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Habitat Use of the Climate-Sensitive Snowshoe Hare (Lepus americanus) In the Manistee National Forest in Michigan's Lower Peninsula

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Habitat Use of the Climate-Sensitive Snowshoe Hare (*Lepus americanus*) In the Manistee National Forest in Michigan's Lower Peninsula

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DEDICATION

I dedicate this thesis to my parents, who despite have five children to bring everywhere, always fostered in us a love of the outdoors. It is the countless hikes, time spent playing outdoors, mornings looking for wildlife in the neighborhood, and vacations that we spent hiking that have encouraged me to pursue this degree. I could not and would not have gotten here without all of your hard work and dedicated parenting.

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ABSTRACT

Snowshoe hares (*Lepus americanus*) are a wide-ranging lagomorph that are important forest herbivores and a popular game species throughout their range. Across the southern boundary of their geographic range, snowshoe hares are experiencing population declines and possible extirpation due to increased predation pressure driven by climate change induced camouflage mismatch, competition for forage, degraded and fragmented habitat. One method of reversing the negative trends in snowshoe hare distribution is to increase and improve available hare habitat. A specific habitat analysis for local regions will most effectively advise managers how to target habitat management. I radio-collared 11 snowshoe hares in the Manistee National Forest in Michigan's Lower Peninsula from August 2017-May 2019 to document their local habitat use. Snowshoe hares used areas of greater understory density than available forest. Regenerating aspen stands provided this type of habitat, as aspen stands also had significantly greater understory density and total stem count than random available forest. We found snowshoe hares to use lower understory density during leaf-off periods, due to a lack of available dense coniferous understory. Snowshoe hare survival increased in areas with greater proportions of aspen stands, but showed no trends associated with coniferous stands. In the Manistee National Forest, regenerating aspen stands will be a large determinant of the persistence, survival, and distribution of snowshoe hares in the immediate future.

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KEY TO SYMBOLS

* or **

Used to indicate varying significance levels for statistical analyses of group comparisons, such as Mann-Whitney U tests.

DSP

Daily survival probability calculated using the Mayfield Method.

n

Sample size. The number of recorded or measured samples for a given experimental or control group.

η^2

Effect size. Value that indicates the impact of effect on differences between two groups.

p

Value that indicates significance in statistical analyses if it is < 0.05.

PC

Principal component, a dimension in an ordination of a Principal Component Analysis that explains a proportion of the variation in the data. PC1 explains the greatest proportion of variation in the data is typically ordinated along the x-axis. PC2 explains the second-greatest proportion of variation in the data and is ordinated along the y-axis. A given PCA contains a number of principal components equal to the number of descriptors in the analysis.

U

Test-statistic from Mann-Whitney U test.

ABBREVIATIONS

CWD = Coarse woody debris

d = Days

F = Female

GPS = Global Positioning System

m = Meters

M = Male

MLP = Michigan's Lower Peninsula

MNF = Manistee National Forest

PCA = Principal Component Analysis

PIT = Passive Integrated Transponder

SD = Standard Deviation

VHF = Very High Frequency

CHAPTER I

INTRODUCTION

Snowshoe Hares

Snowshoe hares (*Lepus americanus*) are a wide-ranging lagomorph with a range extending from Alaska, south to Michigan, Colorado, and Pennsylvania and which generally prefer boreal forests with a thick, brushy understory (Wirsing et al. 2002). Though snowshoe hares occasionally feed on carrion, their diet is almost exclusively herbivorous, foraging on shrubs, grasses, and flowers in the summer and switching to woody browse during winter (Murray et al. 2002). Hares depend on their camouflage, dense cover, and agile movement as a last resort, as they are a common prey item to a variety of predators throughout their range. Snowshoe hares also rely on coat camouflage to avoid predation, as their pelage is a light brown in the summer, molting to white October-November, and returning to light brown in March-April (Merilaita & Lind 2005).

Dense cover is extremely important to snowshoe hare persistence, and is the major habitat variable impacting occurrence and survival (Carreker 1985). Dense understory cover provides visual cover from predators and doubles as their major food source as they are unable to reach vegetation higher in the canopy

Though wildlife species commonly have wide geographic ranges, individuals at the margins of the species' range generally face more ecological challenges and are more sensitive to change than individuals within core range locations (Anderson et al. 2008). This tendency also holds true for snowshoe hares as the habitat at the southern reaches of their range is vastly different from the northern boreal forest (Hansen et al. 2013). Habitat in Michigan's Lower

Peninsula is an example with lower annual snow cover and more temperate deciduous forest (Nagorsen 1985). In addition to the differences in forest type and snow cover, snowshoe hares in Michigan's Lower Peninsula experience potentially higher predation pressures from mesocarnivores. The absence of grey wolves (*Canis lupus*) and mountain lions (*Puma concolor*) in Michigan's Lower Peninsula has had a twofold effect on snowshoe hare populations. First, lack of large predators has resulted in a proliferation of white-tailed deer (*Odocoileus virginianus*) populations (Frawley 2018). At high densities, white tailed deer are able to outcompete snowshoe hares for optimal forage, specifically reducing the available browse during winter (Patterson & Power 2002). Second, absence of apex predators causes an increase in mesocarnivores, such as the eastern coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), and red fox (*Vulpes vulpes*) (Ripple et al. 2013). These mid-sized predators are unlikely to take down a large prey such as a white-tailed deer, and more frequently will choose prey of optimal size, such as snowshoe hare (Mills et al. 1993).

Climate Change

In recent years, climate change has had extensive effects on weather patterns and projections predict impacts to intensify with altered precipitation and sporadic winters in the Midwestern United States (Meehl et al. 2007). Climate change increases minimum air temperature and precipitation, but decreases persistent snow cover, causing drastic effects in the Midwest with its four varying seasons, especially by reducing late-autumn and early-spring snow cover (Mishra et al. 2010). Projections are that future snowfall will decrease in Lower Michigan due to reduction of lake effect snow events. In Michigan's Lower Peninsula, lake effect snow makes up a large proportion of annual snowfall as major Lake Michigan lake effect snow events account for the majority of local annual snowfall. It is also a dominant factor in forest type distribution, and is sensitive to lake ice cover and temperature (Wright et al. 2012). Therefore, climate change will have direct impacts on Michigan's plant communities, significantly changing the structure of forests and land cover at higher rates than any known historic ecosystem changes (Williams & Dumroese 2013).

Loss of persistent snow cover in Michigan's Lower Peninsula increases predation rates of snowshoe hares due to camouflage mismatch which occurs when a species which exhibits a cryptic coloration in its natural habitat no longer matches the local "background" landscape (Mills et al. 2013). In snowshoe hares, camouflage mismatch occurs most frequently in autumn and spring, when their pelage is white but lasting snow cover is absent, presenting a white prey item with a brown background (Zimova et al. 2014). Camouflage mismatch in snowshoe hares increase mortality by predation and greater predation pressure increases stress levels, leading to lower reproductive rates (Sherrif et al. 2009). Dense cover is necessary to allow hares to more effectively hide from predators if they are white while their snow does not cover their surroundings (Beaudoin et al. 2004).

Climate change has already resulted in poleward range shifts of several terrestrial vertebrates, including snowshoe hares in Michigan (Burt et al. 2017). As climate change continues, forests at the southern margins of snowshoe hare range will become unsuitable habitat if left unmanaged. Due to natural barriers (i.e. Lake Michigan & Lake Huron), snowshoe hare populations in Michigan's Lower Peninsula will be unable to disperse northward as southern habitat is degraded (Schloss et al. 2012). Habitat in Michigan's Lower Peninsula is generally suboptimal for snowshoe hares, but some of the best habitat is in aspen stands (*Populus grandidentata* and *Populus tremuloides*) regenerating after timber harvests (Conroy et al. 1979). Understanding the characteristics of aspen stands that both promote use by hares and positively influence survival of hares will allow us to provide management recommendations to the US Forest Service and MI Dept. of Natural Resources as they strive to maintain viable hare populations in Michigan's Lower Peninsula.

Study Area

The study area for this project is located in the northwest region of Michigan's Lower Peninsula. Specifically, this study includes forested regions in the Manistee National Forest and nearby sections of the Pere Marquette State Forest. I chose this study area because the most recently articulated southern boundary of snowshoe hares in Michigan falls within the Manistee National Forest, making it an ideal location to study snowshoe hares at the extreme southern boundary of the species' range (Burt et al. 2017).

Snowshoe hares in Michigan's Lower Peninsula are present in lower densities than in the core of their range (Burt et al. 2017). Dense coniferous understory which is common in the boreal biome, is almost nonexistent in Michigan's Lower Peninsula, causing a shift in snowshoe habitat availability. Instead, the densest understory in Michigan's Lower Peninsula is commonly in regenerating stands of aspen (Roberts & Richardson 1985). Large patches of native coniferous forest are almost nonexistent or heavily over-browsed by white tailed deer.

PURPOSE

Snowshoe hares are an important herbivore and game species in Michigan forests and therefore provide important benefits to both the ecosystem and the hunting community. Dwindling populations at the southern reaches of the snowshoe hare range in other states indicate a need for detailed research and management plans for snowshoe hares in Michigan. Due to their sensitivity to climate change and vulnerability to predation, snowshoe hare numbers may drastically decrease without improved management. The purpose of this thesis was to provide more detailed information on the habitat use by snowshoe hares in the Manistee National Forest of Northern Lower Michigan (Chapter II). This thesis then aimed to compare the habitat used by snowshoe hares to available habitat to identify specific habitat preferences of snowshoe hares. Additionally, comparing survival of snowshoe hares to their surrounding local habitat can provide more knowledge about broad-scale habitat features impacting survival and persistence of snowshoe hares on the landscape (Chapter IV). Managers will be able to use information detailed in this thesis to improve and increase snowshoe hare habitat.

SCOPE

This thesis details habitat use of snowshoe hares in the Manistee National Forest in Lower Michigan, a region at the southern reach of the species' range. The research presented in this thesis details specific differences between used and available in the Manistee National Forest. Additionally, the survival of snowshoe hares is a product of stand-level forest habitat characteristics and has potential to provide insight to other populations located at the southern reaches of the snowshoe hare range.

ASSUMPTIONS

For this thesis, I assumed the snowshoe hares captured and monitored in this study are representative of the population of snowshoe hares throughout the Manistee National Forest in Northern Lower Michigan. I also assumed resting locations found during daylight periods were sufficiently descriptive of snowshoe hare habitat use. For Chapter II, I assumed vegetation characteristics would not change significantly between the time I recorded snowshoe hare locations and measured vegetation characteristics. Additionally, I measured all vegetation characteristics during the leaf-on period for consistency. I therefore assumed that measuring vegetation characteristics in different seasons would not significant alter the results and conclusions of this thesis. Additionally I assumed 2015 land cover data provided by the United States Forest Service remained appropriately descriptive of the study area through this study period.

HYPOTHESIS

This thesis examined three central hypotheses. I hypothesized habitat used by snowshoe hares would differ from available habitat in the Manistee National Forest (Chapter II). I predicted snowshoe hare habitat to exhibit higher horizontal cover, higher overall stem count, but lower conifer stem count than random locations. I also hypothesized snowshoe hare habitat would differ between leaf-on and leaf-off periods, with a higher overall stem count and higher conifer stem count in the leaf-off periods. Lastly, I hypothesized that snowshoe hare survival in the Manistee national forest would vary among habitat type surrounding individual hare locations.

SIGNIFICANCE

This thesis presents new information regarding the habitat use of snowshoe hares in the Manistee National Forest in Northern Lower Michigan. Prior to this thesis, there had been a lack of detailed research describing snowshoe hare habitat requirements and preferences specific to this region. As a wide-ranging species, both the used and available habitat potentially exhibits vast variation across the range. With recent and predicted progressions in climate change, snowshoe hares at the southern reaches of the species' range are at a particularly high risk of population decline. The information in Chapter II present explicit differences between used snowshoe hare habitat and available forest habitat while also presenting more broad-scale stand level characteristics and proportions that influence snowshoe hare survival in the Manistee National Forest. This thesis adds to the newly-focused research on the southern reaches of snowshoe hare range, with the goal of preventing further range contractions and extirpation. Managers can utilize the conclusions of this thesis to improve and adapt management techniques for the benefit of snowshoe hare habitat and populations at the southern reach of its range.

DEFINITIONS

Biplot

An ordination plot of a Principal Component Analyses that displays the variation in the data represented by the two greatest principal components of the analysis.

Eigenvalues

A term used in multivariate analyses. In a principal component analysis, an eigenvalue indicates the amount of variation explained by a specific axis.

Eigenvector

A term used in multivariate analyses. In the case of a principal component analysis, an eigenvector describes the contribution of a given variable to the principal component.

Leaf-off

The seasons (typically surrounding the winter months) in which leaves are not present on local deciduous trees.

Leaf-on

The seasons (typically surrounding the summer months) in which leaves are present on deciduous trees in the local area.

CHAPTER II – Snowshoe Hare Habitat Use and Survival in the Manistee National Forest

ABSTRACT

Snowshoe hares (*Lepus americanus*) utilize forested regions with high understory density, which provides both forage and cover. Through the majority of their geographic range, this dense understory is composed largely of coniferous species, such as fir, cedar, and spruce swamps. However,in the Lower Peninsula of Michigan at the southern reach of the snowshoe hare range, the dense conifer understory is largely absent due to proliferation of white-tailed deer (*Odocoileus virginianus*), and forest loss. I radio-collared 11 snowshoe hares in the Manistee National Forest and compared forest stands they used to the surrounding available forest and aspen stands. Snowshoe hare locations during the leaf-off season were not significantly different from locations during the leaf-on season. Snowshoe hares used areas with greater 0.5-meter and 1-meter horizontal cover, greater overhead cover, deciduous stems, snags, and total stems than available forest. However, snowshoe hare locations showed no significant difference in conifer stem counts when compared to random forest sites, indicating the hares are indeed finding other vegetation stands to replace the typical conifer understory. I found points within aspen stands to have greater horizontal cover, overhead cover, deciduous stems, and total stems than random forest sites, though snowshoe hare locations had 1-meter cover and stem values greater than aspen stand locations.Snowshoe hares in Lower Michigan found high quality habitat in regenerating aspen stands to make up for a lack of dense conifer understory in my study area. The hares may be subject to higher predation risk during winter months as available cover decreases in deciduous stands following leaf off.

INTRODUCTION

Snowshoe hares (*Lepus americanus*) are a wide-ranging lagomorph with populations ranging from Alaska, throughout much of Canada, south to Michigan, Colorado, and Pennsylvania. Snowshoe hares generally prefer boreal forests with a thick, brushy understory (Wirsing et al. 2002). Though known to occasionally feed on carrion, their diet is almost exclusively herbivorous, foraging on shrubs, grasses, and flowers in the growing season and switching to woody browse during winter months (Murray et al. 2002). Snowshoe hares play a key role in the predator-prey cycles with Canada lynx (*Lynx canadensis*) (Tyson et al. 2010) and are a common prey species for many less specialized predators. Predation is the leading stressor of snowshoe hare population fluctuations, despite impacts of available forage (Krebs et al. 1995). Snowshoe hares undergo a seasonal coat color molt to avoid detection by predators, as their pelage is a light brown in the summer, molting to white in October-November, and returning to light brown in March-April (Grange 1932, Merilaita and Lind 2005). Climate change has resulted in more variable weather, creating the potential for mismatch between snowshoe hare coat color and their surroundings.

Though wildlife species commonly inhabit wide geographic ranges, individuals at the margins of the species' range generally face more ecological challenges and experience different habitat than individuals within the range's core (Anderson et al. 2008, Hansen et al. 2013, Nagorsen 1985, Wirsing et al. 2002). Michigan's Lower Peninsula is at the southern reach of the snowshoe hare range and experiences lower annual snow cover and less coniferous forest than the core range (McCann 1991, Cherkaur and Sinha 2010). The extirpation of grey wolves (*Canis lupus*) and mountain lions (*Puma concolor*) in Michigan's Lower Peninsula increased densities of eastern coyote (*Canis latrans var.*), foxes (*Vulpes vulpes; Urocyon cinereoargenteus*), and bobcats (*Lynx rufus*) (Ripple et al. 2013; Ritchie & Johnson 2009) which are unlikely to take down a large prey item, more frequently choosing prey of optimal size, such as snowshoe hares (Boutin et al. 1986, Mills et al. 1993). A dense understory provides visual cover from predators (Wolfe et al. 1982), and a lack of dense cover is the major habitat variable impacting their occurrence and survival (Keith et al. 1984, Carreker 1985, Litvaitis et al. 1985).

A proliferation of white-tailed deer due to the lack of apex predators in Michigan's Lower Peninsula has increased forage competition for snowshoe hares and a decimation of coniferous understory (Frawley 2019). Deer densities in Michigan's Lower Peninsula have also increased in recent decades due to altered management strategies which now maintain and create more early successional forest than is typical in the history of Michigan (Litvaitis 1993). Though early successional forest typically provides snowshoe hare habitat, high densities of white tailed deer are able to outcompete snowshoe hares for optimal forage, specifically reducing the available browse during winter and preventing regeneration of several coniferous species (Telfer 1972, Rooney & Waller 2002, Rawinski 2008). Long-term studies have shown up to 81% loss of understory herbs and shrubs as deer densities increase (Rooney 2001).

In recent years, climate change has altered precipitation cycles and caused variable winter conditions in the Midwestern United States (Meehl et al. 2007, Swanston et al. 2018). Climate change has and will continue to increase minimum air temperature and precipitation in the Midwestern US, therefore decreasing persistent snow cover and reducing late-autumn and early spring snow cover (Mishra et al. 2010). Even though lake effect snow events are projected to increase in Michigan as climate change progresses, higher average temperatures will reduce periods with snow on the ground in late fall and early spring (Wright et al. 2012). Loss of persistent snow cover in Michigan's Lower Peninsula increases predation rates of snowshoe hares due to camouflage mismatch, which occurs when a species with a cryptic coloration in its natural habit no longer matches the local "background" landscape (Mills et al. 2013). Camouflage mismatch occurs most frequently in autumn and spring, while their pelage is white but snow cover is lacking, presenting a white prey item on a brown background (Zimova et al. 2014). The availability of dense cover may help ameliorate increased predation risk during periods of mismatch (Sievert & Keith 1985, Wilson et al. 2019).

Though Lower Michigan contains a lot of conifer forest, the majority is mature and lack the dense understory of younger forests (USFS 2005). However, regenerating aspen (*Populus grandidentata* and *Populus tremuloides*) stands commonly are dense in their understory. Understanding the characteristics of aspen stands that promote their use by hares and buffer survival can potentially improve management practices by local agencies. However, when deciduous trees drop their leaves, cover values within may decrease. Snowshoe hares may require different habitat during the leaf-off season to compensate for the decrease cover values in deciduous stands.

Snowshoe hares in Michigan's Lower Peninsula have already experienced significant range contractions and have the potential for extirpation without management intervention (Burt et al. 2017). The objective of this study was to quantify year-round snowshoe hare habitat use in Michigan's Lower Peninsula in order to improve understanding of local snowshoe hare habitat selection for future research and management. I hypothesized (1) snowshoe hares would use areas of higher understory density than available forest but (2) with no preference for coniferous stands, and (3) aspen stands would exhibit more dense horizontal cover than overall available forest. I hypothesized (4) snowshoe hare locations during the leaf-off season will have lower horizontal cover values than during the leaf-on season, but (5) snowshoe hares will attempt to compensate for this by more commonly selecting for coniferous habitat during the leaf-off season than they do during the leaf-on season.

MATERIALS AND METHODS

Study Area

I conducted this study in the Manistee National Forest in Michigan's Lower Peninsula (Figure 1). Climate data from Manistee, Michigan, the nearest weather station, recorded mean temperatures of 1.0 ± 0.06 °C from October-March and 16.0 ± 3.8 °C from April-September of 2017 (NCEI 2017). October-March had a mean precipitation of 36.8 ± 0.2 cm while April-September was 51.4 ± 0.07 cm (NCEI 2017). Elevation within the Manistee National Forest ranged from 140-521 meters (USGS 2016).

Forest composition in the study area is primarily mixed, including a variety of stand types such as pine plantations, aspen regeneration, and mixed conifer-deciduous. Dominant tree species in the area include red pine (*Pinus resinosa*), white pine (*Pinus strobus*), bigtooth aspen, quaking aspen, red oak (*Quercus rubra*), white oak (*Quercus alba*), red maple (*Acer rubrum*), and American beech (*Fagus grandifolia*). Common vegetation stands throughout the study area include regenerating aspen, mature aspen, red pine plantations, red maple, mixed oaks, sugar maple – beech/yellow birch, open, mixed hardwoods, lowland shrubs, and mixed swamp conifers. The large proportion of deciduous forest stands in the region creates distinct seasonal differences in overhead and thermal cover. I chose this study area because the most recently articulated southern boundary of snowshoe hares in Michigan falls within the Manistee National Forest, making it an ideal location to study snowshoe hares at the extreme southern reaches of their range (Burt et al. 2017).

Live Trapping

I conducted live-trapping for snowshoe hares opportunistically from August 2017 to December 2018. Traps (Tomahawk Live Trap Company, Tomahawk, Wisconsin, model 106) were baited with apples, alfalfa, and cinnamon-scented aspen sticks and were covered with surrounding debris for thermal cover. I checked traps every morning and rebaited as needed. I chose trapping locations based on confirmed sightings of snowshoe hares from camera surveys and from consultations with local hunters.

I transferred hares from the trap into a transportation/recovery box made of plastic PVC pipe, painter's canvas, and a plywood bottom. This box was approximately the same size as the live trap but did not allow the hare to see outside and potentially reduced hare stress and activity during transportation to the mobile lab site. I immobilized hares with gaseous anesthesia of isoflurane and oxygen, and monitored respiration, body temperature, heart rate, and overall condition throughout immobilization. Once immobilized, I sexed and weighed individuals, and implanted a passive integrated transponder tag (AVID Identification Systems Inc., Norco, California) subcutaneously between the shoulder blades. All individuals weighing over 833 grams were fitted with a VHF collar (Advanced Telemetry Systems, Isanti, Minnesota, model M1555). I then placed hares back in the transportation/recovery box to monitor recovery before transporting them to the original point of capture for release. Grand Valley State University Animal Care and Use Committee examined and approved all capture and handling protocols for this project (Project 18-04-A).

Radio Telemetry

Radio-collared hares were tracked on foot using a handheld receiver (Advanced Telemetry Systems, Isanti, Minnesota, model R410) and a three-element Yagi antennae. I tracked hares during the daytime, at least once weekly, until they were visually located, or until I flushed the hare from its original location. I tracked hares until mortality, collar failure, or through the end of the study period. I excluded hunted individuals from survival calculations. Individuals whose final fate was unknown could have been due to collar failure, hunter harvest, depredation, or emigration. I calculated survival as number of days alive from first trapping encounter until mortality or last-located date.

I separated snowshoe hares into four main groups for survival analyses based on geographic location: Stoddard, Saddler, Caberfae, and 25 Rd (Figure 2). I excluded the Stoddard group from analyses as the only collared individual was a confirmed hunter harvest. I analyzed the other three groups and compared using the Mayfield Method (Mayfield 1975). Because of the low sample size, statistical options and power was limited for survival analyses.

I analyzed habitat in ArcGIS (ESRI 2011) by creating 500-meter buffers around the first location of each individual hare to include entire possible home ranges for the individual hares, as well as the forest surrounding those home ranges. Buffers from neighboring individuals overlapped and combined into singular features representing distinct groups. I analyzed the data in Program R (R Core Team, Vienna, Austria) and illustrated using Microsoft Excel (Microsoft Corporation 2019).

Vegetation Sampling

To quantify habitat quality and differences at snowshoe hare locations, I measured horizontal cover at 1 meter and at 0.5-meter heights, overhead cover, and stem count for deciduous, conifer, and snag stems (Clark 2016). I measured vegetation characteristics at every snowshoe hare location, as well as at 50 random locations, and within 50 random aspen (bigtooth aspen or quaking aspen) stands throughout the study area. At each location, I placed a 1-meter tall 1-inch

PVC pole, marking a center point (Figure 3). The pole was marked with orange at 0.5 meters and 1 meter along its length. Using a random number generator, I generated four random bearings from this central pole. For each bearing, using a 4-meter-long chain, I placed an identical PVC pole (the sample pole) 4 meters along the bearing. I used a moosehorn densitometer (Forestry Suppliers, Jackson, Mississippi, Model 41114215) to measure overhead cover and horizontal cover at 0.5 meters and 1 meter, looking towards the central pole for the marking at the corresponding height. Measurements were binary for overhead cover and for each height at each bearing. Through combining the measurements for each bearing, a value of 0%, 25%, 50%, 75% or 100% resulted for each cover characteristic. Using the last random bearing, I measured stem count for each hare location and random sample site. I held a 1-meter PVC pole horizontally at 1 meter height, and moved across the 4-meter distance from the sample pole, recording any stem touching the PVC pole along the 4 meters, giving a final stem count for each site of snags, conifer stems, and deciduous stems.

In addition to the aforementioned vegetation characteristics, I measured separate vegetation characteristics during radio telemetry tracking. Once hares were located, I visually estimated canopy cover, horizontal cover, and tree species composition. Within 50 meters, I recorded overall tree species composition, including percent conifer and percent deciduous. I also recorded season, time of day, ambient temperature, forest type, snowpack, and leaf-on vs leaf-off for each location. Variables recorded for analyses included overhead canopy cover, 3m cover, 1m cover, percent coniferous, percent deciduous, 3m percent deciduous, 3m percent coniferous, understory shrubs, understory herbaceous, understory coniferous, understory deciduous, aspen, red pine, other conifer, and other deciduous (Table 1).

Statistical Analyses

I compared hare locations and randomly sampled locations were compared in Program R (R Core Team, Vienna, Austria), using a principal component analysis (PCA) to compare hare locations, random forest locations, and random aspen locations. I analyzed specific differences between hare locations, aspen sites, and random forest sites using Mann-Whitney tests. I calculated effect sizes along with Mann-Whitney U analyses due to large numbers of hare locations and random sites. When comparing groups, p-values are dependent on both the size of effect and the sample size (Coe 2002). Calculating effect size ensures incorporation of the size of *effect*, and distinguishes when a p-value indicates significance primarily due to size of the sample. I calculated effect size for all analyses between groups using the following formula (Coe 2002):

$$Effect\ Size = \frac{[Mean\ of\ experimental\ group] - [Mean\ of\ control\ group]}{SD}$$

Where *SD* is the standard deviation of all samples, including both the experimental group and control group. When comparing snowshoe hare locations to random forest sites, I assigned the hare locations as the experimental group with random forest sites representing the control group. Hare locations again represented the experimental groups when compared to random aspen stands, which served as the control group in these analyses. When comparing random aspen stands to random forest sites, random aspen stands became the experimental group with random forest sites remaining as the control group.

I also analyzed differences between leaf-on and leaf off for snowshoe hare locations using PCA and made further comparisons between the leaf-off and leaf-on periods using Mann-Whitney tests to analyze for significant differences between the groups due to data being unbalanced and not normally distributed.

RESULTS

Habitat Use

I radio-collared 11 adult snowshoe hares between August 2017 and March 2019. Three individual hares survived to the end of the study period, 3 were depredated (1 by red fox, others unknown), 2 were found dead with no sign of predation, 1 was taken by hunter harvest, 1 unknown fate, and 1 trap-related death. The hares were tracked an average of 17.7 ± 4.87 times for a cumulative 188 times until their respective mortalities or through the end of the study period. I measured vegetation characteristics at every hare location, 50 random forest locations, and 50 random aspen locations.

I found snowshoe hare locations, random forest locations, and random aspen locations to be distinctly different, with the biplot representing approximately 69% of the variation in the dataset (Figure 4; *PC1=0.4095, PC2=0.2808*). Hare locations had high 1-meter horizontal cover and high deciduous stem counts. Random forest sites were associated with lower 1-meter horizontal cover and lower deciduous stem counts. Hare locations and random forest sites showed similar degrees of association with conifer stem counts whereas aspen stands were likely to have lower conifer stem counts (Figure 4). Aspen stands provided higher quality snowshoe hare habitat than random forest sites, with higher horizontal and overhead cover values (Figure 5; *PC1=0.3264, PC2=0.2034*). Horizontal cover at 1-meter and 0.5-meter had greater deciduous stem counts but shared no relationship with conifer stem counts. Aspen stands were more commonly associated with greater deciduous stem counts and horizontal cover (Figure 5). Random forest stands had more conifer stems, lower horizontal cover, and lower overhead cover than aspen stands. PC1 and PC2 together explained 52.98% of the variation in the data due to the inclusion of all vegetation characteristics. Snowshoe hare locations were associated with lower conifer stem counts and higher overhead cover (Figure 6; *PC1=0.2938, PC2=0.2096*). Horizontal cover at 0.5-meter and 1-meter were the most influential of the measured vegetation characteristics (Figure 6). Again, greater deciduous stem counts associated with both 0.5-meter and 1-meter horizontal cover, none of which correlated with conifer stem counts. (Figure 6).

Except for conifer stems, every measured characteristic was significantly greater at snowshoe hare locations than random forest locations (Table 2). Hare locations had greater overhead cover (Mann-Whitney U Test, $p=4.45e^{-5}$, $U=6059$, $\eta^2=0.65$) , 0.5-meter horizontal cover ($p=1.36e^{-5}$, $U=6191.5$, $\eta^2=0.70$), 1-meter horizontal cover ($p=4.03e^{-13}$, $U=7394$, $\eta^2=1.16$), snags ($p=6.25e^{-4}$, $U=5779$, $\eta^2=0.42$), deciduous stems ($p=2.20e^{-16}$, $U=7885$, $\eta^2=1.12$), and total stems ($p=2.20e^{-16}$, $U=7950.5$, $\eta^2=1.16$) than random forest locations (Table 3A). Additionally, hare locations had significantly greater 1-meter horizontal cover (Mann-Whitney U Test, $p=4.33e^{-6}$, $U=6293.5$, $\eta^2=0.74$), deciduous stems ($p=2.44e^{-9}$, $U=6932.5$, $\eta^2=0.85$), snags ($p=7.28e^{-4}$, $U=5762.5$, $\eta^2=0.48$), and total stems ($p=1.40e^{-11}$, $U=7268.5$, $\eta^2=0.91$) than aspen stands (Table 3B). When comparing aspen stands specifically to random forest sites, aspen stands exhibited greater overhead cover (Mann-Whitney U Test, $p=0.01$, $U=1571$, $\eta^2=0.46$), 0.5-meter horizontal cover ($p=9.75e^{-4}$, $U=1685.5$, $\eta^2=0.64$), 1-meter horizontal cover ($p=0.01$, $U=1565$, $\eta^2=0.48$), and total stems ($p=0.03$, $U=1508.5$, $\eta^2=0.48$) than random forest sites (Table 3C).

Seasonal Comparisons

Snowshoe hare locations did not differ between leaf-off and leaf-on seasons (Figure 8; *PC1=0.3706, PC2=0.2963*). 1-meter horizontal cover was equally associated with high deciduous stem counts during both leaf-on and leaf-off seasons, with no indication of a seasonal difference in conifer stem counts (Figure 8). There was no difference in conifer stem counts between leaf-on and leaf-off locations (Mann-Whitney U Test, *p=0.914, U=0.914*). Conversely, leaf-on hare locations had greater total stems than leaf-off locations (Figure 9; $p=1.48e^{-3}$, $U=5074$, $\eta^2=0.42$).

Hares were more commonly found in red pine and coniferous stands during the leaf-off period while they were more likely to be found in aspen during leaf-on periods (Figure 10; *PC1=0.4468, PC2=0.2562; n=118*). Forest composition showed great variability across recorded locations, as represented through high standard deviation values for all variables (Table 5). Snowshoe hares used coniferous forest significantly more frequently during leaf-off periods than during leaf-on periods ($p=5.09e^{-6}$, *U=5397.5, n=181*). Cover density at 1m exhibited significant differences between leaf periods (Mann-Whitney U, $p=7.31e^{-3}$, *U=2493.5, n=181*), while 3m cover and overhead canopy cover did not (Table 4). Snowshoe hare used aspen stands at similar frequency between leaf on and leaf offperiods (*P=0.5806, U=1785*). Red pine use showed slightly more variation between the periods, but again was not significant (Mann-Whitney U, Figure 11; *P=0.1442, n = 176*).

Survival

Using data from 9snowshoe hares, I generated 500-meter buffers around groups overlapping individuals for survival analyses (Table 6). Saddler had the highest average survival (Mayfield Method, 408.33 days, *DSP=0.9992*, n=3), followed by 25 Rd (278 days, *DSP=0.9964*, n=2), and Caberfae exhibited the lowest average survival length (131.25 days, *DSP=0.9924*, n=4). Survival of snowshoe hares increased in correlation with increasing proportions of surrounding aspen stands. The Saddler group exhibited the greatest proportion of aspen stands among the 3 groups, with bigtooth aspen and quaking aspen combining to account for over 50% of the vegetation in Saddler (Figure 12). Both 25 Rd and Caberfae had considerably lower proportions of aspen stands, with the fewest found in Caberfae. Red Pine made up over 37% of the vegetation in 25 Rd, compared to 19% and 29% in Caberfae and Saddler, respectively (Figure 12). The larges contributing vegetation stand in Caberfae was Sugar Maple – Beech/Yellow Birch, accounting for over 62% of the surrounding habitat but was not present in any amounts in Saddler or 25 Rd. Though proportions were lower for all groups, Red maple accounted for 7.5% of vegetation stands in Saddler, 3.8% in 25 Rd, and just 2.5% in Caberfae.

DISCUSSION

Snowshoe hares in Lower Michigan are at great risk due a lack of suitable habitat available. Snowshoe hares require habitat that contains a dense coniferous understory (Boutin et al. 1986, Carreker 1985, Krebs et al. 1995). I found hare locations to have higher mean horizontal cover than randomly-sampled locations (Figure 4) and no correlation with conifer stems, even when compared to the available forest (Figure 4, Figure 6). Snowshoe hare locations were composed of thick aspen saplings and beech thickets, creating a dense understory. Snowshoe hare habitat suitability indices (Carreker 1985) indicate a need for coniferous understory. In our study area, snowshoe hares used habitat that contained a dense understory but lacked the conifer component, which is similar to hare population in Wisconsin (Wilson et al. 2019). Regenerating aspen can be a stand-in for snowshoe hare habitat when dense conifer understory is absent (Litvaitis et al. 1985; Wilson et al. 2019).

Random sites within aspen stands provided habitat of higher quality than random forest locations, but lower quality that the average hare location (Figure 4). Locations within aspen stands do provide better habitat in general than the surrounding forest in the study area, though on average may represent intermediate-quality habitat if hares are only using a subset of aspen stands due to my samples including a variety of aspen age classes. The greater stem counts at hare locations indicate a preference for young aspen stands and may be representative of stands which contain young maples within the understory, further increasing the stem count (Litvaitis et al. 1985, Gigliotti et al. 2018). Regenerating aspen stands are important to the distribution of snowshoe hares in Michigan's Lower Peninsula, and potentially to similar regions across the southern reaches of the historic snowshoe hare range (Wilson et al. 2019). Wolfe et al. (1982) proposed snowshoe hares use early successional aspen stands as they are regenerating from disturbance (i.e. 5-20 year age class). Snowshoe hares in my study area do not alter their habitat use during the leaf-off season suggesting that leaves on aspen trees are not the reason for snowshoe hare use, but rather the stem density. Hares are unable to reach leaves in the canopy, even on young aspen. They do however browse on the bark and twigs of the aspen saplings. Beech saplings in the study area usually retained their leaves until the end of winter, providing important cover in beech thickets. Some of these thickets were found in aspen stands and even in mature red pine stands and may be important to winter survival.

The scope and scale of survival analyses were limited due to low sample size, restricting capability and depth of analyses. Yet, no predation occurred in the Saddler group, with two of the three individuals surviving through the study period, and two individuals surviving over 500 days (Table 6). The Caberfae group was distinctly different, with all four individuals dying within 200 days of collaring. The two hares at the 25 Rd group were both lost to predation, yet both survived longer than all of the Caberfae individuals (Table 6). The snowshoe hares in the Saddler group, which had the highest average survival, experienced the greatest proportion of aspen stands, at over 50% of the surrounding forest. Red pine stands and red maple were the only other stand types present in all three groupings. Red maple was present in lower percentages than aspen, yet still correlated positively with survival across the three groups. The possibility of aspen to buffer snowshoe hare survival is consistent with other populations at the southern range boundary (Wilson et al. 2019). The majority of red pine stands in the area are greater than 50 years old, and lack influential understory .A potential reason for the lacking density of conifer stems is the large amount of mature red pine stands that comprise the majority of coniferous stands in the study area (USFS 2004). These same stands provided substantial snowshoe hare habitat 30-40 years ago when full of dense saplings, are no longer capable of supporting robust hare populations. More frequent management of red pine stands may also provide support for snowshoe hares, as management transitions some stands into young, dense stands full of coniferous saplings. Thinning mature red pine stands would allow openings in the canopy and release understory vegetation (Bender et al. 1997).

When sufficient dense understory is absent, snowshoe hares may find refuge in areas with dense coarse woody debris (hereafter CWD). Bull et al. (2005) indicated that snowshoe hares commonly use areas such as downed trees and limbs from thinning practices. This CWD can provide thermal cover in winter, cover from predation, and even some forage if leaves are still present. Anecdotally, I found hares resting under or near CWD at approximately 35% of the telemetry locations where I visually confirmed the hare. Increasing CWD may therefore increase the perceived dense understory required by snowshoe hares.

My data indicate that snowshoe hares are settling for lower-quality habitat due to a lack of coniferous refugia. As snowshoe hares continue to deal with climate change and increased predation pressure, year-round high-quality habitat will only increase in importance to prevent population declines and local extirpations. This creates a need for higher quality habitat and denser cover to allow hares to more effectively avoid predation during periods of mismatch.

Snowshoe hare populations need management of these habitats particularly at the southern reaches of their range as climate change progresses (Beaudoin et al. 2004).

Yet, aspen stands may not be the most effective habitat for snowshoe hares across the entire southern reach of its range. Regions of the Western US have an entirely different forest structure and vertebrate community. In Wyoming and Utah, snowshoe hares were associated with mid-successional to mature lodgepole pine forests, despite being at the south of their range (Wolfe et al. 1982, Koehler & Brittell 1990, Berg et al. 2012). Nonetheless, the scale of all of these studies, including ours, is extremely dependent on the habitat, available forest, and the vertebrate community. In the past, snowshoe hares in Michigan used lowland shrub, lowland hardwood, lowland conifer, bog, swamp, and mesic conifer stands, making up over half of the habitat types they utilized (Handler et al. 2014). However, lowland conifers have decreased in Michigan's Lower Peninsula to about 25% of their pre-settlement area, with similar decreases seen in other wetland types (Comer 1996; Leahy & Pregitzer 2003). These areas that were once a substantial portion of snowshoe hare habitat are now largely lost throughout the state, may be another key to aiding snowshoe hare populations in the coming decades.

More in-depth analyses are necessary to quantify specific stand age of aspen stands used by snowshoe hares. Snowshoe hares in this area are present in lower densities than at the core of their range and are thus not ideal for determining presence or population density via pellet transects or track surveys, which are common methods throughout their core range (Krebs et al. 1987, Burt et al. 2017). These methods when combined with live-trapping may provide additional opportunities to observe snowshoe hares in the Manistee National Forest and provide further insight to local populations. The results from this study suggest an importance of aspen stands for snowshoe hare habitat. However, the data do show that surrounding habitat may provide potential as a predictor for snowshoe hare survival in the Manistee National Forest. Future work should include intensive live-trapping and GPS-collaring of large sample of snowshoe hares to determine home range and complete habitat use.

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TABLES

Table 1. All variables measured via visual estimation immediately upon a radio telemetry event. Detailed with variables included in and excluded from PCA analysis (Figure 10) of environmental variables and snowshoe hare locations, including detailed collection methodology. Columns are detailed variable name (*Variable*), description of variable (*Description*), whether or not variable was included in PCA (*PCA*, "Yes" if included, "No" if excluded), label name for variable in PCA plot (*PCA Label;* N/A if excluded from PCA), and detailed description of collection/measurement methods (*Methodology*).

Variable	**Description**	**PCA**	**PCA Label in Figure 4**	**Methodology**
Percent Canopy Coniferous	Proportion of overhead canopy comprised of coniferous species	Yes	CanopyCon	Visually estimated by observer calculating species present
Percent Canopy Deciduous	Proportion of overhead canopy comprised of deciduous species	No	N/A	Visually estimated by observer calculating species present
Percent Canopy Cover	Proportion of coverage by overhead canopy	Yes	CanopyCover	Visually estimated by observer calculating percent canopy closure
Percent 3m Subcanopy Coniferous	Proportion of canopy at 3m height comprised of coniferous species	Yes	X3mCon	Visually estimated by observer calculating species present
Percent 3m Subcanopy Deciduous	Proportion of canopy at 3m height comprised of deciduous species	No	N/A	Visually estimated by observer calculating species present
Percent 3m Subcanopy Closure	Proportion of coverage by canopy at 3m height	No	N/A	Visually estimated by observer calculating percent of closure at 3m
Percent 1m Subcanopy Closure	Proportion of coverage by canopy at 1m height	Yes	X1mCover	Visually estimated by observer calculating percent of closure at 3m
Percent Understory Coniferous	Proportion of canopy at 1m height comprised of coniferous species	Yes	UnderCon	Visually estimated by observer calculating species present
Percent Understory Deciduous	Proportion of canopy at 1m height comprised of deciduous species	Yes	UnderDecid	Visually estimated by observer calculating species present
Percent Aspen	Proportion of all trees in the area comprised of Aspen trees	Yes	PerAspen	Visually estimated by observer calculating species present
Percent Red Pine	Proportion of all trees in the area comprised of Red Pine trees	Yes	PerRedPine	Visually estimated by observer calculating species present
Percent Other Coniferous	Proportion of all trees in the area comprised of coniferous trees excluding Red Pine	Yes	PerOthCon	Visually estimated by observer calculating species present
Percent Other Deciduous	Proportion of all trees in the area comprised of deciduous trees excluding Aspen	Yes	PerOthDecid	Visually estimated by observer calculating species present

Forest Type	General forest stand type	No	N/A	Visualized at hare location and surrounding forest
Hare Visual	Whether or not the hare location was visually confirmed	Yes	Circles = No Visual; Triangles = Yes Visual	Recorded if snowshoe hare was seen, or if tracking was aborted due to chase
Snowpack	Amount of snow present on the ground	No	N/A	Measured in cm
Leaf Presence	Whether deciduous trees nearby had leaves still attached	Yes	Filled shapes = Leaf On; Empty shapes = Leaf Off	Visually seen

Table 2. Medians and standard deviations of all measured vegetation characteristics for snowshoe hare locations, random forest sites, and random aspen stands.

	Overhead Cover	**0.5m Horizontal Cover**	**1m Horizontal Cover**	**Conifer Stems**	**Deciduous Stems**	**Snags**	**Total Stems**
Hare Locations	75 ± 23.43	50 ± 26.87	50 ± 26.40	0 ± 0.90	11 ± 8.36	1 ± 1.47	12 ± 8.23
Forest	50 ± 26.75	50 ± 27.40	25 ± 23.15	0 ± 0.98	1 ± 3.15	0 ± 1.18	3 ± 3.30
Aspen	75 ± 22.48	50 ± 26.24	25 ± 29.21	0 ± 0.51	3 ± 4.83	0 ± 0.93	4 ± 5.25

Table 3. P-values and effect sizes for Mann-Whitney tests between **(A)** snowshoe hare locations and random forest sites, **(B)** snowshoe hare locations and random aspen stands, and **(C)** random aspen stands and random forest sites. I tested each group for differences in the medians, whether the test group is greater than the control group, and whether the test group is less than the control group. P-values below 0.05 indicate significance if effect size is *greater than 0.3**, and an additionally large difference if effect size is ***greater than 0.5*****.

A	Hares ≠ Forest (p-value)	Hares > Forest (p-value)	Hares < Forest (p-value)	Effect Size
Overhead Cover	***8.91e^{-5**}***	***4.45e^{-5**}***	1	**0.65**
0.5m Horizontal Cover	***2.71e^{-5**}***	***1.36e^{-5**}***	1	**0.70**
1m Horizontal Cover	***8.07e^{-13**}***	***4.03e^{-13**}***	1	**1.16**
Conifer Stems	2.02^{e-3}	0.99	1.01e^{-3}	-0.18
Deciduous Stems	***3.77^{e-16**}***	***2.20e^{-16**}***	1	**1.12**
Snags	*1.25e^{-3*}*	*6.25e^{-4*}*	0.99	*0.42*
Total Stems	***2.20e^{-16**}***	***2.20e^{-16**}***	1	**1.16**
B	Hares ≠ Aspen (p-value)	Hares > Aspen (p-value)	Hares < Aspen (p-value)	Effect Size
Overhead Cover	0.16	0.08	0.92	0.21
0.5m Horizontal Cover	0.65	0.33	0.67	0.06
1m Horizontal Cover	***8.67e^{-6**}***	***4.33e^{-6**}***	1	**0.74**
Conifer Stems	0.19	0.10	0.90	-0.05
Deciduous Stems	***4.89e^{-9**}***	***2.44e^{-9**}***	1	**0.85**
Snags	*1.46e^{-3*}*	*7.28e^{-4*}*	0.99	*0.48*
Total Stems	***2.79e^{-11**}***	***1.40e^{-11**}***	1	**0.91**
C	Aspen ≠ Forest (p-value)	Aspen > Forest (p-value)	Aspen < Forest (p-value)	Effect Size
Overhead Cover	*0.02**	*0.01**	0.99	*0.46*
0.5m Horizontal Cover	***1.95e^{-3**}***	***9.75e^{-4**}***	0.99	**0.64**
1m Horizontal Cover	*0.02**	*0.01**	0.99	*0.48*
Conifer Stems	7.07e^{-4}	0.99	3.53e^{-4}	-0.07
Deciduous Stems	***2.12e^{-3**}***	***1.06e^{-3**}***	0.99	**0.58**
Snags	0.96	0.48	0.52	-0.06
Total Stems	0.07	*0.03**	0.96	*0.48*

Table 4. Mean, standard deviation, and median (MEAN ± 1 SD [MEDIAN]) of canopy and subcanopy closure variables for recorded locations of snowshoe hares, separated by leaf-off and leaf-on periods.

	Canopy Cover	3m Cover	1m Cover
Year-Round	77.83 ± 15.74 [80]	71.38 ± 18.39 [75]	76.73 ± 56.12 [80]
Leaf Off	77.44 ± 16.54 [80]	72.64 ± 16.49 [72.5]	68.51 ± 17.67 [72.5]*
Leaf On	78.19 ± 15.06 [85]	70.34 ± 19.87 [75]	83.56 ± 73.72 [80]*

** represents significance between groups marked with the same symbol (Mann-Whitney test, P=0.007312)*

Table 5. Mean, standard deviation, and median (Median ± 1 SD [MEDIAN]) of visual estimation forest composition variables for recorded locations of snowshoe hares, separated by leaf-off and leaf-on periods.

	Canopy Conifer	Canopy Deciduous	Percent Aspen	Percent Red Pine	Percent Other Conifer	Percent Other Deciduous
Year-Round	27.03 ± 25.28 [20]	72.60 ± 25.20 [80]	38.66 ± 24.97 [40]	16.75 ± 24.78 [5]	11.25 ± 16.50 [5]	32.91 ± 21.49 [30]
Leaf Off	36.01 ± 27.67 [30]*	63.99 ± 27.67 [70]	37.53 ± 24.82 [40]	20.70 ± 28.00 [5]	13.25 ± 17.72 [2.5]	28.01 ± 21.07 [37.5]
Leaf On	18.83 ± 19.71 [15]*	80.47 ± 19.80 [85]	40.52 ± 21.74 [40]	10.25 ± 16.62 [5]	7.96 ± 13.83 [10]	40.90 ± 19.87 [25]

** represents significance between groups marked with the same symbol (Mann-Whitney test, P<0.001)*

Table 6. Fate and survival of radio-collared snowshoe hares in the Manistee National Forest from August 2017 through May 2019. Snowshoe for this study fell within four main grouping areas. Individuals lost to hunter harvest were not included in analyses. M or F in the *HareID* column indicates sex of the individual as male or female, respectively.

Hare ID	Fate	Survival (days)	Group
180M	Survived through study period	>595	Saddler
423F	Natural Causes	538	
306F	Survived through study period	>92	
222M	Predation	144	Caberfae
513M	Predation	197	
674F	Unknown	156	
001M	Climate mortality	28	
561M	Predation	334	25 Rd
782F	Predation	222	
288M	Hunter harvest	45	Stoddard

FIGURE LEGENDS

Figure 1. Hare locations within the Manistee National Forest in Michigan. Green stars represent hare locations, and a black line depicts the border of the Manistee National Forest. Snowshoe hares were radio-collared and monitored at their respective locations from August 2017 until March 2019.

Figure 2. Map of the study area within the Manistee National Forest in Michigan's Lower Peninsula. The black line depicts the border of the Manistee National Forest, and the excerpt details the locations of the three distinct snowshoe hare groupings used in survival comparisons.

Figure 3. Diagram detailing the vegetation sampling method for snowshoe hare locations and randomly sampled locations. Vegetation characteristics were sampled in June 2019 using a moosehorn densitometer, three 1-meter PVC poles, and a 4-meter chain to measure horizontal cover at 0.5-meter and 1-meter, overhead cover, and deciduous, conifer, and snag stem counts.

Figure 4. Principal component analysis of all snowshoe hare locations, random forest sites, and random aspen stands. Vectors represent vegetation characteristics, while points indicate sample sites. This figure explains approximately 69.03% of the variation in the data (Scaling=2; *PC1=0.4095, PC2=0.2808*).

Figure 5. Principal component analysis of random forest sites and random aspen stands. Vectors represent vegetation characteristics, while points indicate sample sites. This figure explains approximately 52.98% of the variation in the data represented on the plot (Scaling=2; *PC1=0.3264, PC2=0.2034*).

Figure 6. Principal component analysis of all sampled snowshoe hare locations. Vectors represent vegetation characteristics, while points indicate snowshoe hare locations. This figure explains approximately 50.34% of the variation in the data (Scaling=2, *PC1=0.2938, PC2=0.2096*).

Figure 7. Box-plots of *(a)* 0.5-meter horizontal cover, *(b)* 1-meter horizontal cover, *(c)* overhead cover, and *(d)* total stems for snowshoe hare locations, randomly forest sites, and random aspen stands. Boxes represent the inter-quartile ranges and medians of the data. Bars indicate the range of the data, and points represent extremes.

Figure 8. Principal component analysis of leaf-on and leaf-off use by snowshoe hares. Vectors represent vegetation characteristics, while points indicate snowshoe hare locations. This figure explains 66.69& of the variation in the data (Scaling=2; *PC1=0.3706, PC2=0.2963*).

Figure 9. Boxplot of Mann-Whitney U test comparing number of total stems in leaf-on hare locations to leaf-off hare locations. Leaf-on locations had significantly greater total stems than leaf-off locations ($p=1.48e^{-3}$). Boxes represent the inter-quartile ranges and medians of the data, bars indicate the range, and points represent extremes.

Figure 10. Principal component analyses of 118 snowshoe hare locations and associated vegetative characteristics (Scaling = 2; *PC1=0.4468*, *PC2=0.2562*). Each shape represents a recorded location, with filled shapes recorded during leaf-on period and unfilled shapes recorded during leaf-off. Triangles represent records with confirmed visual observation of the hare, whereas circles represent records I did not visually observe the hare. Arrows indicate strength of specific variables on the variation among sites.

Figure 11. Boxplots of Mann-Whitney tests between leaf-off and leaf-on groups for (A) percent aspen, (B) percent red pine, (C) percent coniferous, and (D) percent 1m closure. Dark bars indicate median values, boxes extend to inter-quartile range, and bars represent extremes of data. Circles represent outliers. Significant differences are present in 5C and 5D ($p<0.001$), but not 5A and 5B.

Figure 12. Proportions of vegetation stands in the three main snowshoe hare groupings studied from August 2017-May 2019.

FIGURES

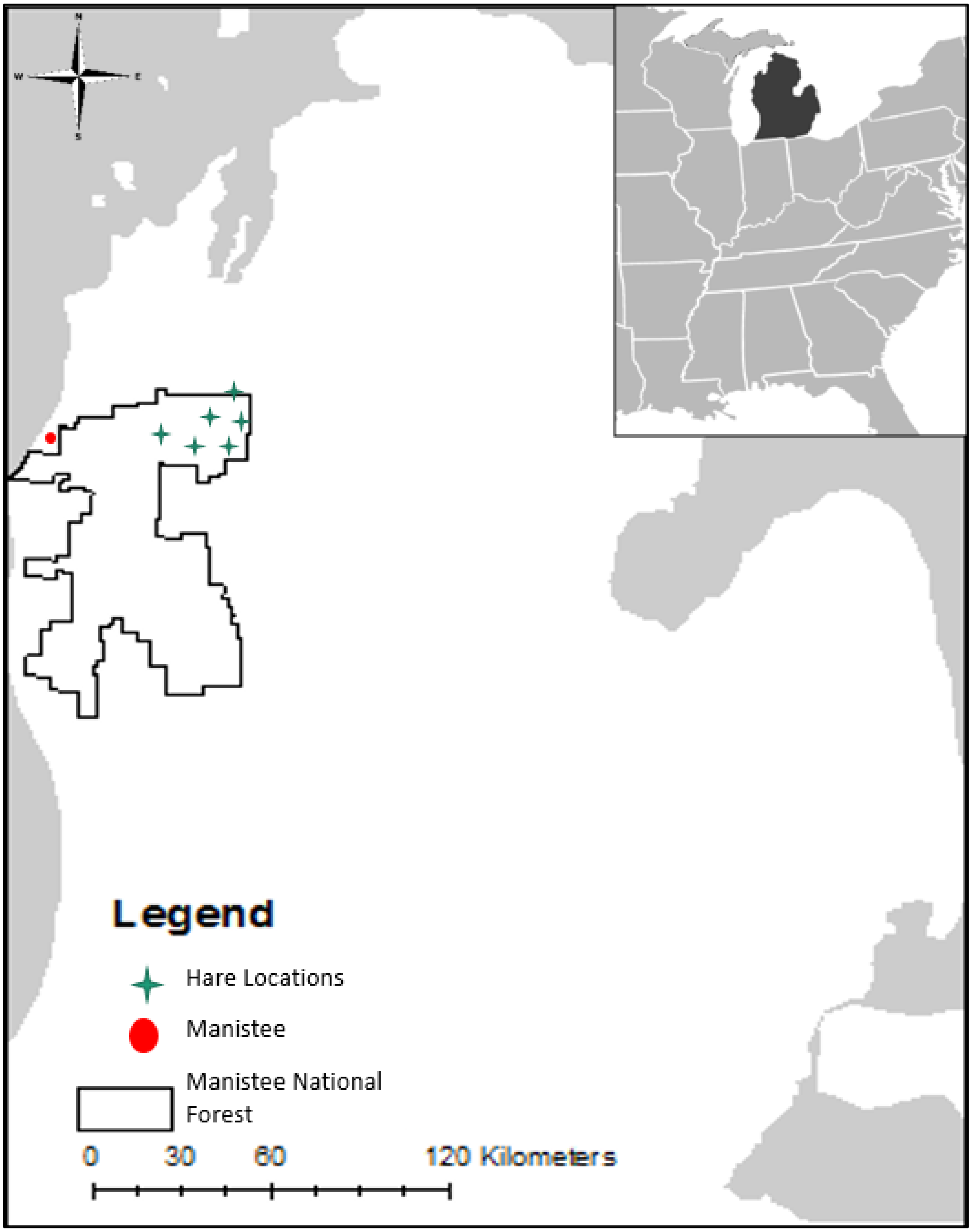

Figure 1.

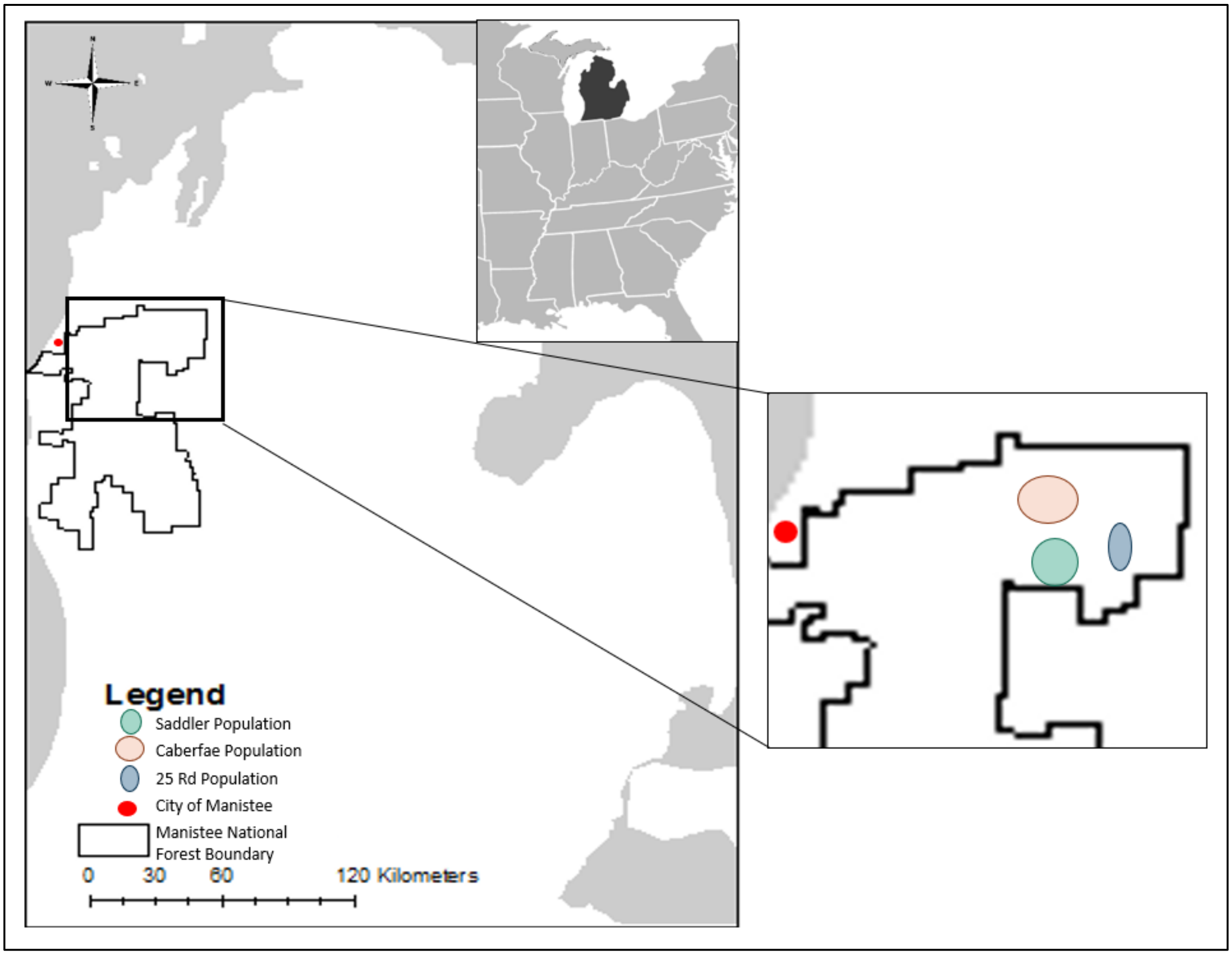
Legend
Saddler Population
Caberfae Population
25 Rd Population
City of Manistee
Manistee National
Forest Boundary
0
30
60
120 Kilometers

Figure 2.

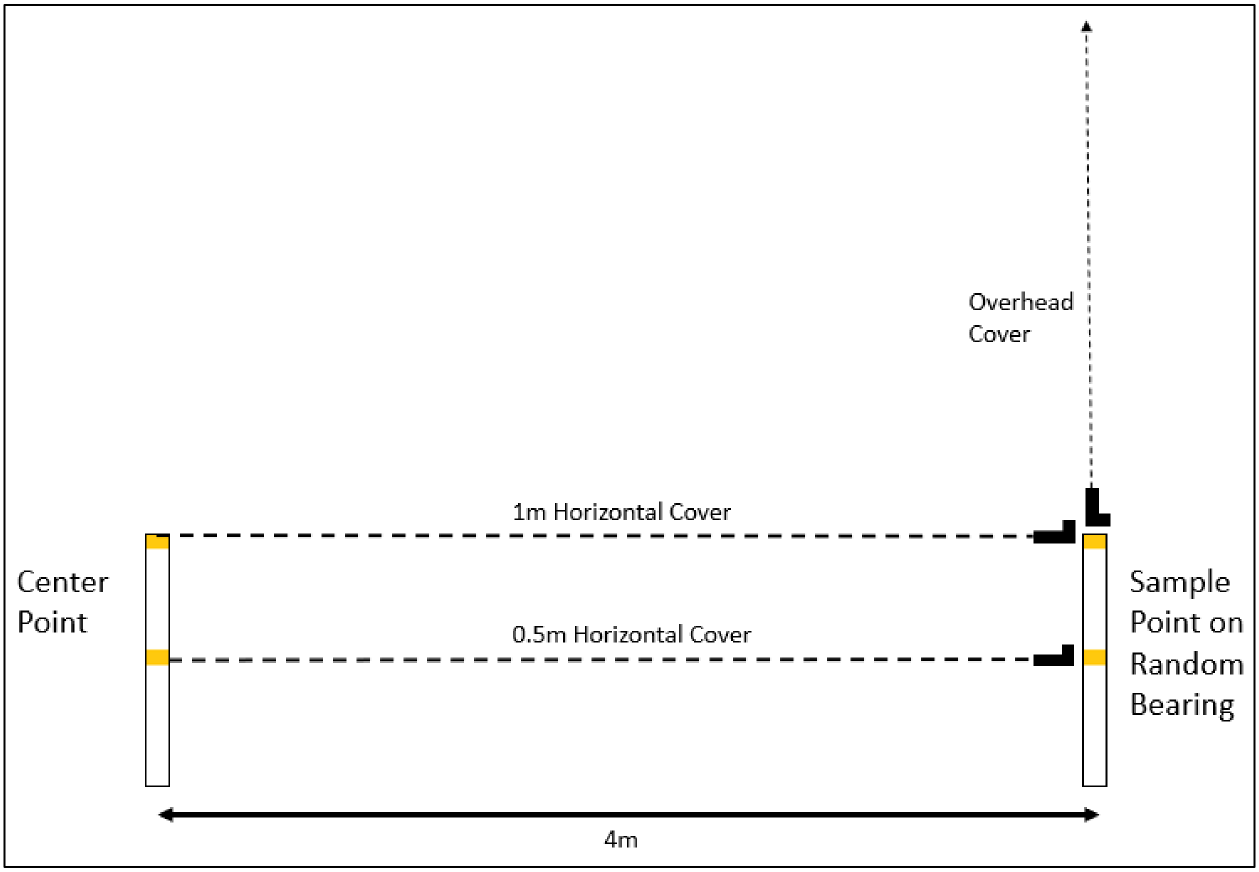
Overhead
Cover
1m Horizontal Cover
Center
Point
0.5m Horizontal Cover
Sample
Point on
Random
Bearing
4m

Figure 3.

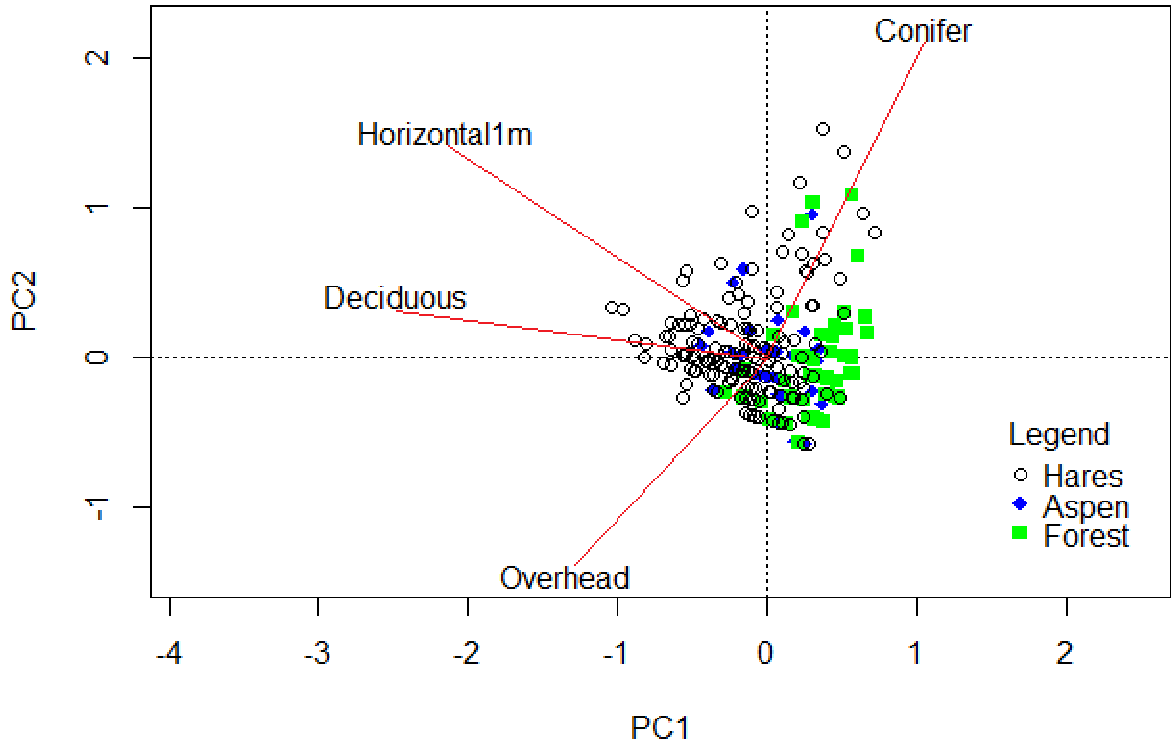
Conifer
Horizontal1m
Deciduous
Overhead
Legend
Hares
Aspen
Forest
PC2
PC1
2
1
0
-1
-4
-3
-2
-1
0
1
2

Figure 4.

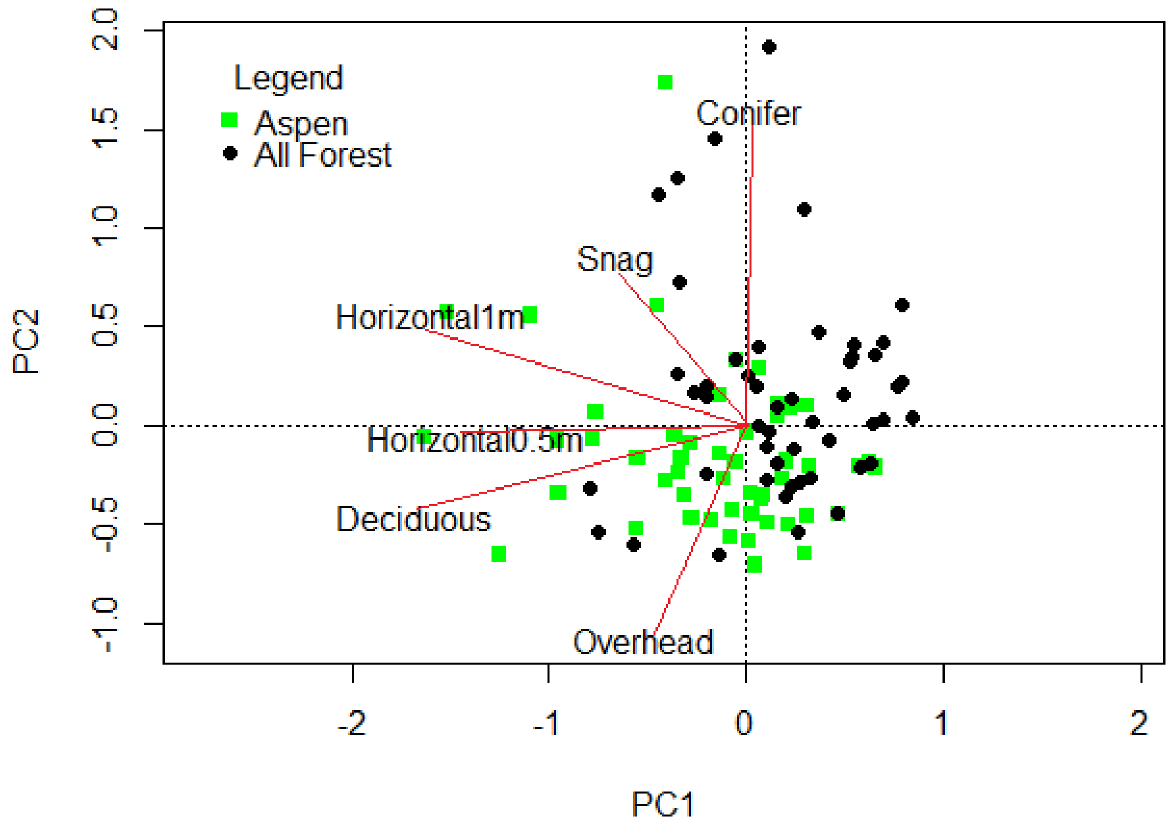
Legend
Aspen
All Forest
Conifer
Snag
Horizontal1m
Horizontal0.5m
Deciduous
Overhead
PC2
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-2
-1
0
1
2
PC1

Figure 5.

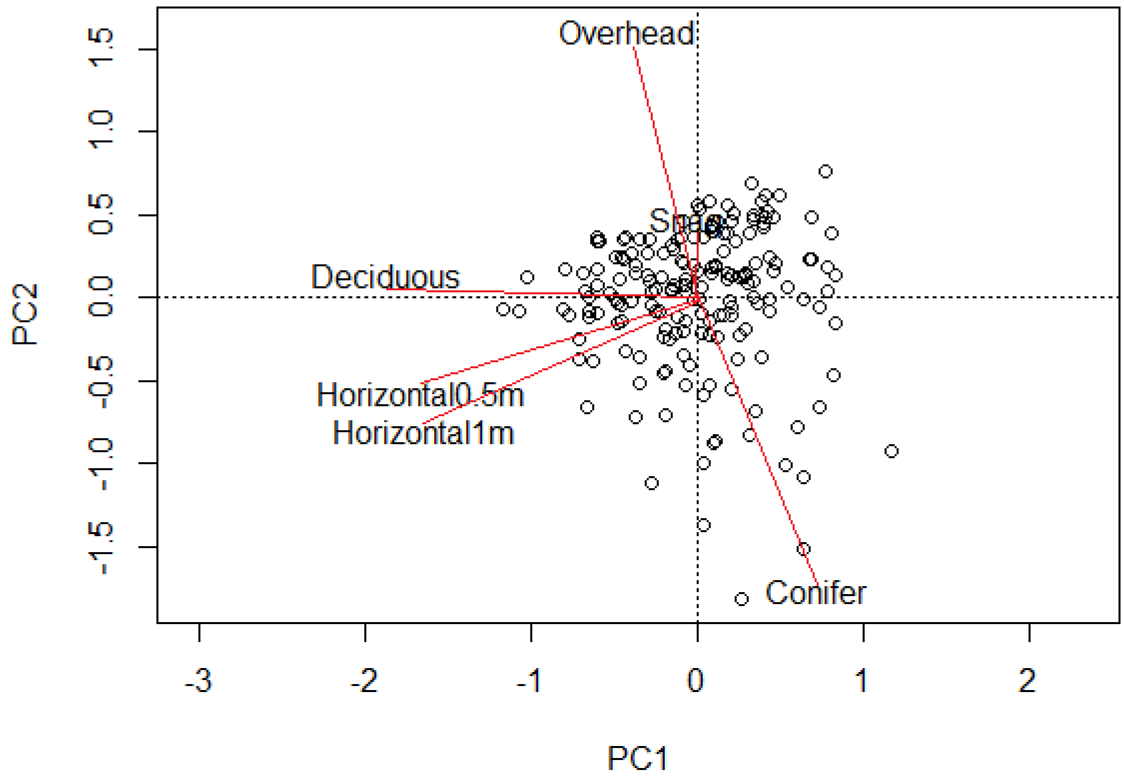
Overhead
Snag
Deciduous
Horizontal0.5m
Horizontal1m
Conifer
PC2
PC1
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-3
-2
-1
0
1
2

Figure 6.

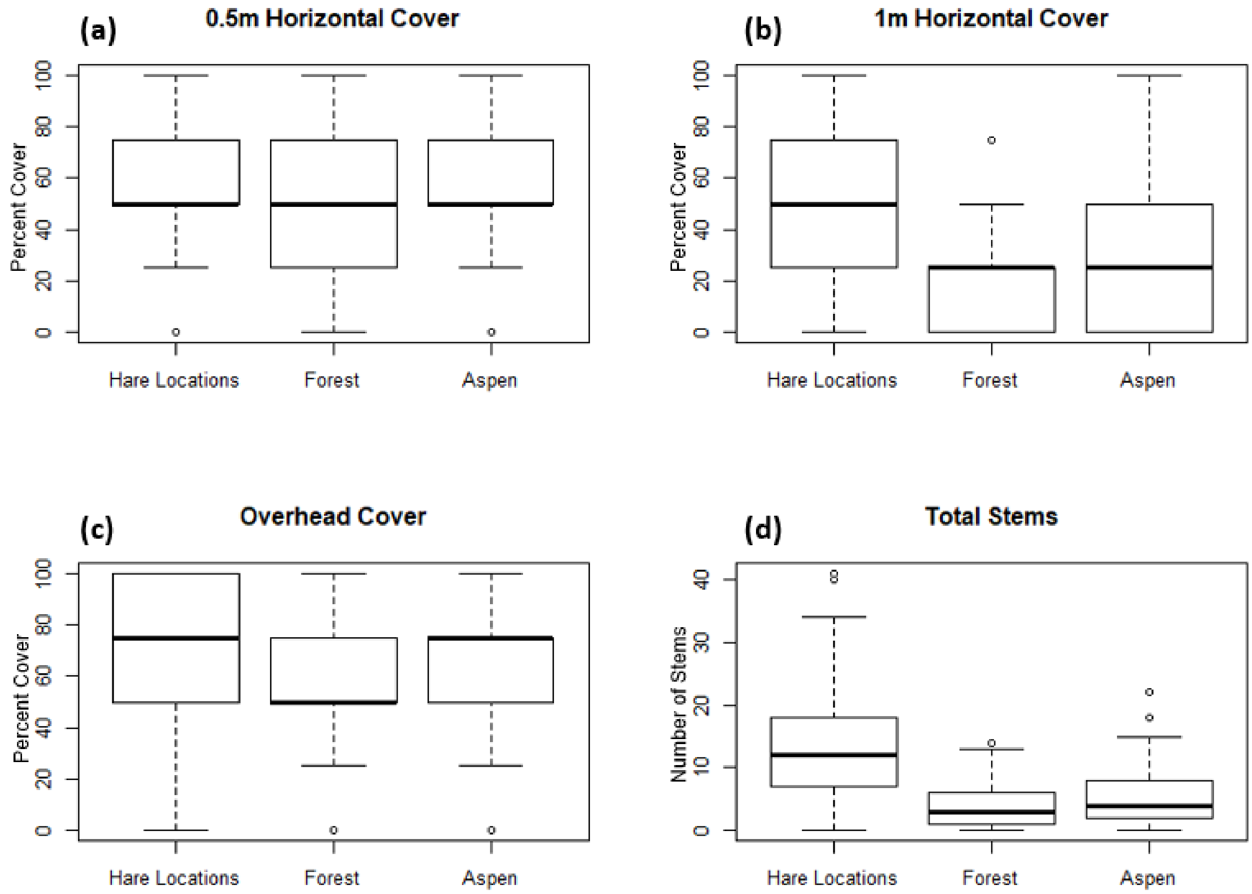
(a)
0.5m Horizontal Cover
Percent Cover
0
20
40
60
80
100
Hare Locations
Forest
Aspen
(b)
1m Horizontal Cover
Percent Cover
0
20
40
60
80
100
Hare Locations
Forest
Aspen
(c)
Overhead Cover
Percent Cover
0
20
40
60
80
100
Hare Locations
Forest
Aspen
(d)
Total Stems
Number of Stems
0
10
20
30
40
Hare Locations
Forest
Aspen

Figure 7.

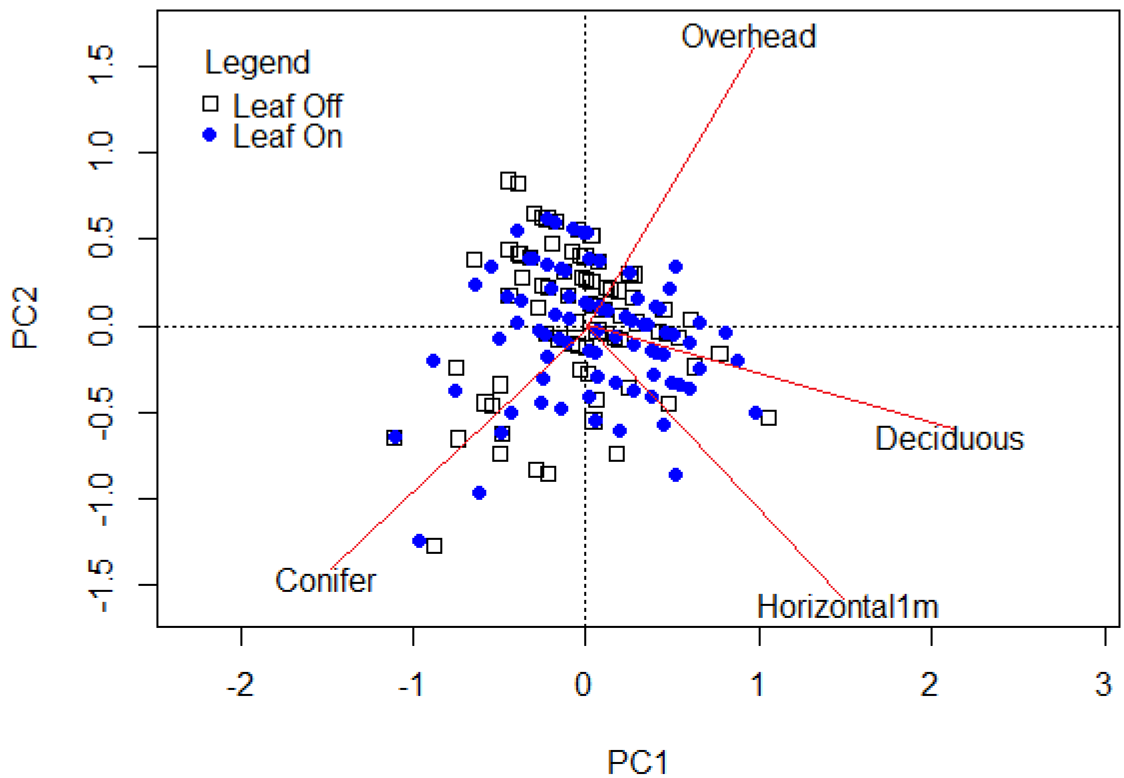
Legend
Leaf Off
Leaf On
Overhead
Deciduous
Conifer
Horizontal1m
PC2
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2
-1
0
1
2
3
PC1

Figure 8.

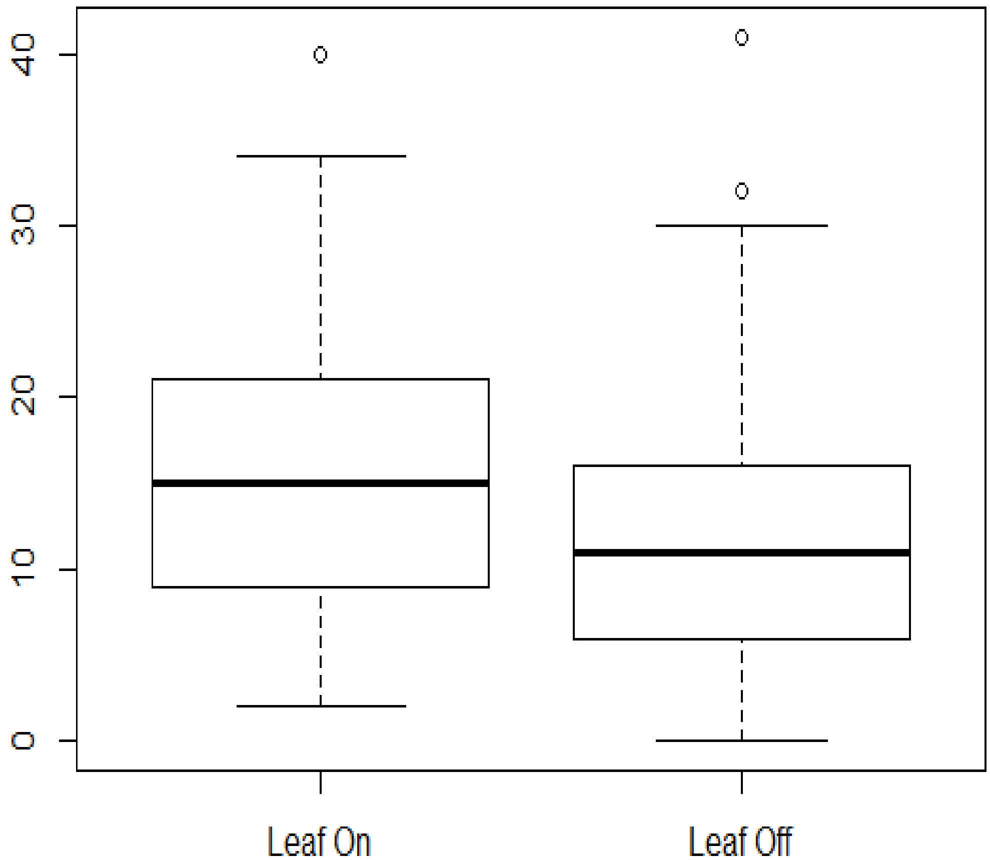

Figure 9.

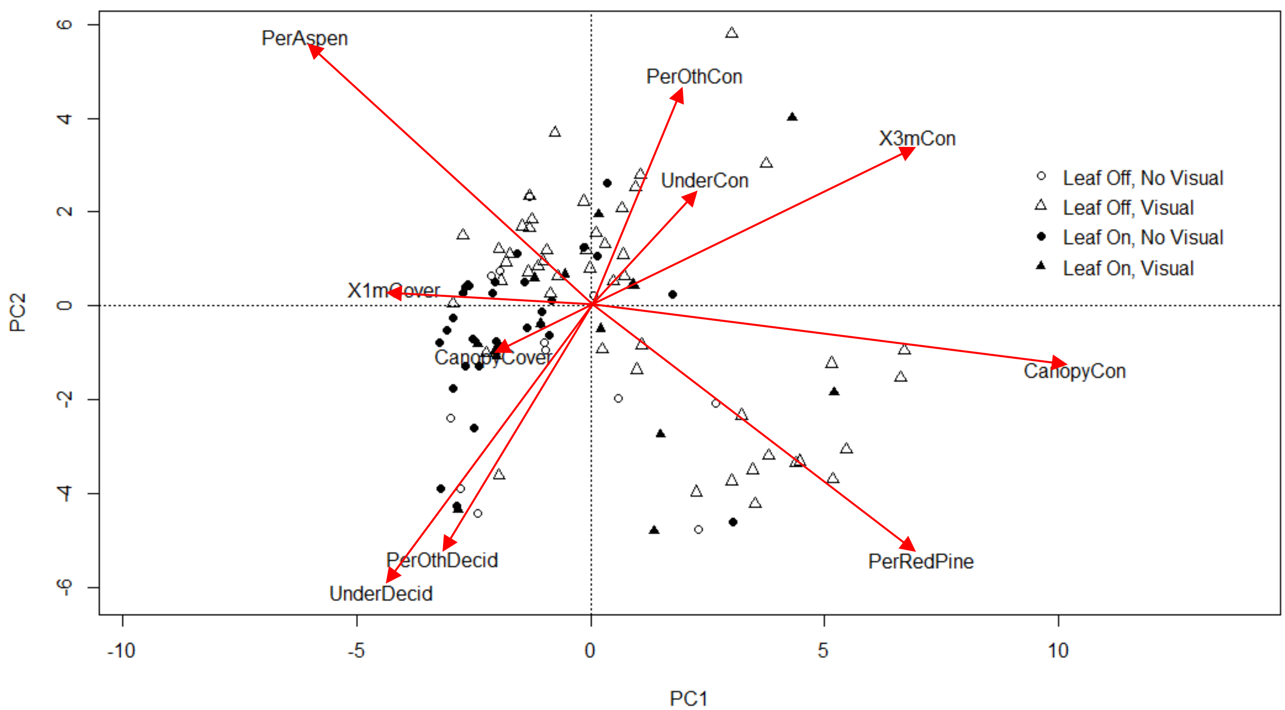
PerAspen
PerOthCon
X3mCon
UnderCon
X1mCover
CanopyCover
CanopyCon
PerOthDecid
UnderDecid
PerRedPine
Leaf Off, No Visual
Leaf Off, Visual
Leaf On, No Visual
Leaf On, Visual
PC1
PC2
-10
-5
0
5
10
6
4
2
0
-2
-4
-6

Figure 10.

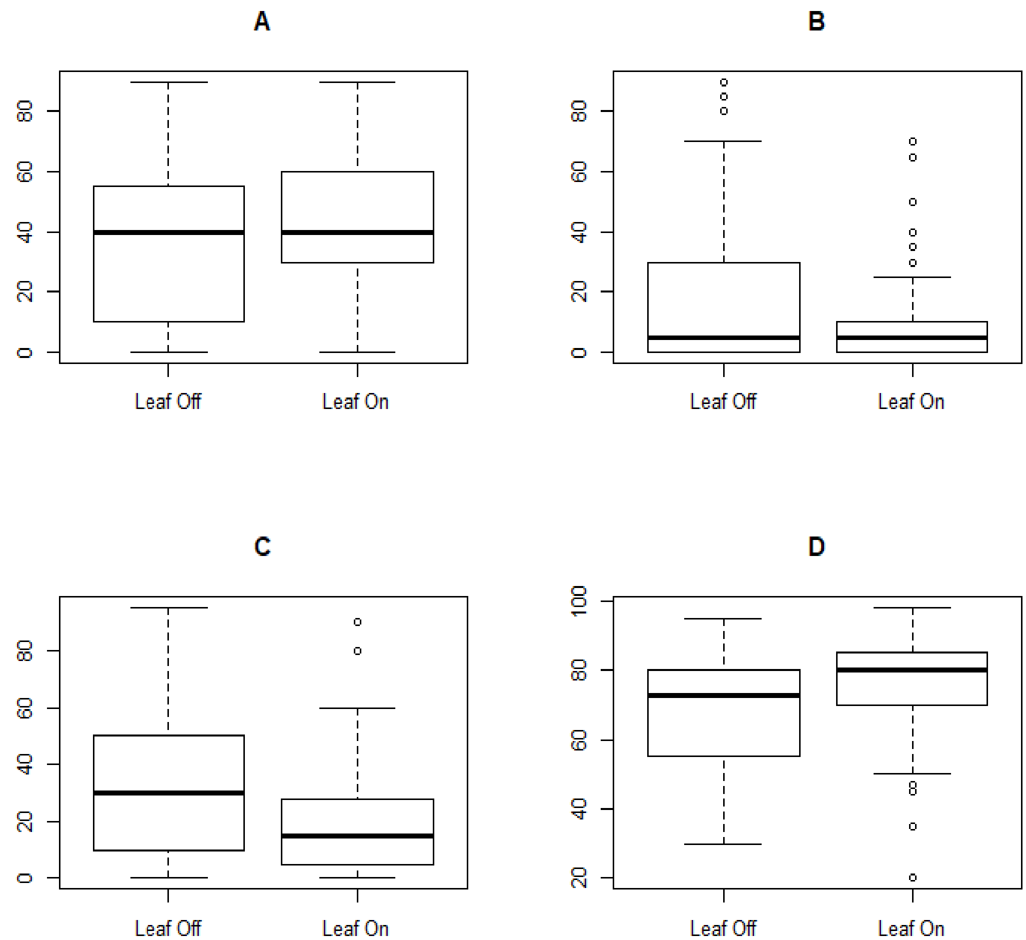

Figure 11.

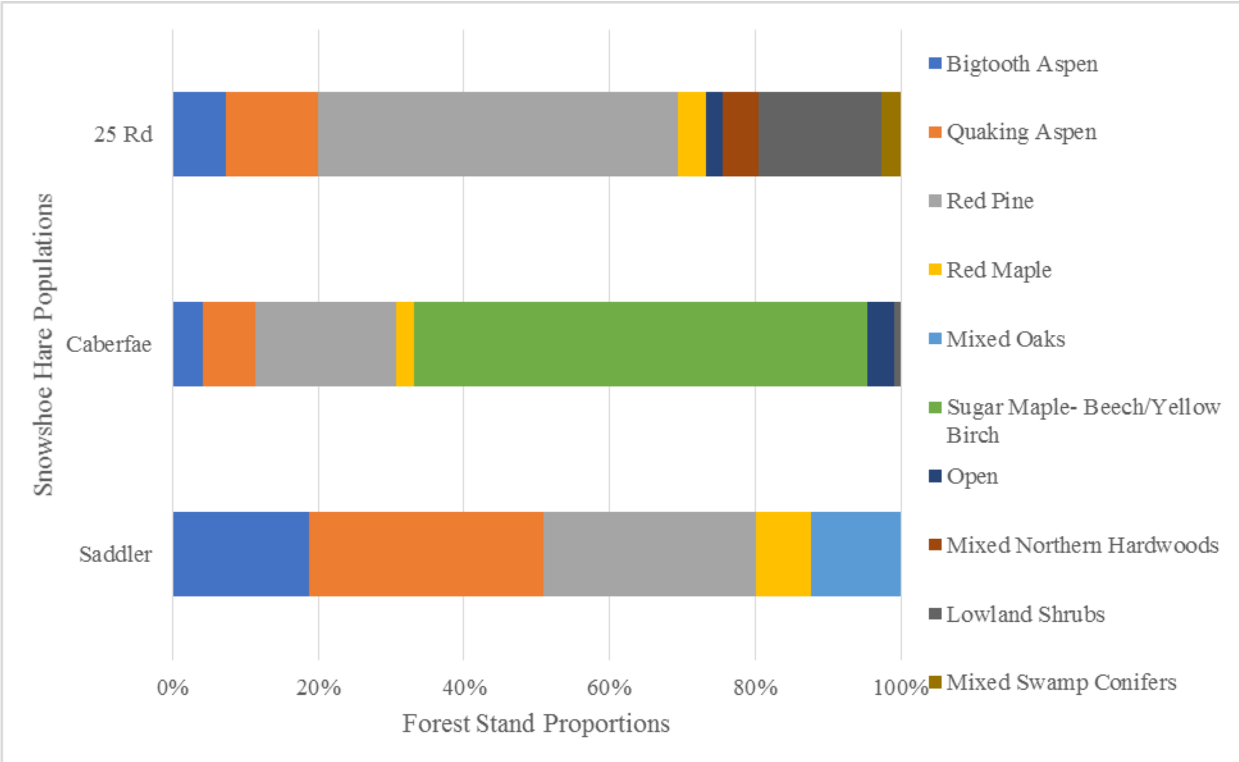
25 Rd
Caberfae
Saddler
Snowshoe Hare Populations
0%
20%
40%
60%
80%
100%
Forest Stand Proportions
Bigtooth Aspen
Quaking Aspen
Red Pine
Red Maple
Mixed Oaks
Sugar Maple- Beech/Yellow Birch
Open
Mixed Northern Hardwoods
Lowland Shrubs
Mixed Swamp Conifers

Figure 12.

CHAPTER III – Management Recommendations for the Persistence and Proliferation of Snowshoe Hares in the Manistee National Forest

This thesis presents novel documentation on the under-studied snowshoe hares in the Manistee National Forest in Northern Lower Michigan. Habitat use by snowshoe hares in the Manistee National Forest is largely lacking of substantial research. Snowshoe hares in the Manistee National Forest appear to select strongly for aspen stands, a trend that was common throughout the course of this study. We trapped all hares within or near regenerating aspen stands, and found to use these types of habitat regularly (Figure IV-2). Hares in the Manistee National Forest were able to find areas of higher understory density than the surrounding available forest, yet were not selecting for habitat with greater coniferous component (Chapter II). Instead, snowshoe hares more commonly in areas with a greater number of deciduous stems. In general, aspen stands were host to higher understory density and stem counts than random forest sites (Figure II-4 & Figure II-6). Snowshoe hare locations exhibited stem counts and understory density even greater than aspen stands.

Therefore, snowshoe hares are potentially selecting for a particular cohort of aspen stands, specifically regenerating aspen. Regenerating aspen is especially of note as it can provide habitat for other local game species (Palmer, 1956). Other studies have found snowshoe hares to utilize aspen stands at their southern range boundary, especially 5-20 years after disturbance (Wilson et al. 2019, Wirsing et al. 2002). There are several mature aspen stands throughout the Manistee National Forest that no longer exhibit high understory density and therefore do not provide quality snowshoe hare habitat. Managing these aspen stands more frequently by way of periodic clear-cuts can increase available habitat for snowshoe hares. A more intense rotation of aspen management can increase snowshoe hare habitat, potentially increasing their population densities and allowing them to persist further south, maintaining stable populations for local hunting. The increased regenerating aspen stands would also provide habitat for more game species and wildlife that utilize early successional forest. While reintroduction of apex predators in Michigan's Lower Peninsula is unlikely, managers should also consider strategies that may reduce white-tailed deer or alter harvest goals to curtail deer densities.

A significant finding of Chapter II was the lack of dense coniferous understory in the Manistee National Forest. Unless agencies reintroduce gray wolves, or white-tailed deer harvest numbers are dramatically increased this absence of conifer understory is unlikely to change in the near future. High densities of white-tailed deer are able to immediately outcompete snowshoe hares for optimal coniferous forage in the understory. Not only are the deer reducing available forage for snowshoe hares, but by eliminating understory coniferous stems they are drastically reducing available cover for snowshoe hares. Therefore, it may not be plausible for managers to attempt to increase the amount of available coniferous understory.

If snowshoe hares are heavily using deciduous stands, particularly regenerating aspen, they may be increasingly vulnerable during the winter months, when the deciduous trees shed their leaves. A potential solution would be to maintain areas of beech thickets near or within regenerating aspen stands. As a southern-adapted tree species, American beech saplings hold onto their leaves through most of the winter, sometimes not dropping their leaves until the new buds poke through. Providing occasional beech thickets can enhance available cover for snowshoe hares during the otherwise leaf-off period.

Not only was aspen found to provide habitat with higher understory density and stem counts than random forest, but snowshoe hares actually had higher survival when surrounding habitat contained greater proportions of aspen stands. Increasing the amount of aspen on the landscape, or preventing it from succeeding out, can potentially buffer snowshoe hare survival in the Manistee National Forest. Within aspen stands there is room for variation in management types. Snowshoe hares are likely to continue using aging aspen stands if a managers maintain a dense understory underneath the canopy. Seeding maple trees to grow in the shade of the aspen trees and will temporarily keep the stem density at an appropriate level for snowshoe hare use. By managing more areas for aspen, forest managers can maintain or increase forest production levels while also providing more high-quality habitat for snowshoe hares and other wildlife species.

CHAPTER IV

EXTENDED LITERATURE REVIEW

Climate Change

In the past several years, climate change has had extensive effects on weather cycles and patterns and projections predict impacts to worsen in coming years (Meehl et al. 2007). Changing climate has caused more extreme heat events and more sporadic winters in the Midwestern United States, also impacting precipitation events (Luber & McGeehin 2008). Climate change is increasing minimum air temperature and precipitation, but decreasing snow water equivalent, with more drastic effects in the Midwest and its four varying seasons, especially autumn and spring (Mishra et al. 2010). This will result in higher summer temperatures and decreased snowfall during late fall, early winter, late winter, and early spring. Projections show that snowfall is likely to decrease in future years in the northern Midwest as warmer winter air temper will reduce lake effect snows (Wuebbles & Hayhoe 2004).

In Michigan, lake effect snow makes up a large proportion of annual snowfall, thus being very important to the ecosystem in the region (Zhao et al. 2012). While Michigan does receive snowfall that is not from lake effect snow of the Great Lakes, several major Lake Michigan lake effect snow events account for the majority of annual snowfall in Michigan's lower peninsula. (Hjelmfelt & Braham 1983). In Michigan, lake effect snow is a dominant factor in the control and distribution of mesic forests (Henne et al. 2007). With lake-effect snow being extremely sensitive to ice cover on the lakes and temperature in the Great Lakes region, the impacts of climate change in Michigan are drastically increased (Wright et al. 2012). With less lake effect snow projected as climate change continues, Michigan is likely to lose a large portion of its mesic forests (Brandt et al. 2016). Not only will Michigan lose its mesic forests, the entire region will be more vulnerable, changing the structure and land cover significantly and effectively altering species' ability to exist in the changing ecosystems (Williams & Dumroese 2013).

With climate change not only impacting temperature, weather, and precipitation, but also land cover and forest structure, it threatens to have devastating impacts on wildlife and has already resulted in range shifts of several terrestrial vertebrates (Chen et al. 2011). Some species have been shifting their ranges, with the only other outcomes being adaptation and extirpation/extinction, which can depend on numerous factors (Tacoli 2009). The changes brought about by climate are forcing some species' ranges to contract to higher elevations and other species to shift poleward (Davis & Shaw 2001). Warming temperatures are causing poleward range contractions in several species that have certain temperature and weather restrictions in their natural history (Hellmann et al. 2010). Vertebrates in the northern hemisphere are experiencing northward range contractions, as areas in the southern parts of their historical range are becoming unfit for the species (Hitch & Leberg 2007).

Other than causing range shifts and contractions, climate change is also creating isolation for wildlife species in areas where they once had vast, uninterrupted populations (Heller & Zavaleta 2009). Because of changing temperature and precipitation cycles, trees and other plants are having difficulty adapting to suddenly unstable ecosystems, making habitat stands more fragmented and thus isolating wildlife populations (Krebs & Berteaux 2006). Gilg et al. (2009) indicate that climate also affects most predator-prey cycles, which creates another pathway through which climate change has been affecting the range, distribution, and abundance of wildlife (Gilman et al. 2010). Several species are more vulnerable to climate change, making their management of high importance in future years (Mawdsley et al. 2009).

Snowshoe Hares

Due to many features of their biology and natural history, Snowshoe Hares (*Lepus americanus*) at the southern reaches of their range are highly vulnerable to the effects of climate change (Kielland et al. 2010; Diefenbach et al. 2016). Snowshoe hares live mostly in boreal forests with thick, brushy undergrowth and some deciduous forests (Maser et al. 1981). They typically range between 40 and 52 cm long, and 0.75-2.00 kg and have hind legs and ears with black tufts than rabbits (O'Donoghue 1994). The hairs undergo a change of pelage every winter, switching from a light brown to snow-white and then back to brown again in the spring (Merilaita & Lind 2005). Snowshoe hares are fast to avoid predators, making them agile while feeding on shrubs, grasses, trees, and other plants (Murray et al. 2002).

Snowshoe hares have historically inhabited most of the northern continental United States such as Michigan, Colorado, Virginia, and Iowa, and as far north as northern Canada (Wirsing et al. 2002; Murray 2000). Commonly known through the predator-prey cycle of snowshoe hares and Canadian lynx (*Lynx canadensis*), the abundance and distribution of snowshoe hares in their southern range is far more complicated than the cycling populations in core range (Wirsing et al. 2002). While the hares are able to move throughout large expanses of high-quality habitat in the core of their range, they settle in stands of less-favorable habitat in southern portions of their range (Feierabend & Kielland, 2014). Diefenbach et al. (2016) showed ranges of snowshoe hares are indeed contracting further north in Pennsylvania, a southern part of their range. While climate can explain hare locations, occurrence of hares is more dependent on suitable habitat (Diefenbach et al. 2016), which is impacted by climate fluctuations (Stenseth et al. 2002). In the limited and fragmented habitat at the southern reaches of snowshoe hare range, stands of suitable habitat are more favorable when surrounded with mostly dense stands and fewer open-structured areas within 300 meters (Lewis et al. 2011), indicating that increased fragmentation negatively affects hare abundance.

Factors Impacting Snowshoe Hare Distribution

Forest management has been a common practice in Michigan since early settlement, and continues to affect the wildlife and land use (Heinen & Currey 2000). While snowshoe hares are unlikely to use stands for the first 15 years after a clear-cut or even mature forests, they frequently occur in stands 20-30 years after a clear-cut (Newbury & Simon 2005), but not after management practices using fire (Allard-Duchêne et al. 2014). Hares will sometimes use residual forest left behind after clearcutting due to the high stem and browse density which offers plentiful forage (St-Laurent et al. 2008). Due to the effects of fragmentation, forest management has several impacts on snowshoe hare abundance and distribution (Cheng et al. 2014).

The changes in snowfall due to climate change impact snowshoe hares by accentuating the problem of camouflage mismatch, an instance when hares are in their snow-white winter pelage in early spring although the snow is already melted, presenting a stark contrast (Mills et al. 2013). This mismatch may make hares more vulnerable to predation and increase mortality rates (Griffin et al. 2005). While camouflage mismatch is as a possible cause in increased predation on hares, it is not certain whether or not the mismatch is contributing to population decline. Snowshoe hares do not display phenotypic plasticity for adapting color morphs to warmer spring weather due to low genetic variation (Zimova et al. 2014). Even if camouflage mismatch does not currently factor into decreasing hare abundance, it will certainly have compounding impacts as climate change impacts snowfall and weather in Michigan (Thomas 2010).

In core snowshoe hare range, Schmitz et al. (2003) showed that climate change is already affecting predation rates on hares. Without wolves in Michigan's Lower Peninsula a mesopredator release has resulted in more mid-size carnivores such as coyotes and foxes, which prefer to prey on hares (Ripple et al. 2013). In areas of higher predation risk, snowshoe hares are likely to select habitat based on cover and show a definitive difference in habitat selection between perceived low-risk and high-risk areas (Beaudoin et al. 2004). If hares are selecting habitat based on predation risk, it will require specialized management for predator species to be included in hare management, especially as climate change proceeds (Groves et al. 2012).

Snowshoe Hare Management and Considerations

Forest structure plays an important role in snowshoe hare habitat selection as there typically is not a single stand that meets all of the population's needs; rather, they typically use separate smaller stands within a habitat for varying purposes (Fuller & Harrison 2013). As habitat becomes less suitable and more fragmented due to climate change, it is possible that snowshoe hares will enter into a source-sink population dynamic with fewer high-quality habitats being the main sources of the hare populations across Michigan's Lower Peninsula (Griffin & Mills 2009).

David Burt (2014) recently studied hares in Michigan's Upper Peninsula and portions of Michigan's Lower Peninsula. Burt (2014) worked to find historic records of snowshoe hare occurrence in Michigan, and discover which methods are efficient and effective for estimating hare presence and abundance. Winter track surveys of transects 150 m in length with 100 m spacing are the most efficient and successful method for determining hare presence and abundance in a given area (Burt 2014). Clark & Rohloff (2016) are also continuing work on snowshoe hares in Michigan and have further record of current hare abundance in some areas, although most are in Michigan's Upper Peninsula. Burt (2014) also investigated climatic and habitat features impacting snowshoe hare abundance and occurrence. These records as well as future investigation will be necessary to develop a habitat map and model, as well as a presence/absence map of snowshoe hares. Burt (2014) showed that snowshoe hare abundance and occurrence have both declined in Michigan's Lower Peninsula, showing a need for further investigation and management of snowshoe hares.

EXTENDED METHODOLOGY

Study Site Selection

I chose the Manistee National Forest in Michigan's Lower Peninsula as the study site for this project due to its location at the southern reach of the snowshoe hare historic range. Within the Manistee National Forest, I selected more specific study sites through camera trap surveys. Camera traps (various models) were baited with alfalfa pellets, apples, and cinnamon-scented aspen twigs and were placed at nonrandom locations for 3 weeks. When I found snowshoe hares via camera traps, I conducted live-trapping at the camera site and the surrounding area. There were multiple camera sites with confirmed snowshoe hare visits but zero live-trapping success. Pellet surveys were a proposed method but we did not employ pellet surveys due to a complete lack of persistent snow cover in the winter of 2017-2018 across the study area.

Live-trapping

I conducted live-trapping sessions opportunistically depending on availability, resources, and confirmed snowshoe hare locations. I placed in areas believed to be most locally ideal for snowshoe hares, and not in a grid fashion as this project did not aim to conduct any population or density analyses. Live-trapping success was <0.02% (Unpublished data). Snowshoe hares are a high stress species, so I anesthetized trapped individuals using isoflurane gas. Adult snowshoe hares are large animal for isoflurane anesthetization, so recovery was quick and without issue. At the end of the radio telemetry period, animals that were still alive and collared were live-trapped to remove the collars.

I did experience a single snowshoe hare trap mortality during March of 2019 when temperatures were unusually cold overnight. However, I captured other hares the same night as the trap death, and the other individuals were all alive and in good condition. Despite that, I immediately pulled all traps for the remainder of the trapping session to prevent further trap mortalities. Trapping bycatch included but was not limited to eastern cottontail (*Sylvilagus floridanus*), red squirrel (*Tamiasciurus hudsonicus*), grey squirrel (*Sciurus carolinensis*), American marten (*Martes americana*), North American porcupine (*Erethizon dorsatum*), striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), Virginia opossum (*Didelphis virginiana*).

Vegetation Sampling

I measured multiple sets of vegetation characteristics for the snowshoe hare radio telemetry locations. Immediately after locating an animal via walk-in radio telemetry, visual estimations were made to record percent canopy coniferous, percent canopy deciduous, percent canopy cover, percent 3-meter subcanopy coniferous, percent 3-meter subcanopy deciduous, percent 3-meter subcanopy closure, percent 1-meter subcanopy closure, understory (1-meter) species composition of grasses/forbs, woody shrubs, coniferous saplings, deciduous saplings, and other, overall species composition, lean on or leaf off, and forest type. Other characteristics immediately measured included hare visual, season, daylight, snowpack, and ambient temperature.

I measured the second set of vegetation characteristics measured in June of 2019. Eric Clark developed these methods and showed there to be extremely high positive correlation between winter and summer measurements of these characteristics in Michigan's Upper Peninsula (Clark, 2018). Therefore, measuring vegetation characteristics for all sample sites within a single season would not skew results. The vegetation characteristics measured within this period were 1-meter horizontal cover, 0.5-meter horizontal cover, overhead cover, deciduous stem count, conifer stem count, and snag count.

Survival Analyses

The statistical options for analyzing survival of snowshoe hares (Chapter II) were extremely limited due to a number of factors, primarily related to low sample size. Only five of the radio-collared hares produced a number of telemetry locations great enough to allow for home range estimation. Therefore, I used buffers around the first known locations of all hares and extrapolated the habitat within those buffers rather from true home ranges. A model was not appropriate to estimate survival in this scenario due to autocorrelation of vegetation stand proportions, resulting in the decision to use the Mayfield Method. I did not make further comparisons between groups, including multivariate analyses, due to the low number of objects (sites).

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