Lepus americanus*, occupancy, snowshoe
hare, snow track surveys, Program Unmarked.

**3.1. INTRODUCTION**

Snowshoe hares (*Lepus americanus*) depend on dense forest vegetation (i.e., >60% visual obstruction) for concealment, escape, and thermal cover (Litvaitis et al. 1985, Sievert and
Keith 1985, Hodges 2000, Jacqmain et al. 2007, Berg et al. 2012). For example, hare survival was
lower in areas with sparse horizontal cover in Maine (Litvaitis et al. 1985), and hare populations
were less likely to go extinct in areas with dense vegetation cover in Idaho (Thornton et al.
2013). Orr and Dodds (1982) found that hare habitat use was higher in areas dominated by
conifers, with total canopy cover <60%, and with trees <12m tall in Nova Scotia. Presumably
this vegetation structure provided high amounts of ground cover and abundant palatable food
sources (Orr and Dodds 1982). Recent assessments have identified snowshoe hares as
vulnerable to climate change (Hoving et al. 2013, Mills et al. 2013), and wildlife agencies have
expressed interest in managing habitats to potentially mitigate negative climate impacts.
In areas of fragmented snowshoe hare habitat, especially with small patch sizes and sparse cover, the probability of localized extinction increases primarily due to predators (Buehler and Keith 1982, Sievert and Keith 1985, Keith and Bloomer 1993, Keith et al. 1993, Hodges 2000). These fragmented patches can provide adequate cover from predators if they consist of dense spruce (\textit{Picea} spp.) or willow-alder (\textit{Salix} spp. – \textit{Alnus} spp.) thickets (Wolff 1980). Multi-layered habitat structure that provides both vertical and horizontal cover is important to snowshoe hares. Berg et al. (2012) found that multi-storied forests dominated by spruce and fir (\textit{Abies} spp.) supported higher densities of snowshoe hares compared to even-aged stands. In addition, Ivan et al. (2014) recommended managing for multi-layered mature spruce-fir and early seral lodgepole pine (\textit{Pinus contorta}) to benefit snowshoe hares in Colorado. In some locations, these multi-layered habitat conditions take decades to develop following timber harvest or fire. For example, Thompson et al. (1989) and Newberry and Simon (2005) found that snowshoe hares were considerably more abundant in 30-year-old boreal mixedwood clearcuts compared to clearcuts ≤20 years in Ontario and Labrador, Canada, respectively, with stands <5 years having the lowest abundance. Collectively these studies indicate that land cover type, especially those types that contain conifers, and habitat structure in the form of vertical and horizontal cover are important to hares. Less is known on how land management history and resultant patterns in land cover types influence hare.

Snowshoe hare habitats on the southern edge of the range distribution in the Great Lakes region of the United States are generally fragmented in small (relative to more northward landscapes) patches (Buehler and Keith 1982, Sievert and Keith 1985, Keith et al. 1993). For example, a coarse, broad-scale habitat assessment corresponding to the late 1990s and early
2000s in the Upper Peninsula of Michigan indicated that hare habitat quality ranged from poor to marginal with only small, isolated areas of higher quality habitat (Linden et al. 2011). This model portrayed potential hare densities in Michigan as about half of what is considered high density in the southern habitats of hare range (Hodges 2000, Linden et al. 2011). The isolated spatial arrangement of high quality habitats that occur in a matrix of low quality habitats, coupled with a patchy distribution of hare densities across the landscape suggests that hare populations in Michigan may have a metapopulation structure. In metapopulations localized extinction and colonization tend to be affected by patch size and isolation (MacArthur and Wilson 1967).

In Michigan, the current southern edge of snowshoe hare distribution has apparently moved northward by ~45km over the last 20 years, presumably due to the negative impacts of climate change (Burt 2014: Chapter 2). However, Burt (2014: Chapter 2) also documented localized hare extinctions over the past 60 years throughout hare range in Michigan, indicating that vegetation and climate are likely interacting to determine site occupancy. Whereas climate change apparently affects hares over multi-year time frames (Burt 2014: Chapter 2), the time frames resulting in isolation and fragmentation of hare habitats are less understood. My objectives were to: 1) quantify the effects of historical land cover changes on localized snowshoe hare occupancy, and 2) rank the ability of current land cover and within patch habitat measures to predict localized occupancy. I used a combination of local ecological knowledge, air photo interpretation, GIS analyses, logistic regression, and Akaike Information Criteria (AIC). My results help inform land management and conservation decisions for a climate vulnerable species.
3.2. STUDY AREA

The field portion of my study occurred in the Upper and northern Lower Peninsulas of Michigan on publically owned lands during the winter of 2013 (Fig. 3.1). The spatial extent of my study corresponds to the known historic distribution of snowshoe hares in Michigan (Fig. 3.1). The study area included 3 broad biogeoclimatic regions: 1) western Upper Peninsula, 2) eastern Upper Peninsula, and 3) northern Lower Peninsula. Landforms of the western Upper Peninsula consist of glacial moraines, lake plains, outwash channels and plains, and glacially scoured bedrock ridges (Albert 1995). Primary vegetation types include northern hardwoods, aspen (*Populus* spp.), pine (*Pinus* spp.), and conifer swamps (Albert 1995). The western Upper Peninsula experiences the most extreme winters and shortest growing seasons of the three regions I studied (Albert 1995). Monthly average temperatures ranged from -10°C to 17°C, with average annual precipitation of 90 cm, including 435 cm of snowfall (NOAA 2012).

Landforms of the eastern Upper Peninsula consist mostly of flat lake plain with areas of exposed bedrock (Albert 1995). Vegetation types include northern hardwoods, upland conifers (white pine (*P. strobus*), red pine (*P. resinosa*), jack pine (*P. banksiana*)), hardwood-conifer swamps, rich conifer swamps, and northern wet meadows (Albert 1995). Monthly average temperatures vary from -10°C to 18°C with average annual precipitation of 80 cm, including 194 cm of snowfall (NOAA 2012).

Landforms in the northern Lower Peninsula (NLP) consist of large, sandy outwash plains and large glacial moraines (Albert 1995). The climate of coastal areas in the NLP is moderated by Lakes Huron and Michigan resulting in warmer and cooler temperatures in winter and summer, respectively. Interior areas are subjected to more extreme temperature fluctuations.
Forest types include northern hardwoods, aspen, oak (*Quercus* spp.), pine, and lowland conifer (Albert 1995). Monthly average temperatures range from -8°C in January to 20°C in July, with average annual precipitation of 90 cm, including 169 cm of snowfall (NOAA 2012).

### 3.3. METHODS

#### 3.3.1. Site Selection

I interviewed 45 individuals that had knowledge of historical snowshoe hare locations in Michigan. Interviewees included Michigan Department of Natural Resources employees, hare hunters, and tribal members. I identified potential interviewees by contacting various hunt clubs, attending sportsperson coalition meetings, talking with colleagues, and by individuals providing contact information for hare hunters they personally knew. Each interviewee was asked to map locations that to their knowledge were unequivocally occupied by snowshoe hares sometime in the past. Unequivocal evidence included tracks, harvested hares, or observed hares. Each interviewee was asked to estimate the year of last confirmed occupancy within 5 yrs. I also checked museum records (e.g. VertNet or MaNIS) for historical snowshoe hare collection locations, but opted not to use these records because the locational error was generally large (i.e. >1km). I compiled potential study sites from the interviews and selected a subset of locations that encompassed broad spatial (throughout hare range in Michigan; Fig. 3.1) and temporal (1955-2010; Fig. 3.2) domains. The 332 ha study sites were separated by >1.6 km (mean = 10.2 km, SE = 0.7). My interview protocol was reviewed and approved by the Human Research Protection Program, Institutional Review Board, at Michigan State University (IRB# x11-805).
3.3.2. Field Sampling

Winter track counts along transects are commonly used to document snowshoe hare occupancy and habitat use (Brocke 1975, Conroy et al. 1979, Thompson et al. 1989). However, transect dimensions and configurations are inconsistent among studies. I evaluated the effects of transect number (2-9), length (10-150m), and spacing (25-125m) on my ability to accurately portray site occupancy using a known number of telemetered snowshoe hares in a 6 ha enclosure during the winters of 2012 and 2013 (Burt 2014: Chapter 1). Prior to releasing telemetered hares, I surveyed the enclosure to ensure that no hares were present. I demarcated 9 transects, spaced 25 m apart, ranging in total length from 225-250 m (Burt 2014: Chapter 1). Track surveys were conducted 12-65 hours after fresh snowfall; survey results were standardized to 12 hours (Burt 2014: Chapter 1). Track locations along transects were mapped to the nearest 5m and random sub-sampling of transect lengths and spacing was used to identify the most efficient transect configuration, where efficiency was defined as the highest probability of correctly denoting site-level occupancy with minimal distance traveled (Burt 2014: Chapter 1). I replicated transect sampling at densities ranging from 0.2 to 1.5 hares/ha. These densities represented low to high snowshoe hare densities recorded at the southern edge of hare range (Hodges 2000). Snowshoe hare trapping and radio-collaring were conducted by the Michigan Department of Natural Resources – Wildlife Division following internal animal use and care guidelines that were consistent with the American Society of Mammalogists Animal Care and Use Guidelines (Sikes et al. 2011).

I implemented the most efficient transect methodology from my enclosure study at a subset of locations selected from the interview process (Fig. 3.1). My selected transect
configuration (9 transects, 125m length, 75m spacing) resulted in the correct designation of occupancy status 95% of the time based on my enclosure study results (Burt 2014: Chapter 1). My transect configuration was centered on the historic location of hares from the interviews. I then randomly oriented the set of transects and visually confirmed that transects occurred on public lands. Sampling for snowshoe hares occurred on a single day and was completed 12-72 hours after fresh snowfall to allow for track accumulation. If a track was detected on ≥1 transect at a site, I designated the site as occupied. Sites without tracks were deemed unoccupied and presumed to have experienced localized extinction since the time of last known occupancy. For transect-level analyses, I designated transects as used (a track was documented) or unused (no tracks documented) by hares.

At all sites, I measured woody stem density and species composition (i.e., conifer or hardwood) as important habitat elements for hare (Litvaitis et al. 1985). I conducted counts of stem densities for each site along a 6 x 2m transect at the first hare track location or at a randomly generated location along each transect if no hares were present. In addition to direct measurements of stem density, I also calculated equivalent stem density (3x coniferous stem count + 1x deciduous stem count; Litvaitis et al. 1985). I quantified visual obstruction using a modified Robel pole at 3 different height classes above the snow (Robel et al. 1970). The Robel pole was placed at the center of the sample location and subsequently viewed from 4m away from 2 opposing directions along the transect. I tallied the number of 10cm demarcations; represented by alternating colors along the pole, visible at 0.0-0.5m, 0.51-1.0m, and 1.01-1.5m above the snow. I also tallied the number of snowshoe hare predators encountered along each transect by families (canids, felids, and mustelids) as an index to potential predation pressure.
A priori, I identified 5 site-level and 7 transect-level variables potentially related to snowshoe hare occupancy (Table 3.1). To generate the site level covariates, I buffered the 9 transects at each site by 812m, resulting in ~332ha around the transects. I selected 812m based on the reported dispersal distance of snowshoe hare (Gillis and Krebs 1999). I used National Agricultural Imagery Program (NAIP) infrared aerial imagery to map patches of 6 different land cover types within the buffer; 1) coniferous, 2) deciduous, 3) mixed coniferous and deciduous, 4) water, 5) urban, and 6) open. These land cover types were consistent with Michigan Department of Natural Resources mapping guidelines (Michigan Department of Natural Resources 2009). I calculated average patch sizes for the 3 forested land cover types and the proportion of total forest in the buffer, where the forest designation was based on a visible tree canopy regardless of canopy height. The 3 non-forested vegetation types were grouped together as a single “open” category. Lastly, I used program Fragstats v. 4.2 (McGarigal et al. 2012) to calculate the forest to open edge ratio. An edge was mapped as a boundary between land cover type stands; this could be a transitional zone between two separate cover types or when there was a noticeable difference between the same cover type, such as differing age classes of stands. The same process was used with the open category. I hypothesized that this ratio declined over time as openings from timber management and land conversion became more prevalent.

I calculated all land cover metrics from aerial photos that most closely corresponded to the year of last known snowshoe hare occupancy (historical) and from 2012 photos (current). Historical photos included 2005 and 2010 from the Remote Sensing and GIS Laboratory at Michigan State University (http://www.rsgis.msu.edu/) and 1977, 1987, and 1997 from the
Michigan Department of Natural Resources aerial photography library. I hypothesized that forsted patch size decreased over time, consistent with a trend in smaller-sized clearcuts and greater forest fragmentation that potentially results in localized snowshoe hare extinction. I further hypothesized that forest type changed to a more deciduous dominated landscape in some locations as a result of past land management and climate effects. Current photos were from 2012 NAIP. I evaluated 2 scenarios for site-level effects on snowshoe hare occupancy: 1) the net change in land cover variables over time, and 2) current land cover.

3.3.3. Data Analysis

I analyzed possible combinations of site and transect-level covariates for collinearity using Pearson’s correlation coefficient (Sokal and Rohlf 2011); covariates were considered correlated if \( r \geq |0.15| \) and \( p \leq 0.05 \). For land use change over time (Table 3.1), I modeled the likelihood that a localized (approximately 7.5 ha) snowshoe hare population went extinct from year of last known occupancy using logistic regression. I created a candidate set of models (n=17; Table 3.2) from all possible combinations (additive terms) of uncorrelated site variables. Models were ranked based on Akaike Information Criterion (AIC) and parameter estimates were deemed significant if the 95% confidence intervals did not overlap 0 (Burnham and Anderson 2002, Nakagawa and Cuthill 2007).

For current land cover, I modeled the likelihood of snowshoe hare occupancy at a site and use at the transect level using a 2-level occupancy model (MacKenzie et al. 2002), where the first level corresponded to site occupancy probability and the second level corresponded to transect level habitat use. I assumed minimal detection error, i.e., if a transect was occupied my ability to detect the track was high. I implemented the model in the R package “unmarked” (R
The 2 levels in my model were parameterized with 6 site level variables and 7 transect level variables (Table 3.1). I created a candidate set of models (n=41; Table 3.5) from possible combinations (additive terms) of uncorrelated site and transect variables. Potential models included 3 scenarios: 1) site level variables only, with transect set as intercept-only, 2) transect level variables only, with site set as intercept-only, and 3) site level and transect level variables combined. Models were ranked based on Akaike Information Criterion (AIC) and parameter estimates were deemed significant if the 95% confidence intervals did not overlap 0 (Burnham and Anderson 2002, Nakagawa and Cuthill 2007).

3.4. RESULTS

My interviews resulted in 386 potential study sites with year of last known hare occupancy ranging from 1955 to 2010; land cover and vegetation data were compiled for 117 of those sites (Fig. 3.1). I documented a range of minimum and maximum values for land cover change, current land cover conditions, and transect-level covariates (Table 3.1). Relative to the size of my assessment area (332ha), change in forest proportion over time exhibited the broadest range of impacts (loss of 14% to gain of 64%) but the average change was low (4% gain) with low variability (SE=1%). The historical changes in patch sizes only varied from -12.6 to 7.8ha, influencing <4% of my assessment area at each site (Table 3.1). On average, I observed a reduction in patch sizes for all forest cover types I evaluated, but that reduction was small (<1.7ha). On average, forest to open edge ratio reflected a gain in forest that was generally consistent across sites (mean=0.40, SE=0.16). My historical land cover change analysis collectively indicated that Michigan forest patch sizes in snowshoe hare range have declined slightly over the last ~35 years and that the amount of forest has slightly increased.
Current land cover indicated that all sites had ≥25% forest (Table 3.1). Most sites had high forest amounts (mean=84%, SE=2%; Table 3.1). The deciduous patch sizes tended to be higher than coniferous and mixed forest patch sizes with deciduous forests occurring at all sites (Table 3.1). My sites usually contained more forest edge compared to open edge, with the average being nearly 3 times more forest edge (Table 3.1). My results indicate that deciduous forests are a dominant component of the sites I surveyed.

At the transect-level, conifer stem counts (averages and maximums) were typically lower than deciduous stem counts by a factor of 4-5 (Table 3.1). On average the equivalent stem density was higher than the deciduous stem counts, suggesting that transects generally contained a mixture of coniferous and deciduous stems (Table 3.1). Predators were typically absent from transects (mean families detected=0.22), but all 3 predator families were present at some locations. Visual obstruction averages were low, but some sites exhibited complete obstruction at all 3 height strata (Table 3.1).

Statewide, I found that 45 of 117 sites (38%) became unoccupied by snowshoe hares over the time span of my study (1955-2013). In the northern Lower Peninsula 32 of 66 sites (~48%) were unoccupied during 2013. Only 13 out of 51 (~25%) sites were unoccupied in the Upper Peninsula. My results indicate almost a two-fold decrease in localized occupancy from south to north in Michigan, with the greatest concentration of unoccupied sites at the southern edge of the range (Fig. 3.1).

3.4.1. Land Cover Change Over Time

All candidate models for describing localized occupancy of snowshoe hares based on changes in land cover over time received little support (i.e., ΔAIC ≤ 4.0 and ωi ≤ 0.12), with no
clear top-ranking model (Table 3.2). Additionally, all candidate models received some minimal level of support (i.e., \( \omega_i \geq 0.02 \)). No significant parameters were identified in any of the candidate models. My results indicate that historic changes in land cover at a ~332ha scale did not affect changes in localized snowshoe hare occupancy.

3.4.2. Current Land Cover and Habitat Structure

Of the 41 candidate models for describing current snowshoe hare occupancy, 6 received some support (i.e., \( \omega_i \geq 0.01 \)), but a clear top-ranking model emerged that included a combination of transect and site-level covariates (Table 3.3). The top 4 models included both site and transect level covariates, with the 5th and 6th models containing only transect level covariates (Table 3.3). My top-ranking model accounted for 51% weight of evidence and consisted of the site level covariate forest to open edge ratio (\( \beta = 0.33, 95\% \text{ CI} = -0.006 - 0.669 \)) and the transect level covariates of visual obstruction at the 1.0-1.5m height strata (\( \beta = 0.25, 95\% \text{ CI} = 0.18 - 0.31 \)) and equivalent stem density (\( \beta = 0.019, 95\% \text{ CI} = 0.008 - 0.030; \text{Table 3.3} \)). My results indicate that in the absence of edge (e.g., 100% coniferous forest) site level occupancy for snowshoe hares was >0.40 (Fig. 3.3A). However, forest edge (e.g., a conifer and deciduous mix) increased occupancy probability to near 1 indicating that diverse forest conditions enhance site-level suitability for hares (Fig. 3.3A).

Visual obstruction between 1.0-1.5m above the snow had the greatest effect on snowshoe hare transect use, and this effect was almost linear (Fig. 3.3B). Without visual obstruction the likelihood of transect level habitat use was approximately 0.20 (Fig. 3.3B), indicating that visual obstruction is not a necessity for hare habitat use. High visual obstruction alone can result in transect-level habitat use >0.80 (Fig. 3.3B). The effect of equivalent stem
density on transect use was positive but less pronounced than the observed relationship for visual obstruction (Fig. 3.3C). My results indicate that in a forested patch, snowshoe hares will use areas without coniferous or deciduous stems (~0.30 use probability), presumably if sufficient horizontal cover is provided, such as brush piles or windfalls.

The second ranked model (ΔAIC = 1.9) accounted for 19% weight of evidence and was based on the same variables as the top-ranking model but also included number of predator families (Table 3.3). Similar to the top-ranking model, the forest to open edge ratio was not significant (β = 0.33, 95% CI = -0.007 – 0.670) but visual obstruction (β = 0.24, 95% CI = 0.18 – 0.31) and equivalent stem density (β = 0.019, 95% CI = 0.008 – 0.030) were significant. The number of predator families was not significant (β = -0.031, 95% CI = -0.351 – 0.289), but the sign of the parameter estimate suggested that with increased predator presence, the likelihood of snowshoe hare occupancy decreased. My results suggest that the primary determinants of snowshoe hare occupancy and habitat use in Michigan relate to habitat structure and composition at local scales and not on larger scale land cover variables.

3.5. DISCUSSION

My results indicate that land cover change over time in the area encompassed by average snowshoe hare dispersal distance was having no effect on current occupancy status for hares in Michigan. Given this finding, I contend that in forest-dominated landscapes, current land cover and habitat structure are more important determinants of hare occupancy because this species is relatively short-lived (e.g., 5 years; Kurta 1995), highly mobile (maximum documented dispersal distances of 20 km; Hodges 2000), and evolved in disturbance-prone environments (Thompson et al. 1989, Newberry and Simon 2005). Snowshoe hares are an
obligate forest species and hence some minimum forest amount across larger landscapes is likely important; my sites apparently were not below that minimum amount. My study landscapes were dominated by forests (84% forested on average) and most timber harvest operations (except large jack pine cuts) were relatively small scale (8-20ha). Coupled with the relatively large area of my analysis (~332ha), the change in patch sizes and configurations over time at my sites was generally subtle potentially explaining why historical changes in land cover was not related to localized hare occupancy. Thornton et al. (2012) also observed that the relatively small size of forest cutting in Idaho did not cause local hare populations to become extirpated.

Although not significant, my results suggest that more forest edge (as opposed to open edge) has a positive influence on snowshoe hare occupancy. I was somewhat surprised that current land cover metrics were not more important determinants of occupancy. Others have found land cover metrics to be correlated with hare occurrence. For example, Buehler and Keith (1982) found that the proportion of forest at a site influenced hare occurrence and mean number of hare tracks found in Wisconsin. The primary determinant of snowshoe hare occupancy depends on whether an area is forested with a conifer component that provides cover close to the ground (Wolff 1980, Buehler and Keith 1982, Berg et al. 2012, Ivan et al. 2014). Snowshoe hares typically avoid openings, but can often be found near forest edges (Pietz and Tester 1983). While land cover of conifers is important to snowshoe hares, the vegetation structure (i.e. vegetation density or height) within the patch is critical (Brocke 1975).

The most influential variables on snowshoe hare occupancy in my study were fine-scale measures of habitat structure and composition. Consistent with other studies (Litvaitis 1985), I
found positive relationships between stem density and visual obstruction and small-scale habitat use by hares. Areas exhibiting highest use contained conifer-dominated or mixed understories with equivalent stem densities of ~37,066/ha. In some instances, abundant horizontal cover (typically in the form of trees that were blown down) was observed to compensate for lower stem counts, suggesting that both habitat elements interact to effect hare space use. My results that forest types with adequate cover 1.0-1.5m above the snow support snowshoe hare are consistent with Wolfe et al. (1982) who also found that this horizontal cover measure accounted for 85% of winter habitat use by hares. Equivalent stem density and horizontal cover were not correlated in my study, presumably because a small number of conifers can create abundant visual obstruction (depending on branching characteristics and snow depth).

Some researchers have suggested that hares in the southern part of the distribution are subjected to higher mortality rates from predation because a warming climate and increased anthropogenic activities have allowed predators not adapted to deep snows to expand into hare range (Gese et al. 2013, Dowd et al. 2014). My simplified assessment of predators lends support to this observation in Michigan, with the number of predator families detected on a site being negatively related to hare occupancy. I caution that although my predator covariate occurred in the second-ranked model (19% weight of evidence), the parameter estimate was not significant and hence this relationship warrants further evaluation. It is generally accepted that stem densities and horizontal cover influences predation rates on snowshoe hares (Sievert and Keith 1985, Keith et al. 1993). With recent attention devoted to the coloration mismatch of hares to their environment under current climate change scenarios (Mills et al. 2013, Zimova et
al. 2014), vegetation management may be one of the few management actions available to reduce predation rates. In addition to protection from predators, dense vegetation also provides thermal cover, allowing hares to thermoregulate with less movement (Brocke 1975, Sievert and Keith 1985, Keith et al. 1993).

I suspect that my observations of localized changes in occupancy status are likely an interaction between a changing climate (Burt 2014: Chapter 2), habitat structure, and predators. The geographical range of snowshoe hares is moving northward, likely related to direct and indirect effects of climate change, with predators identified as a likely proximate cause of localized extirpations (Sievert and Keith 1985, Hodges 2000). The relationships among climate, patch configuration, habitat structure, and predators are complex, with managers having direct influence over patch configuration, habitat structure, and predator abundance. I contend that large patch sizes with suitable habitat structure can help ameliorate negative predator effects on snowshoe hares in the southern part of their range. Future research should focus on whether modifying vegetation can help alleviate the negative effects on snowshoe hare occupancy apparently linked to climate change (Burt 2014: Chapter 2) and predation.

3.6. MANAGEMENT IMPLICATIONS

My results stress the importance of habitat structure on snowshoe hare occupancy. To achieve >90% probability of snowshoe hare occupancy for 3 stand categories (conifer dominated, deciduous dominated (including shrubs like *Rubus* spp.), and an equal mix of conifer and deciduous; Table 3.4), managers can focus on equivalent stem density and visual obstruction. In the Lake States region, visual obstruction should be provided at 3m height above the ground to account for varying snow conditions. This recommendation is consistent
with Brocke (1975) who recommended dense vegetation at 3.5m height. Visual obstruction does not have to be provided by living vegetation, other alternatives include jack-strawing or hinge-cutting trees. Brush piles may also be used, but these alone may not provide enough effective refugia for survival compared to sites without brush piles. (Cox et al. 1997).

Land managers most frequently implement prescriptions based on tree stem densities. Based on my data, I related equivalent stem density to horizontal cover as a means to provide general guidance to land managers on when forests should be supplemented with horizontal cover (Table 3.4). For example, in a dense conifer-dominated patch (>37,000 stems/ha) visual obstruction is high (9-10 demarcation on the Robel pole are covered) and thus no additional horizontal cover is needed (Table 3.4). Conversely, in dense deciduous dominated patches (59,305 stems/ha), 6 Robel demarcations are visible and managers should consider supplementing the patch with horizontal cover (Table 3.4). I caution that my deciduous densities include trees and shrubs and thus managers should have some knowledge of understory deciduous shrub abundance to effectively use Table 3.4.

In the Lake States region, I contend that the stem density table could be used in coordination with management of other species (e.g., Kirtland’s warbler (Setophaga kirtlandii) or ruffed grouse (Bonasa umbellus)) to potentially improve those habitats for snowshoe hare. For example, Cade and Sousa (1985) found a suitability index of 1 at an equivalent stem density of ~4,900 – 16,000 stems per hectare for ruffed grouse habitat. After factoring in shrubs being valued at 0.25 times a tree stem, this range falls within my recommended stem densities (Table 3.4). The Michigan Department of Natural Resources et al. (2014) recommends a jack-pine (i.e. conifer) density of at least 3,588 trees per hectare for Kirtland’s warbler management, which is
~62% of our lowest conifer estimate, but does not count shrub stems. Moreover, horizontal obstruction recommended for snowshoe hare could provide drumming logs for ruffed grouse, which benefit from at least 3 logs per hectare for a potential drumming site (Sargent and Carter 1999).

3.7. ACKNOWLEDGEMENTS

I thank P. Nelson for serving as a field technician during the winter of 2013. I appreciate the numerous interviewees who graciously made themselves and their knowledge available for identifying historic hare sites. Also, thanks to T. Minzey for coordinating my attendance at sportsperson coalition meetings and S. Beyer for helping me manage the social and political aspects of the project. Funding for this project was provided by the Michigan Department of Natural Resources – Wildlife Division through the Michigan Federal Aid in Wildlife Restoration program grant F13AF01268 in cooperation with the U.S. Fish and Wildlife Service, Wildlife and Sport Fish Restoration Program and Safari Club International Michigan Involvement Committee.
APPENDIX
Table 3.1. Sample level, means (SE), and ranges of land cover and habitat covariates used for estimating localized snowshoe hare occupancy (site level only) or habitat use (transect level) in Michigan.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Level&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Change from Historical to Current</th>
<th>Current (2012)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean</td>
<td>SE</td>
</tr>
<tr>
<td>Forest Proportion</td>
<td>Site</td>
<td>0.04</td>
<td>0.01</td>
</tr>
<tr>
<td>Average Deciduous Patch Size (ha)</td>
<td>Site</td>
<td>-1.71</td>
<td>0.55</td>
</tr>
<tr>
<td>Average Coniferous Patch Size (ha)</td>
<td>Site</td>
<td>-0.81</td>
<td>0.42</td>
</tr>
<tr>
<td>Average Mixed Forest Patch Size (ha)</td>
<td>Site</td>
<td>-1.31</td>
<td>0.34</td>
</tr>
<tr>
<td>Forest to Open Edge Ratio</td>
<td>Site</td>
<td>0.40</td>
<td>0.16</td>
</tr>
<tr>
<td>Conifer Stem Density (stems/12m&lt;sup&gt;2&lt;/sup&gt;)</td>
<td>Transect</td>
<td>.</td>
<td>.</td>
</tr>
<tr>
<td>Deciduous Stem Density (stems/12m&lt;sup&gt;2&lt;/sup&gt;)</td>
<td>Transect</td>
<td>.</td>
<td>.</td>
</tr>
<tr>
<td>Total Predator Genera</td>
<td>Transect</td>
<td>.</td>
<td>.</td>
</tr>
<tr>
<td>Visual Obstruction 0.0-0.5m&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Transect</td>
<td>.</td>
<td>.</td>
</tr>
<tr>
<td>Visual Obstruction 0.5-1.0m&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Transect</td>
<td>.</td>
<td>.</td>
</tr>
<tr>
<td>Visual Obstruction 1.0-1.5m&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Transect</td>
<td>.</td>
<td>.</td>
</tr>
<tr>
<td>Equivalent Stem Density (stems/12m&lt;sup&gt;2&lt;/sup&gt;)</td>
<td>Transect</td>
<td>.</td>
<td>.</td>
</tr>
</tbody>
</table>

<sup>a</sup> Site = ~332ha area surrounding a set of 9 transects; Transect = 125m long.

<sup>b</sup> Historical data on transect level covariates unavailable.

<sup>c</sup> Values range from 0-10 with 0 being no visual obstruction 10 being complete visual obstruction.
Table 3.2. Candidate model set for estimating the likelihood of a localized site being occupied by snowshoe hare in Michigan. $\Delta$AIC = difference in AIC value from top-ranking model, $k = $ model parameters, $\omega_i =$ Akaike weight of evidence.

<table>
<thead>
<tr>
<th>Candidate Model</th>
<th>$\Delta$AIC</th>
<th>$k$</th>
<th>$\omega_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest Proportion + Deciduous Patch Size</td>
<td>0.0</td>
<td>3</td>
<td>0.118</td>
</tr>
<tr>
<td>Deciduous Patch Size</td>
<td>0.1</td>
<td>2</td>
<td>0.114</td>
</tr>
<tr>
<td>Forest Proportion</td>
<td>0.2</td>
<td>2</td>
<td>0.105</td>
</tr>
<tr>
<td>Deciduous Patch Size + Mixed Patch Size</td>
<td>0.3</td>
<td>3</td>
<td>0.099</td>
</tr>
<tr>
<td>Null Model</td>
<td>0.5</td>
<td>1</td>
<td>0.093</td>
</tr>
<tr>
<td>Deciduous Patch Size + Forest to Open Edge Ratio</td>
<td>0.9</td>
<td>3</td>
<td>0.075</td>
</tr>
<tr>
<td>Forest:Open Edge Ratio</td>
<td>1.3</td>
<td>2</td>
<td>0.062</td>
</tr>
<tr>
<td>Mixed Patch Size</td>
<td>1.4</td>
<td>2</td>
<td>0.058</td>
</tr>
<tr>
<td>Mixed Patch Size + Forest to Open Edge Ratio</td>
<td>1.9</td>
<td>3</td>
<td>0.045</td>
</tr>
<tr>
<td>Deciduous Patch Size + Coniferous Patch Size</td>
<td>2.0</td>
<td>3</td>
<td>0.042</td>
</tr>
<tr>
<td>Deciduous Patch Size + Coniferous Patch Size + Mixed Patch Size</td>
<td>2.3</td>
<td>4</td>
<td>0.037</td>
</tr>
<tr>
<td>Coniferous Patch Size</td>
<td>2.5</td>
<td>2</td>
<td>0.034</td>
</tr>
<tr>
<td>Deciduous Patch Size + Coniferous Patch Size + Mixed Patch Size + Forest to Open Edge Ratio</td>
<td>2.7</td>
<td>5</td>
<td>0.030</td>
</tr>
<tr>
<td>Deciduous Patch Size + Coniferous Patch Size + Forest to Open Edge Ratio</td>
<td>2.9</td>
<td>4</td>
<td>0.028</td>
</tr>
<tr>
<td>Coniferous Patch Size + Forest to Open Edge Ratio</td>
<td>3.3</td>
<td>3</td>
<td>0.023</td>
</tr>
<tr>
<td>Coniferous Patch Size + Mixed Patch Size</td>
<td>3.4</td>
<td>3</td>
<td>0.022</td>
</tr>
<tr>
<td>Coniferous Patch Size + Mixed Patch Size + Forest to Open Edge Ratio</td>
<td>3.9</td>
<td>4</td>
<td>0.016</td>
</tr>
</tbody>
</table>
Table 3.3. Top 6 ranking models with variables from site and transect levels from the 41 candidate models (Table 3.5) for estimating the likelihood of a site being currently occupied by snowshoe hare in Michigan. ΔAIC = difference in AIC value from top-ranking model, k = model parameters, ω_i – Akaike weight of evidence.

<table>
<thead>
<tr>
<th>Candidate Modela</th>
<th>ΔAIC</th>
<th>K</th>
<th>ω_i</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site: Forest to Open Edge Ratio Transect: Visual Obstruction 1.0-1.5m + Equivalent Stem Density</td>
<td>0.0</td>
<td>5</td>
<td>0.51</td>
</tr>
<tr>
<td>Site: Forest to Open Edge Ratio Transect: Visual Obstruction 1.0-1.5m + Equivalent Stem Density + Predators</td>
<td>1.96</td>
<td>6</td>
<td>0.19</td>
</tr>
<tr>
<td>Site: Forest Proportion Transect: Visual Obstruction 1.0-1.5m + Equivalent Stem Density</td>
<td>2.38</td>
<td>5</td>
<td>0.16</td>
</tr>
<tr>
<td>Site: Forest Proportion Transect: Visual Obstruction 1.0-1.5m + Equivalent Stem Density + Predators</td>
<td>4.35</td>
<td>6</td>
<td>0.058</td>
</tr>
<tr>
<td>Transect: Visual Obstruction 1.0-1.5m + Equivalent Stem Density</td>
<td>4.43</td>
<td>4</td>
<td>0.056</td>
</tr>
<tr>
<td>Transect: Visual Obstruction 1.0-1.5m + Equivalent Stem Density + Predators</td>
<td>6.40</td>
<td>5</td>
<td>0.021</td>
</tr>
</tbody>
</table>

a Site = ~332ha area surrounding a set of 9 transects; Transect = 125m long.
Table 3.4. The relationship between visual obstruction and stem densities in 3 forest types. Compiled from stem densities and visual obstruction measured at 117 sites in the northern Lower and Upper Peninsulas of Michigan, winter of 2013.

<table>
<thead>
<tr>
<th>Visual Obstruction(^a)</th>
<th>Conifer Dominated(^b) (Stems per Hectare)</th>
<th>Mixed Stand(^b) (Stems per Hectare)</th>
<th>Deciduous Dominated(^b) (Stems per Hectare)</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>5,765</td>
<td>11,530</td>
<td>16,472</td>
</tr>
<tr>
<td>9</td>
<td>9,059</td>
<td>17,297</td>
<td>27,182</td>
</tr>
<tr>
<td>8</td>
<td>13,178</td>
<td>24,711</td>
<td>37,889</td>
</tr>
<tr>
<td>7</td>
<td>16,472</td>
<td>32,124</td>
<td>48,596</td>
</tr>
<tr>
<td>6</td>
<td>19,768</td>
<td>39,537</td>
<td>59,305</td>
</tr>
<tr>
<td>5</td>
<td>23,885</td>
<td>45,302</td>
<td>70,012</td>
</tr>
<tr>
<td>4</td>
<td>27,182</td>
<td>52,715</td>
<td>80,719</td>
</tr>
<tr>
<td>3</td>
<td>30,475</td>
<td>60,128</td>
<td>91,429</td>
</tr>
<tr>
<td>2</td>
<td>34,595</td>
<td>67,541</td>
<td>102,136</td>
</tr>
<tr>
<td>1</td>
<td>37,889</td>
<td>74,954</td>
<td>112,843</td>
</tr>
<tr>
<td>0</td>
<td>41,183</td>
<td>81,545</td>
<td>127,727</td>
</tr>
</tbody>
</table>

\(^a\) The number of Robel pole demarcations (10cm) that are visible.
\(^b\) Includes shrub species.
Table 3.5. List of all 41 candidate models used in current occupancy modeling for estimating the likelihood of a site being currently occupied by snowshoe hare in Michigan.

<table>
<thead>
<tr>
<th>Model Rank&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Site-level Covariates</th>
<th>Transect-level Covariates</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Forest to open edge ratio</td>
<td>Visual obstruction 1.0-1.5m; Equivalent stem density</td>
</tr>
<tr>
<td>2</td>
<td>Forest to open edge ratio</td>
<td>Visual obstruction 1.0-1.5m; Equivalent stem density; Total predator genera</td>
</tr>
<tr>
<td>3</td>
<td>Forest proportion</td>
<td>Visual obstruction 1.0-1.5m; Equivalent stem density</td>
</tr>
<tr>
<td>4</td>
<td>Forest proportion</td>
<td>Visual obstruction 1.0-1.5m; Equivalent stem density; Total predator genera</td>
</tr>
<tr>
<td>5</td>
<td>.</td>
<td>Visual obstruction 1.0-1.5m; Equivalent stem density</td>
</tr>
<tr>
<td>6</td>
<td>.</td>
<td>Visual obstruction 1.0-1.5m; Equivalent stem density; Total predator genera</td>
</tr>
<tr>
<td>7</td>
<td>.</td>
<td>Visual obstruction 1.0-1.5m</td>
</tr>
<tr>
<td>8</td>
<td>.</td>
<td>Visual obstruction 1.0-1.5m; Total predator genera</td>
</tr>
<tr>
<td>9</td>
<td>.</td>
<td>Visual obstruction 0.5-1.0m</td>
</tr>
<tr>
<td>10</td>
<td>.</td>
<td>Deciduous stem count; Visual obstruction 0.5-1.0m</td>
</tr>
<tr>
<td>11</td>
<td>.</td>
<td>Visual obstruction 0.5-1.0m; Total predator genera</td>
</tr>
<tr>
<td>12</td>
<td>.</td>
<td>Deciduous stem count; Visual obstruction 0.5-1.0m; Total predator genera</td>
</tr>
<tr>
<td>13</td>
<td>.</td>
<td>Visual obstruction 0.0-0.5m</td>
</tr>
<tr>
<td>14</td>
<td>.</td>
<td>Visual obstruction 0.0-0.5m; Total predator genera</td>
</tr>
<tr>
<td></td>
<td>Description</td>
<td></td>
</tr>
<tr>
<td>---</td>
<td>-----------------------------------------------------------------------------</td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>. b Conifer stem count</td>
<td></td>
</tr>
<tr>
<td>16</td>
<td>. b Conifer stem count; Total predator genera</td>
<td></td>
</tr>
<tr>
<td>17</td>
<td>. b Equivalent stem density</td>
<td></td>
</tr>
<tr>
<td>18</td>
<td>. b Equivalent stem density; Total predator genera</td>
<td></td>
</tr>
<tr>
<td>19</td>
<td>Forest to open edge ratio</td>
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</tr>
<tr>
<td>20</td>
<td>Forest proportion</td>
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</tr>
<tr>
<td>21</td>
<td>Average conifer patch size; Average mixed forest patch size</td>
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</tr>
<tr>
<td>22</td>
<td>Average mixed forest patch size</td>
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</tr>
<tr>
<td>23</td>
<td>. d Equivalent stem density</td>
<td></td>
</tr>
<tr>
<td>24</td>
<td>Forest proportion; Average mixed forest patch size</td>
<td></td>
</tr>
<tr>
<td>25</td>
<td>Forest to open edge ratio</td>
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</tr>
<tr>
<td>26</td>
<td>. b Total predator genera</td>
<td></td>
</tr>
<tr>
<td>27</td>
<td>Average conifer patch size</td>
<td></td>
</tr>
<tr>
<td>28</td>
<td>. b Deciduous stem count</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Average conifer patch size; Average mixed forest patch size</td>
<td>Visual obstruction 1.0-1.5m; Equivalent stem density</td>
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<tr>
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<td></td>
<td></td>
</tr>
<tr>
<td>30</td>
<td></td>
<td>Deciduous stem count; Total predator genera</td>
</tr>
<tr>
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<td>Average mixed forest patch size</td>
<td>Visual obstruction 1.0-1.5m; Equivalent stem density</td>
</tr>
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<td>32</td>
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<td>Visual obstruction 1.0-1.5m; Equivalent stem density; Total predator genera</td>
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<td>Visual obstruction 1.0-1.5m; Equivalent stem density; Total predator genera</td>
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<td>34</td>
<td>Average deciduous patch size; Average mixed forest patch size</td>
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</tr>
<tr>
<td>35</td>
<td>Forest to open edge ratio; Average deciduous patch size; Average mixed forest patch size</td>
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</tr>
<tr>
<td>36</td>
<td>Forest proportion; Average deciduous patch size; Average mixed forest patch size</td>
<td>.</td>
</tr>
<tr>
<td>37</td>
<td>Average deciduous patch size</td>
<td>.</td>
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<tr>
<td>38</td>
<td>Average deciduous patch size; Average conifer patch size; Average mixed forest patch size</td>
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Table 3.5. (cont’d)

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<td>Average conifer patch size</td>
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<tr>
<td>40</td>
<td>Forest to open edge ratio;</td>
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<td></td>
<td>Average deciduous patch size</td>
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<tr>
<td>41</td>
<td>Forest proportion; Average</td>
</tr>
<tr>
<td></td>
<td>deciduous patch size</td>
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</tbody>
</table>

\(^{a}\) Based on AIC.
\(^{b}\) Only transect-level covariates.
\(^{c}\) Only site-level covariates.
\(^{d}\) Null model.
Figure 3.1. Location and occupancy status of snowshoe hare survey sites throughout the northern Lower and Upper Peninsulas of Michigan, USA, winter 2013. The geographic range of snowshoe hares and Michigan are portrayed in the map inset as adapted from the International Union for Conservation of Nature (www.iucnredlist.org/technical-documents/spatial-data#mammals).
Figure 3.2. Number of study sites by 5-year groupings (through 2010) of last confirmed snowshoe hare occupancy in the northern Lower and Upper Peninsulas of Michigan, USA.
Figure 3.3. Snowshoe hare site occupancy probability and (A) forest to open edge ratio, and transect level probability of use by (B) visual obstruction 1.0-1.5m above snow level, and (c) equivalent stem density in Michigan, USA and the 95% confidence intervals. The points along the x-axes represent the values of each study site.


CONCLUSIONS

My thesis addresses 2 distinct questions: 1) what is the optimal transect configuration for effectively and efficiently sampling a snowshoe hare population using snow track surveys, and 2) what factors are driving snowshoe hare localized extinctions, current occupancy, and current habitat use in Michigan. Chapter 1 of my work is the first to experimentally manipulate hare densities and determine the accuracy of track surveys. As such, Chapter 1 adds to the literature on using snow track surveys to monitor snowshoe hare populations (Hodges and Mills 2008). Chapter 2 focused on climate covariates that have been linked to snowshoe hare demographics. I found that climate correlated with localized extinctions and offered some potential mechanisms for how climate is negatively affecting hares. In Chapter 3 I concentrated on how various land cover and habitat factors were associated with localized hare occupancy over time. The primary contributions of Chapter 3 included an assessment of historical and current land cover and which is more important for influencing snowshoe hare occupancy and a ranking of land cover and habitat structure variables to help guide where management should be focused.

In Chapter 1, my results indicated that snow track surveys, if configured correctly, can be efficiently implemented and provide accurate data on snowshoe hare occupancy status. I recommended 3 designs for use in broad-scale snowshoe hare monitoring programs. Additionally, results from the 3 transect configurations appeared to correlate with snowshoe hare density across the full range of densities I evaluated. This relationship was not observed
over a narrower range of densities (e.g., like those found at the southern distribution). I used transects that were 125m in length with 75m spacing for Chapters 2 and 3 of my thesis.

In Chapter 2, I found that of 134 sites sampled in Michigan, 39% of the sites experienced localized snowshoe hare extinction, with higher probabilities in the Lower Peninsula of Michigan compared to the Upper Peninsula. I found that maximum temperature between May 15 and January 19 and the number of days with snow on the ground were the primary factors influencing localized extinction. The hypothesized mechanisms of these covariates were a decrease in litter size and coat color mismatch to the environment, respectively. Study sites with the highest maximum temperatures and/or fewest days with snow on the ground were approximately 3 times more likely to experience extinction.

In Chapter 3, I found that out of the 117 sites that I compiled land cover and habitat data for, 62% of the sites were occupied in 2013. Results suggested that long-term land cover change over time at a 332ha scale did not affect snowshoe hare occupancy status. I also found that occupancy status was most influenced by a single site and 2 transect level covariates. While the 1 site covariate (forest to open edge ratio) appeared in the top-ranked model, it was not significant, with current snowshoe hare occupancy in Michigan being primarily influenced by the transect-level covariates of visual obstruction 1.0-1.5m above snow level (~3m) and an equivalent stem density (3x conifer stems + 1x deciduous stems). These results are consistent with a growing body of research that show hares mostly depend on dense vegetation for survival (Litvaitis et al. 1985, Sievert and Keith 1985, Hodges 2000, Berg et al. 2012). I provided specific recommendations that can help managers succeed in increasing snowshoe hare occupancy in forests throughout Michigan.
The relationships among climate, land cover, vegetation structure, and predators are complex. Future research is needed to assess if directly managing patch configuration, vegetation structure, or predator abundance can help mitigate the apparent extinction process related to climate change. I contend that while the range of snowshoe hares will continuously contract northward due to climate change, the rate of this contraction could be slowed with designated habitats being targeted to aid snowshoe hares. Overall, this research provides firm guidelines for increasing snowshoe hare occupancy probabilities.


