Snowshoe Hare (*Lepus americanus*) Abundance in Relation to Habitat and Predator Assemblage Across the Apostle Islands

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Dedication

To my family.

Acknowledgments

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Abstract

Snowshoe hares (*Lepus americanus*) are a climate sensitive species that have a southern range boundary moving northward. Snowshoe hares are found on the Apostle Islands, Wisconsin which are near their southern boundary and differ by island in vegetative and carnivore communities. The archipelago serves as a natural laboratory to assess how top-down and bottom-up forces interact and impact snowshoe hare populations. The objectives of this study were to determine the influence of vegetative characteristics, specifically visual obstruction, and the presence of predators on snowshoe hare abundances across the Apostle Islands. We conducted fecal pellet surveys to estimate hare abundance, measured visual obstruction to assess vegetative cover, and quantified predators using camera trap data on seven islands and the nearby mainland. Hares were found at 10 of our 18 sampling grids, which included 6 of the 7 islands sampled, along with on the mainland, all primarily at low densities. Grids where snowshoe hares were found provided higher levels of visual obstruction than those that without hares. Hare abundance was positively correlated with visual obstruction, along with several carnivore abundances including total carnivore relative abundance, raccoon (*Procyon lotor*), gray wolf (*Canis lupus*), and most strongly with coyote (*Canis latrans*) and was negatively correlated with marten (*Martes americana*) and gray fox (*Urocyon cinereoargenteus*). At their current low densities, hares were found in areas with high levels of visual obstruction. The positive correlation between hares and multiple predator abundances suggest predators are cuing to the presence of hares as potential prey. Hare abundance was nearly 10 times higher on Devils island, which has limited potential predation pressure, which highlights the release from top-down forces. However, its high abundance was coupled with lower habitat quality than other locations where snowshoe hares were found, which may be a result of hares overgrazing and preventing regeneration. Both

top-down and bottom-up forces are interacting to determine snowshoe hare abundance across the Apostle Islands.

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Chapter 1

Introduction

Introduction

Snowshoe hares (*Lepus americanus*) are a wide-ranging important prey species. Hares are found from Alaska through Canada, extending down into the northern United States, with their southern boundary passing through central Wisconsin and the Great Lakes Region (Murray, 2000). While commonly associated with boreal forests, understory density appears to be the most important component in determining habitat usage, rather than species composition (Litvaitis *et al.*, 1985; Ferron and Ouellet, 1992). The most commonly supported trend in habitat usage by hares is that hare use is correlated with understory cover (Hodges, 2000). Areas able to provide 90% visual obstruction during the winter are considered optimal, whereas values below 40% provide no suitable habitat during the winter months (Wolfe *et al.*,1982; Carreker, 1985). High levels of cover up to 3 m are important, as heavy cover 3 m above the ground provides protection from potential avian predators, while cover below 1 m provides concealment from potential terrestrial predators (Wolff, 1980). As a species adapted to snowy winter conditions, hares are facing a southern range limit that is moving northward, likely due to changing climate conditions (Diefenbach *et al.*, 2016; Sultaire *et al.*, 2016; Burt *et* al., 2017).

As a species that seasonally molts, changing climatic conditions pose a great potential risk. Snowshoe hares molt from brown to white pelages to better match their surrounding (*i.e.*, snow / no snow), however this molting process is initiated by photoperiod, not snow cover and therefore hares are an facing increasing number of days where they are mismatched from their surroundings (*i.e.,* brown hair and snow / white hair and no snow) (Mills *et al.*, 2013). Additionally, mismatched hares do not modify their predatory avoidance behavior, indicating

mismatched individuals are more at risk of predation and experience weekly survival decreases up to 7%, which could contribute to population declines (Zimova *et al.*, 2014; Zimova *et al.*, 2016).

Temperatures throughout the Great Lakes Region are expected to increase, with substantial increases in all seasons by the end of the century due to climate change (Kling *et al.*, 2003). In Wisconsin, this warming temperature trend is most pronounced in the winter months (Kucharik *et al.*, 2010). As changing climatic conditions lead to mismatched hares, and therefore lower survival rates (Zimova *et al.*, 2016), areas of high-quality habitat will be important in maintaining at risk populations, such as those near range limits. Snowshoe hares rely on abundant understory vegetation for concealment and escape cover from predators, as well as thermal cover from the elements and winter browse (Buehler and Keith, 1982; Carreker, 1985; Litvaitis *et al.*, 1985).

The Apostle Islands archipelago serves as a natural laboratory to see how top-down and bottom-up forces interact and impact snowshoe hare populations near their southern range limit. An extensive list of carnivores has been documented within the Apostle Islands National Lakeshore, with carnivore communities varying by island (Allen *et al.*, 2017). Vegetative communities also vary across the archipelago as a result of microclimatic effects due to location, being located along the northern boreal coniferous and deciduous forest transition, and historical disturbances including logging and fire history (Craven and Lev, 1987; Judziewicz and Koch, 1993). These differences among islands allow for us to study how bottom-up and top-down processes are acting upon snowshoe hares along their southern range limit. In general bottom-up control, a resource/food driven system, is the primary standard for population control in species, but can be overridden or severely modified by secondary processes, such as top-down processes

from predators (Sinclair and Krebs, 2002). Research near a species' range limit is crucial, as these areas may serve as testing grounds to better understand the conditions by which populations can potentially adapt (Sexton *et al.*, 2009). Our knowledge of the snowshoe hare populations inhabiting the Apostle Islands is currently limited but provides an opportunity to expand upon our knowledge of southern hare populations which will be important with continued changing climate.

Purpose

The purpose of this study was to gain a better understanding of the dynamics controlling the snowshoe hare populations across the Apostle Islands. Very little is known about hare populations on the islands, other than their presence on several islands from ongoing camera surveys and small mammal trapping. I wanted to identify if vegetative characteristics or the presence of predators were affecting snowshoe hare abundances across the Apostle Islands archipelago. Understanding the influence of vegetation and predation in limiting snowshoe hare populations will help guide future management decisions by the National Park Service.

Scope

Snowshoe hares (*Lepus americanus*) are a wide-ranging climate sensitive species. Hares are found from Alaska through Canada, typically associated with boreal forests, and extend into the northern United States, with their southern boundary passing through central Wisconsin. This study takes place in the Apostle Islands National Lakeshore, which includes the majority of the Apostle Islands archipelago, making up the northern most area of Wisconsin. The natural laboratory that the Apostle Islands provide, allow an in-depth look at bottom-up and top-down

processes acting as population controls along snowshoe hares' southern range limit. While our abundance estimates are site specific, habitat usage and relation to predator assemblages can be used by managers across the snowshoe hares' range.

Assumptions

I made the following assumptions while completing this study:

1.) If snowshoe hare populations are cycling or fluctuating, densities from both field seasons are comparable.

2.) Snowshoe hare pellets decompose at similar rates, and therefore last similar amounts of time on different islands.

3.) The locations of the cameras used to determine predator abundances depict similar habitat and predator usage as our sampling grids.

Hypothesis

My objectives for this study were to identify the relative influence of vegetative characteristics and presence of predators on snowshoe hare abundances across the Apostle Islands archipelago. I hypothesized both vegetation and predation affect an island's snowshoe hare abundance. Specifically, I hypothesized 1.) local snowshoe hare abundance would increase with increasing understory cover, measured in terms of visual obstruction provided and 2.) decrease with increasing predation risk, as defined by the relative abundance of potential predator species.

Significance

This study serves as critical baseline data regarding the snowshoe hare populations found across the Apostle Island archipelago. These findings will provide the National Park Service with information allowing them to better manage for this climate sensitive species, along with providing abundance estimates which can be compared to future years' estimates. This will allow management techniques to be evaluated and possible cyclical population trends to be identified. My research contributes to the compilation of snowshoe hare research, while providing additional information near the species southern boundary, where limited research has been conducted.

Definitions

Relative abundance: How common a species is, relative to the other species in a defined location. Calculated here as: RA = (D/ TN) x 100, where D is the number of detections and TN is the number of camera nights.

Leveret: A young hare.

Chapter II

Manuscript

RH: Snowshoe Hares Across the Apostle Islands

Snowshoe Hare (*Lepus americanus*) Abundance in Relation to Habitat and Predator Assemblage Across the Apostle Islands

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Abstract

Snowshoe hares (*Lepus americanus*) are a climate sensitive species that have a southern range boundary moving northward. Snowshoe hares are found on the Apostle Islands, Wisconsin which are near their southern boundary and differ by island in vegetative and carnivore communities. The archipelago serves as a natural laboratory to assess how top-down and bottom-up forces interact and impact snowshoe hare populations. The objectives of this study were to determine the influence of vegetative characteristics, specifically visual obstruction, and the presence of predators on snowshoe hare abundances across the Apostle Islands. We conducted fecal pellet surveys to estimate hare abundance, measured visual obstruction to assess vegetative cover, and quantified predators using camera trap data on seven islands and the nearby mainland. Hares were found at 10 of our 18 sampling grids, which included 6 of the 7 islands sampled, along with on the mainland, all primarily at low densities. Grids where snowshoe hares were found provided higher levels of visual obstruction than those that without hares. Hare abundance was positively correlated with visual obstruction, along with several carnivore abundances including total carnivore relative abundance, raccoon (*Procyon lotor*), gray wolf (*Canis lupus*), and most strongly with coyote (*Canis latrans*) and was negatively correlated with marten (*Martes americana*) and gray fox (*Urocyon cinereoargenteus*). At their current low densities, hares were found in areas with high levels of visual obstruction. The positive correlation between hares and multiple predator abundances suggest predators are cuing to the presence of hares as potential prey. Hare abundance was nearly 10 times higher on Devils island, which has limited potential predation pressure, which highlights the release from top-down forces. However, its high abundance was coupled with lower habitat quality than other locations where snowshoe hares were found, which may be a result of hares overgrazing and preventing regeneration. Both

top-down and bottom-up forces are interacting to determine snowshoe hare abundance across the Apostle Islands.

INTRODUCTION

Snowshoe hares (*Lepus americanus*) are a wide-ranging climate sensitive species with a southern range limit moving northward, likely due to changing climate conditions (Diefenbach *et al.*, 2016; Sultaire *et al.*, 2016; Burt *et al.*, 2017). Hares are found from Alaska through Canada, typically associated with boreal forests, and extend into the northern United States, with their southern boundary passing through central Wisconsin (Murray, 2000). Throughout their range, hares are an important prey species and are preyed upon by numerous predators including Canada lynx (*Lynx canadensis*), coyotes (*Canis latrans*), bobcat (*Lynx rufus*), gray fox (*Urocyon cinereoargenteus*) and red fox (*Vulpes vulpes*) (Hodges, 2000). As a prey species adapted to snowy winter conditions, snowshoe hares rely on a seasonal molt (brown to white pelage) and abundant cover for concealment, escape and thermal cover (Carreker, 1985; Litvaitis *et al.*, 1985). In the northern portions of their range, hares have well documented population cycles of about 10 years, although the cyclical trend is less pronounced in southern populations (Hodges, 2000). Causes of the cycles and population control are debated and include a bottom-up (*i.e.,* food/resource controlled) hypothesis, top-down (*i.e.,* predator controlled), and a three-trophic level (*i.e.,* combination of top-down and bottom-up) hypothesis (Krebs *et al.*, 2018).

Bottom-up hypotheses are the most basic explanation of the snowshoe hare population cycles and population controls. Population growth rates are determined by the food supply and as the population increases, the food available per capita decreases, therefore decreasing the growth rate (Sinclair and Krebs, 2002). In the case of snowshoe hares, there is limited evidence of food quantity being limited (Krebs *et al.*, 2001a), although the addition of food has been shown to increase hare densities but failed to stop the decline phase from happening (Krebs *et al.*, 1986;Krebs *et al.*, 1995). Additional attention was directed toward examining the impact of

secondary chemical defense of browsed trees. After heavy browsing by hares, some species produce advantageous sprouts that contain higher terpene and phenolic resins concentrations that act as hare repellents (Bryant, 1981). Resin decreases protein digestibility, but this is unlikely to cause the decline in hare populations (Sinclair *et al.*, 1988). While food supply is typically thought to control animal population growth rates, this bottom-up control can be overridden or modified by secondary processes, including top-down processes from predators (Sinclair and Krebs, 2002).

Top-down approaches have focused on higher level consumers (*i.e.,* predators), their interactions such as predation, and how those influences cascade down to lower trophic levels. As an important prey species, hare populations face extreme top-down pressure, which makes this a likely agent for causing population cycles and control. In Wisconsin, near their southern boundary, predation accounted for over 90% of hare mortality (Sievert and Keith, 1985; Cox *et al.*, 1997). Predatory influence on hares extends past direct mortality. Predation may have indirect effects which negatively impact snowshoe hares, such as increased stress which has been shown to lower reproductive output (Sheriff *et al.*, 2009). Krebs *et al.* (1995) were also able to show hare densities doubled in the absence of predators. In this same study, Krebs *et al.* (1995) demonstrated food addition also increased hare densities, but when adding food and removing predators the results were additive, indicating a three-trophic level interaction (Krebs *et al.*, 2001a).

The Apostle Islands archipelago serves as a natural laboratory to see how top-down and bottom-up forces interact and impact snowshoe hare populations near their southern range limit. The Apostle Islands National Lakeshore, located off the tip of the Bayfield Peninsula, Wisconsin is comprised of 21 islands. Vegetative communities vary widely across the archipelago as a

result of microclimatic effects due to their location relative to the archipelago, being located along the northern boreal coniferous and deciduous forest transition, and historical disturbances including logging and fire history (Craven and Lev, 1987; Judziewicz and Koch, 1993). An extensive number of carnivore species has recently been documented on the Apostle Islands National Lakeshore, with carnivore communities varying by island (Allen *et al.*, 2017).

Our knowledge of the snowshoe hare populations inhabiting the Apostle Islands and the northern portion of the Bayfield Peninsula of Wisconsin is currently limited, however this island ecosystem provides an opportunity to expand upon our knowledge of southern hare population distribution and abundances (Fig. 1). Our objectives were to quantify vegetative cover levels and predator assemblages on several of the islands and determine how they were affecting snowshoe hare abundances. We hypothesized both vegetation and predation would affect snowshoe hare abundance. We predicted local snowshoe hare abundance would increase with understory cover and decrease with increasing predation risk, as defined by the relative abundance of potential predator. Understanding the influence of vegetation and predation in limiting snowshoe hare populations will help guide future management decisions by the National Park Service, which manages the Apostle Islands.

METHODS

STUDY SITE

The Apostle Islands National Lakeshore is located off the coast of Wisconsin along the southern shore of Lake Superior and is comprised of 21 islands (Fig. 1). We sampled 7 islands, as well as the nearby mainland (Fig. 1). Islands sampled ranged in distance offshore from 2.12 to 23.83 km and in size from 119 to 4069 ha (Table 1). Mean temperatures range from 19.33 C in July to -9.67 C in January, with mean annual amounts of rainfall of 83.85 cm and 184.39 cm of

snow (National Centers for Environmental Information, 2019). Vegetative communities present on individual islands consisted of northern boreal coniferous and deciduous forests, and differed in composition (Table 1) and structure due to varying disturbance histories and microclimate effects of their location within the archipelago (Craven and Lev, 1987; Judziewicz and Koch, 1993). Devils and Raspberry Islands, along with northern portions of Outer Island have been spared from extensive logging due to their status as government lighthouse reservations, whereas remaining islands have seen extensive logging and fires which have replaced pre-settlement forests (Judziewicz and Koch, 1993). Carnivore communities also vary, ranging from simplistic communities on Ironwood Island, only having black bear (*Ursus americanus*) documented, to a very rich community on Stockton Island, which contains black bear, bobcat, coyote, fisher (*Martes pennanti*), red and gray fox, marten (*Martes americana*), raccoon (*Procyon lotor*), short-tailed weasel (*Mustela ermine*), and gray wolf (*Canis lupus*) (Table 1) (Allen *et al.*, 2017).

We sampled the mainland, Devils, Raspberry, and Stockton Islands during June through August 2018. In July 2019, we sampled Ironwood, Oak, Outer, and South Twin Islands. Islands were selected due to snowshoe hares being previously documented as present (Allen *et al.*, 2017). All sampling was conducted after full leaf emergence. Sampling during the winter months was not feasible due to the difficulty of transportation around the Apostle Archipelago during the winter months caused by changing ice conditions and storms.

SAMPLING GRIDS

Our sampling grids (20 ha) were composed of 160 sampling points and were used for fecal pellet surveys and visual obstruction measurements (following Cheng *et al.*, 2017). Each grid consisted of eight 500 m transects, spaced 50 m apart. Each transect had 20 sampling points, spaced 25 m apart (Fig. 1). One grid covered a large portion of Devils (129 ha)

(47°04’30.7416”N, 90°43’44.0125”W), Ironwood (267 ha) (46°59'55.4532"N 90°36'46.116"W), Raspberry (119 ha) (46°58’26.5080”N, 90°47’42.0162”W), and South Twin (146 ha) (47°01'58.4472"N 90°38'47.177"W) Islands, but Stockton(4069 ha), Oak (2055 ha), and Outer (3237 ha) Islands were much larger and required more sampling grids in order to better represent hare abundance. Two grids (Oak 1-2) were used on Oak Island (46°56'55.2804"N 90°43'01.056"W, 46°56'24.7812"N 90°44'37.446"W) which were 1760 m apart. Three grids (Outer 1-3) were used on Outer Island (47°01'09.6276"N 90°26'34.85"W, 47°00'21.6972"N 90°26'31.852"W, 47°00'18.7272"N 90°27'13.0052"W) which were spaced a minimum of 671 m apart. Seven grids (Stockton 1-7) were used on Stockton Island, which were a minimum of 1600 m apart (46°55’37.0020”N, 90°34’00.1380”W, 46°56’06.2412’’N, 90°32’33.0612”W, 46°54’42.7356”N, 90°32’45.8160”W, 46°57’24.7968”N, 90°32’38.6412”W, 46°54’45.1404”N, 90°37’22.4256”W, 46°56’10.4640”N, 90°37’14.0124”W, 46°55’11.3232”N, 90°35’41.9676”W). This spacing ensured each grid sampled was independent of one another, as O’Farell (1965) found 95% of recaptured hares within 335 m of their last capture. Additionally, hares have been found to have relatively small home ranges, from 0.5 – 6.1 ha (Hodges, 2000). In addition, two grids (mainland 1-2) were sampled on Bayfield County owned land on the Bayfield Peninsula (46°55’19.5744”N, 90°57’12.9279”W), (46°54’19.0836”N, 90°47’53.3140”W) (Fig. 1). Grids were only sampled once during the study.

PELLET COUNT SURVEYS

We estimated snowshoe hare abundance using fecal pellet count surveys. At each site, the total number of pellets was counted and recorded within a 0.155-m^2 (5.08 cm x 305 cm) pellet plot (following Krebs *et al.*, 1987; Hodges and Mills, 2008). Plots were constructed of PVC pipe (1.905 cm diameter) and placed perpendicular to transect lines. All intact snowshoe hare pellets

at least half way in the plot were counted, as multiple observers have been shown to identify old pellets inaccurately (Prugh and Krebs, 2004; Hodges and Mills, 2008). Pellets were known to be from snowshoe hares, as eastern cottontail rabbits (*Sylvilagus floridanus*) haven't been documented on the Apostle Islands, and white-tailed deer (*Odocoileus virginianus*) are also absent or at low densities on many of the islands sampled and have different shaped pellets. The mean number of pellets within plots was used with the Yukon equation (Krebs *et al.*, 2001b):

$$1.567 * \exp(-1.203 + 0.889 * \ln[\text{mean pellets}])$$

which produces estimates similar to locally derived equations, to predict hare densities (Mills *et al.*, 2005).

CARNIVORE ABUNDANCE

Relative carnivore abundance was determined as part of an ongoing remote camera study conducted by personnel from the University of Wisconsin – Madison, Northland College and the Apostle Islands National Lakeshore (Allen *et al.*, 2017). Relative abundances (RA) were calculated as:

$$RA = (D/ TN) \times 100$$

where D was the number of detections and TN is the number of camera nights. Additional detections of a species within 30 minutes of a previous detection were considered the same detection. Relative abundances were calculated from the camera placed closest to the center of each of our sampling grids. Distances from the center of a sampling grid to a camera ranged from 210 to 1350 m, with the mean distance of 568 m. While some of the cameras were located outside of our sampling grids, we do believe the cameras still represent similar habitat and predator usages. We were unable to calculate relative carnivore abundances for our second mainland location, as there was not a camera in close proximity.

VISUAL OBSTRUCTION

Visual obstruction was measured from all vegetation at each sampling site up to a height of 3 m (following Carreker, 1985). A modified cover pole (3.175 cm x 3 m) was used in place of a profile board, as recommended by Nudds (1977), as it could be collapsed, was lightweight and found to produce comparable data (Griffith and Youtie, 1973). The cover pole was painted in alternating white and orange 0.5 m increments (Nudds, 1977). A photo of the cover pole was taken 15 m from the sampling point in a random direction at a standard height of 1 m, to be scored at a later time (Nudds, 1977; Carreker, 1985). Each 0.5 m increment was given a visual obstruction score ranging from 1 (0-20% covered) to 5 (81-100% covered) (Nudds, 1977). All visual estimates were made by the same individual (JR) to limit any potential observer bias. Six points (one from each mainland grid, one from Devils Island, two from Stockton 3, and one from Stockton 6) were removed due to missing or unclear images.

STATISTICAL ANALYSIS

We used the program R version 3.4.4 (R Core Team, 2018) for all statistical analyses. An alpha value of 0.05 was used for all statistical tests. A Shapiro Wilks test was used to test for normality of each visual obstruction height increment for each of the sampling grids. Various transformations were attempted, but normality could not be achieved, resulting in non-transformed data being used for analyses. Kruskal - Wallis tests were used to test for differences in visual obstruction among grids at each height increment. Mann-Whitney U tests were used to compare visual obstruction scores of grids with and without snowshoe hares.

In an attempt to identify how hares were selecting locations within areas they were found, Mann-Whitney U tests were used to test for differences in visual obstruction measurements of sampling points containing snowshoe hare pellets and those without pellets. This was done for

each grid with multiple sampling points containing pellets. Our first mainland grid and first Oak Island grid only had one sampling point with pellets, and therefore were excluded from this analysis. Extremely small sample sizes of points with snowshoe hare pellets on most grids limits our ability to identify significant differences. To address this, we also calculated effect sizes for each comparison using pooled standard deviations, in order to quantify differences. An effect size of 0.2 is considered 'small', while an effect size of 0.5 is described as 'medium' and is 'large enough to be visible to the naked eye', and effect sizes greater than 0.8 are considered ‘large’ (Cohen, 1969). Comparisons with effect sizes that were at least ‘medium’ (≥ 0.5) were treated as they were different.

Principal component analyses (PCA) were used to summarize the relationships between snowshoe hare abundances, vegetation, and potential predators. PCA was run using correlation matrices of visual obstruction scores (1-5) for each height increment (0 – 0.5 to 2.5 – 3 m) for each sampling site. Each site had six values associated with it, one for each height increment. Envfit, from the R package Vegan, was then used to overlay environmental variables (snowshoe hare abundance, number of pellets, carnivore richness, and relative abundances for weasel, marten, gray fox, black bear, bobcat, gray wolf, raccoon, coyote, and red fox, and hare abundance from camera survey) onto the PCA.

The initial PCA included all sampling grids except our second mainland grid, which did not have carnivore data available. The ordination appeared to be heavily skewed by Devils Island due to its much higher snowshoe hare abundance estimate and lower cover values in comparison to other grids containing snowshoe hares. Devils Island appeared to be an outlier, so it was removed in a second PCA.

RESULTS

We found snowshoe hare fecal pellets at 10 of the 18 grids sampled, which included 6 of 7 islands sampled along with the mainland (Fig. 1). Ironwood Island was the only island where snowshoe hare pellets were not found, although the mainland, Oak and Stockton Islands, which had multiple sampling grids due to size, contained grids where snowshoe hares were also absent. Grids where snowshoe hare pellets were found had pellet counts within single pellet plots ranging from 0 to 48. Grid means (±SE) (160 sampling points) for those containing snowshoe hare pellets ranged from 0.008±0.01 pellets per plot on Oak Island to 2.29±0.40 on Devils Island, and estimated abundances ranged from 0.007 to 0.98 hares per ha (Table 2). If abundance estimates for grids were extrapolated across entire islands, estimated total hare numbers on islands range from 13 hares on Raspberry Island to 236 hares on Stockton Island, which would represent maximum estimates as habitat suitability wouldn't be constant across entire islands.

We detected visual obstruction differences among grids at every height (Kruskal – Wallis tests, $P \leq 2.2e\text{-}16$, $258.82 \leq H \leq 420.75$, df=17). Visual obstruction was highest from 0 – 0.5 m with means (±SE) ranging from 3.33±0.09 to 4.93±0.03 on our 5-point scale and decreased as height increased, ranging from 2.27±0.13 to 4.03±0.09 above 2.5 m (Table 3). Grids with snowshoe hares had greater visual obstruction scores at every height increment compared to grids without hares (Mann-Whitney U, $P \leq 4.425e\text{-}09$, $U=1037700 \leq \geq 1131100$)

While hares were found at grids with higher levels of visual obstruction, sampling points that contained hare pellets tended to provide less visual obstruction than those without pellets (Table 4). Sampling points containing hare pellets provided less visual obstruction than sampling points that did not contain pellets at heights below 1 m at Devils Island (Mann-Whitney U, $P \leq 0.01555$, U=3776.5, 3817, Effect size 0 – 0.5 m = 0.50) and also the second Outer Island grid

(Mann-Whitney U, P≤0.02524, U=303.5, 332.5, Effect sizes = 1.04, 1.06). Medium effect sizes also indicated this pattern, as sampling points with pellets had lower visual obstruction levels from 0 – 0.5 m on the Outer Island 3 grid (Effect size = 0.52) and from 0.5 – 1 m on the Outer Island 1 grid (Effect size = 0.71). However, on the Stockton 7 grid, sampling points with snowshoe hare pellets had higher levels of visual obstruction between 1 – 1.5 m (Effect size = 0.52) and 2 – 2.5 m (Effect size = 0.63) than points without pellets based on medium effect sizes.

Predators documented in the vicinity of our study grids included black bear, bobcat, coyote, red and gray fox, fisher, gray wolf, marten, raccoon, and short-tailed weasel. Carnivore richness ranged from 1 on Devils Island, Ironwood Island, and Outer Island 3 to 5 on the mainland with an average of 2.47 species per grid (Table 5). Relative carnivore abundances varied by grid, with relative abundances of species ranging from 0 – 13.2 detections per 100 trap nights, with black bear generally being the most common species followed by coyote. Total carnivore relative abundances ranged from 0.14 detections per 100 trap nights at Outer Island 3 to 21.97 on the mainland, with an average of 5.70 (Table 5).

The initial PCA, which included Devils Island, indicated that increasing snowshoe hare abundance was not correlated with increasing visual obstruction as predicted, but was inversely correlated with most carnivore species and carnivore richness (Fig. 2).The proportion of variation explained by the first two axes of the initial PCA was 76.71%, with the first axis explaining 60.15% and the second explaining 16.57%. PC1 was influenced by visual obstruction measurements from 0.5 – 2.5 m, with 1.0 - 2.0 m contributing the most, whereas PC2 was influenced by measurements from 0 – 0.5 m and 2.5 – 3 m. Increasing hare abundance was aligned with the samples representing Devils Island and not the majority of grids with snowshoe hares. Devils Island had an abundance estimate that was nearly 10 times greater than any other

sampling grid, and therefore had a disproportionate effect on the relationship between visual obstruction measurements and hare abundance.

In the PCA which excluded results from Devils Island, snowshoe hare abundance was now positively correlated with locations providing higher visual obstruction (Fig. 3). The proportion of variation explained by the first two axes of the PCA ordination without Devils Island and mainland 2 was 76.60%, with the first axis explaining 60.09% and the second explaining 16.51%. This ordination demonstrates grids with snowshoe hares were similar, having higher visual obstruction levels than grids that did not (Fig. 3). PC1 was still influenced by visual obstruction measurements from 0.5 – 2.5, with 1.0 – 2.0 m contributing the most, and hare abundance was positively correlated with these measurements. PC2 was influenced by measurements from 0 – 0.5 m and 2.5 – 3 m. The vector representing hare abundance has a slight upward slope on the ordination which indicates abundances are more positively correlated with visual obstruction from 2.5 – 3 m, than from 0 – 0.5 m. Hare abundance was now weakly correlated with several carnivore variables, including relative abundances of coyotes, raccoons, gray wolves, and overall carnivore abundance, whereas showing an inverse correlation with marten and gray fox relative abundance, as well as carnivore richness (Fig. 3).

The extent to which some of the carnivores documented, such as black bears and raccoons, may prey on hares is unclear. To address this, black bear and raccoon abundances were removed and an additional PCA was ran. The relationships remained the same, however the correlation between total carnivore relative abundance and snowshoe hare abundance became stronger, as coyote now made up a larger portion (63%) of the total carnivore abundances.

Discussion

We documented snowshoe hare fecal pellets at 10 of the 18 grids sampled, which included 6 of the 7 islands sampled, along with the mainland. Hare abundance was low (< 0.3 hares/ha) at all the locations besides on Devils Island (sensu Mills *et al.*, 2005). The low abundance of snowshoe hares across the Apostle Islands we sampled raises concerns regarding the fate of these populations. It is unknown whether these island populations cycle like northern hare populations. While historical records did not estimate hare densities, documentation of hares on the archipelago date back to 1919 (Jackson, 1920). Populations may be currently declining, or at a low phase in their cycle, as park rangers have noticed steady declines in the number of snowshoe hares feeding on the Raspberry Island lighthouse's lawn over the last several years (NPS Ranger, pers. comm.). Given the low number of hares, even on the larger islands, there is a limited source of individuals to disperse among islands. Along with our sampling on the Bayfield Peninsula, finding limited signs of hares, local biologists have noticed the mainland hare densities declining as well (Red Cliff Tribal Biologist, pers. comm.), which would also limit the mainland source of hares to the islands. Dispersal to and between these island populations is likely further limited due to the distance between most islands (~1600+ m) and their dispersal window being restricted to winter months when ice coverage permits. Ice coverage duration in the area is declining by approximately three days per decade, further shrinking their narrow dispersal window (Howk, 2009). These small populations, with limited influxes of new individuals, may be at risk of genetic issues. In small or fragmented populations, genetic variation is finite, and further decreased from generation to generation, leading to inbreeding (Allendorf *et al.* 2013). Inbreeding has been shown to often significantly affect birth weight,

survival, reproduction and resistance to disease, predation and environmental stresses in animal populations (Keller and Waller 2002).

While snowshoe hares are inhabiting areas across the Apostle Islands that provide higher levels of cover, it appears that predation may be limiting hare abundances more so than habitat quality. Devils Island is essentially a predator free environment in comparison to the other islands sampled and demonstrates the release from top-down forces. Devils Island was similar to the grids without hares, in terms of cover, yet has abundance estimates nearly 10 times higher than the other locations. Krebs *et al.* (1995) found hare density doubled in the absence of predators in the Yukon. Predatory influence on the hares on other islands may extend past direct mortality. Increased stress resulting from predation risk lowers reproductive output, with females exposed to stress producing smaller and lighter young than control females (Sheriff *et al.* 2009). Female hares, stressed only during gestation, also have 30% lower survival rates themselves, and produced 1.5 less offspring that made it to weaning age (MacLeod *et al.* 2018). The elevated stress levels of the dam can also be inherited by their offspring, carrying these effects into the next generation (Sheriff, Krebs, and Boonstra, 2010).

We predicted snowshoe hare abundances would decline with increasing predation risk, however hare abundance was weakly positively correlated with several carnivore relative abundances, including coyote, gray wolf, raccoon, and total carnivore relative abundance (Fig. 3), which may indicate they are acting as an important source of prey on the Apostle Islands. Cameras and small mammal trapping have identified a limited subset of potential prey species on the Apostle Islands, which includes southern red-backed vole (*Myodes gapperi*), red squirrel (*Tamiasciurus hudsonicus*), woodland deer mouse (*Peromyscus maniculatus gracilis*), masked shrew (*Sorex cinereus*), meadow vole (*Microtus pennsylvanicus*), northern short-tailed

shrew (*Blarina brevicauda*), and white-footed mouse (*Peromyscus leucopus*) (Smith and Maragi, 2004; Smith and Fawver, 2005; Allen *et al.*, 2017). Of the carnivore species documented, hare abundance was the most closely correlated with coyote relative abundance. Coyotes are known to be one of the most important predators of hares where they co-occur (Sievert and Keith, 1985; Theberge and Wedeles, 1989; Cox *et al.* 1997; O'Donoghue *et al.*, 1998). Red fox also commonly prey heavily on hares, however in our study red fox abundance had a weak and nonsignificant relationship with our ordination and hare abundance (Fig. 3). Red fox have been shown to turn to alternate prey more than coyotes when hare populations are low (Theberge and Wedeles, 1989).

We only considered terrestrial carnivores in this study, but avian predation also accounted for a large portion of snowshoe hare mortality in Wisconsin (Sievert and Keith, 1985). Hare remains have been found in Bald Eagle (*Haliaeetus leucocephalus*) nests within the Apostle Islands National Lakeshore (Kozie and Anderson, 1991), and the list of potential avian predators found near the islands is extensive including Northern Goshawks (*Accipiter gentilis*), Great Horned (*Bubo virginianusand*), Long-eared Owls (*Asio otus*), Cooper's (*Accipiter cooperii*), Red-shouldered (*Buteo lineatus*) and Broad-winged Hawks (*Buteo platypterus*) (Beals, 1958). Whereas larger predators may prey on adult hares, leverets may be vulnerable to the smaller hawks as well (Hodges, 2000). Future avian dietary studies and population estimates for these species may help provide clarity on avian predation pressure on snowshoe hares across the Apostle Islands.

Habitat quality, in terms of the visual obstruction provided, appeared to be determine where snowshoe hares were found across the Apostle Islands. Grids where snowshoe hares were present had higher visual obstruction measurements for every height increment compared to

grids without snowshoe hares. These differences were more pronounced above 0.5 m, as the differences in means was 0.23 (our scale of 1-5) below 0.5 m and around 0.5 (our scale of 1-5) for height increments above. Based on our scoring system (1 = 20%), grids with snowshoe hares were providing nearly 5% more visual obstruction in the first 0.5 m above the ground, and 10% more visual obstruction at each increment above that. This was further supported in our PCA used to summarize our abundance estimates, visual obstruction, and predator abundances, as hare abundance was positively correlated with visual obstruction.

Areas able to provide 90% (4.5 on our scale of 1-5) visual obstruction during the winter are considered optimal habitat, whereas values below 40% (2 on our scale of 1-5) provide no suitable habitat during the winter months (Wolfe *et al.*, 1982; Carreker, 1985). Direct comparisons from summer cover to winter cover aren't possible, but winter cover values would likely be less, as most deciduous vegetation will no longer provide visual obstruction as it was during our sampling period. Although winter habitat is assumed to be more limiting, areas of viable cover are crucial year-round. Whereas grids with snowshoe hares provided higher amounts of visual obstruction, the grids without snowshoe hares that we sampled would likely still provide adequate cover, but less ideal. No grid sampled had a mean visual obstruction score below 2 (equivalent to 40%) on our scale at any height increment, indicating it provided some suitable habitat. Given the current low densities of hares, this suboptimal habitat may not be used, as hares will disperse as densities increase in optimal habitat, filling into the less suitable areas (Wolff, 1980). This was further supported as Wirsing *et al.* (2002) found the greatest number of hares in Idaho where the habitat featured a dense understory, which provided above 57% understory cover during the summer, but found areas providing below 40% virtually empty.

We found hares present in areas that provided thicker cover, however within these 'thicker' areas we found hares using locations that provided less cover than what was available (Table 4). On Devils and all 3 Outer Island grids, sampling points with snowshoe hare pellets provided lower amounts of visual obstruction below a height of 1 m than the points that did not have pellets. Being a prey species generally associated with high levels of cover, this came as a surprise, however this may be a result of reduced predatory pressure. All of these sampling grids had lower than average relative total carnivore abundances, and low (≤0.18) relative abundances for species that are likely the main predators of hares (*i.e.,* coyote & fox) and therefore low predation risk. Conversely, grid 7 on Stockton Island had above average relative total carnivore abundances as well as higher bobcat and coyote relative abundances. On this grid, sampling points with hare pellets had higher visual obstruction measurements from 1 – 1.5 m and 2 – 2.5 m than sampling points that did not have pellets. The reduced predation risk at some of our sampling grids may alter habitat usage and cover requirements of hares. In Maine, hare visits to sites marked with coyote urine decreased, and the number of visits to these sites decreased as vegetation density increased with the thought that dense vegetation may inhibit the scanning ability of hares for predators that use dense vegetation to conceal themselves while stalking prey (Lankist, 2019). However, in the Yukon, reduced predation risk did not correlate with less protected habitats being used (Hodges and Sinclair, 2005). An alternative explanation for this finding may be due to extensive herbivory by snowshoe hares when top-down forces are absent or minimal. Hares depend heavily on woody browse during the winter, and during population peaks may browse all the terminal shoots within their reach, effectively preventing regeneration (Sinclair, 2003). Whereas white-tailed deer are often associated with preventing regeneration, in northern Wisconsin and the Upper Peninsula of Michigan, hemlock (*Tsuga canadensis*)

regeneration was limited by snowshoe hares in deer exclosures, which would be similar to the Apostle Islands as deer are absent or at low densities across the archipelago (Alverson *et al.* 2019).

We must also address several limitations associated with our study. The relative carnivore abundances used here served only as a proxy, as the camera study objectives were not to evaluate predator numbers and usage at our specific sampling locations. In addition, at low densities (< 0.3 hares/ha) (Mills *et al.*, 2005), accurate population density estimates for hares are difficult to obtain. Every grid sampled besides Devils Island was estimated at 0.14 hares per ha or less (Table 2), which falls into this category. Given the time restraints associated with this study, we used a pellet equation developed elsewhere, and were not able to previously clear plots to insure pellets were from the previous year, which may limit the accuracy of our estimates. A locally derived regression equation and a pellet decomposition study would help increase estimate accuracy, as the Yukon equation used assumes all pellets survive a year, which may not be the case in the humid environment of the Apostle Islands (Prugh and Krebs, 2004). Even with the limitations described, we feel confident in saying hare numbers were low at the majority of our sampling grids. Our sampling approach can however be used by National Park Service staff to quickly evaluate areas in terms of low, medium, or high hare densities, without conducting a labor intense mark-recapture study (Mills *et al.*, 2005).

We suggest continued monitoring of snowshoe hare populations throughout the Apostle Island archipelago as we only sampled a portion of the islands, but it appears to be a balance of bottom-up and top-down forces interacting to control hare populations in their southern reaches. The low abundances of hares documented, along with declining hare trends being noticed on the islands (NPS Ranger, pers. comm.) and nearby mainland (Red Cliff Tribal Biologist, pers.

comm.) call for further monitoring of the species. Additional ecological community information along with these base-line findings on what habitat is being used, and how predators are influencing populations will allow biologists and the National Park Service to better manage snowshoe hares. The future management of these populations requires an understanding of complex ecological interactions but will be important in order to prevent continued range shifts of this climate sensitive species.

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Table 1. Study site descriptions of each island sampled including the dominant vegetation found in the understory and canopy, and carnivore community documented on the island. Vegetation descriptions are from Judziewicz and Koch (1993) and carnivore community are from an ongoing camera survey (Allen *et al.*, 2017)

Location	Vegetation Description	Carnivores Documented
Devils Island (129 ha)	Balsam-fir (*Abies balsamea*), White cedar (*Thuja occidentalis*), White spruce (*Picea glauca*), Black spruce (*Picea mariana*), White birch (*Betula papyrifera*) with scattered white pine (*Pinus strobus*) and hemlocks (*Tsuga canadensis*). Interior sites are open, whereas coastal regions are wind-blasted and stunted, forming a thick Krumholtz community	Short-Tailed Weasel (*Mustela ermine*), Otter (*Lontra canadensis*)
Ironwood Island (267 ha)	Balsam-fir, white cedar, white and yellow birch (*Betula alleghaniensis*), with smaller amounts of sugar maple (*Acer saccharum*), red maple (*Acer rubrum*) and hemlock dominate the forest. Canada yew (*Taxus canadensis*) is the dominate understory shrub, along with mountain maple (*Acer spicatum*)	Black Bear (Ursus americanus)
Mainland	Dominated by quaking aspen (*Populus tremuloides*), white birch, sugar maple, balsam-fir and white spruce	Black Bear, Bobcat (*Lynx rufus*), Coyote (*Canis latrans*), Fisher (*Martes pennanti*), Red Fox (*Vulpes vulpes*), Gray Fox (*Urocyon cinereoargenteus*), Raccoon (*Procyon lotor*), Short-Tailed Weasel, Gray Wolf (*Canis lupus*)
Oak Island (2055 ha)	Sugar maple is common on the summit, while white birch is abundant on slopes of all aspects, and red oak (*Quercus rubra*) preferring southwest facing slopes. Bigtooth aspen (*Populus grandidentata*), red maple, yellow birch, hop-hornbeam (*Ostrya*), and basswood are also part of the diverse mix. Conifers are generally unimportant, with the exception of hemlock, white cedar and balsam fir in areas. Beaked hazelnut (*Corylus cornuta*) and fly honeysuckle (*Lonicera canadensis*) are common in the understory, with mountain maple and thimbleberry (*Rubus parviflorus*) being less common	Black Bear, Bobcat, Coyote, Fisher, Red Fox, Gray Fox, Raccoon
Outer Island (3237 ha)	White birch, quaking aspen, balsam-fir, red maple, and red oak are common in the southern portion of the island. Beaked hazelnut, fly honey suckle, and bush honeysuckle (*Lonicera tatarica*) are common in the understory, along with Canada yew in portions	Black Bear, Coyote, Marten (*Martes americana*), Short-Tailed Weasel
Raspberry Island (119 ha)	Canada yew dominates the understory whereas dominant tree species include white cedar, balsam-fir, white and yellow birch along with scattered sugar-maple, hemlock, basswood (*Tilia americana*), showy mountain-ash (*Sorbus decora*), and black ash (*Fraxinus nigra*)	Coyote, Red Fox, Otter
South Twin (146 ha)	White cedar, yellow and white birch, red maple, and balsam-fir dominate the forest. Mountain maple, beaked hazelnut, and red-berried elder (*Sambucus racemosa*) are common in the understory, with occasional Canada yew	Red Fox
Stockton Island (4069 ha)	Currently white birch, sugar maple, and red maple are the dominant trees, whereas white cedar, balsam-fir, and quaking aspen are also frequent. Hemlock and yellow birch have declined from their pre-settlement importance	Black Bear, Bobcat, Coyote, Fisher, Red Fox, Gray Fox, Marten, Raccoon, Short-Tailed Weasel, Gray Wolf

Table 2. Snowshoe hare fecal pellet survey summaries used to estimate hare abundances. Intact pellets that were at least half inside a 0.155-m^2 (5.08 cm X 305 cm) plot were counted at 160 sampling points per grid. Hares per ha were estimated using the Yukon regression equation (Krebs *et al.*, 2001b). Total number of hares estimated as hares/ha x island size (ha)

Grid	Sampling Points	Points with Pellets	Mean (± 1 SE) pellets	Hares/ha	Island Size (ha)	Total Number of Hares
Devils	160	89	2.29±0.40	0.977	129	126
Ironwood	160	0	-	-	267	-
Mainland 1	160	1	0.019±0.02	0.014	-	-
Mainland 2	160	0	-	-		
Oak Island 1	120	1	0.008±0.01	0.007	2055	14
Oak Island 2	160	0	-	-		-
Outer 1	160	4	0.056±0.03	0.036	3237	117
Outer 2	80	6	0.088±0.04	0.054		175
Outer 3	160	3	0.025±0.02	0.018		58
Raspberry	160	18	0.2±0.06	0.113	119	13
South Twin	160	24	0.25±0.06	0.137	146	20
Stockton 1	160	0	-	-	4069	-
Stockton 2	160	0	-	-		-
Stockton 3	160	10	0.088±0.03	0.054		220
Stockton 4	160	0	-	-		-
Stockton 5	160	0	-	-		-
Stockton 6	160	0	-	-		-
Stockton 7	160	8	0.094±0.04	0.058		236

Table 3. Mean (± SE) visual obstruction estimated using a modified cover pole from a random direction at a distance of 15 m from a height of 1 m. Obstruction was scored from 1 (0-20% covered) to 5 (81-100% covered). Grids are separated based on snowshoe hare (SSH) presence. All height increments were significantly different (Present v. Absent) (Mann-Whitney U tests, P≤ 4.425e-09, U=1037700≤ ≥1131100)

		Height					
SSH	**Location**	**0 – 0.5 m**	**0.5 – 1 m**	**1 – 1.5 m**	**1.5 – 2 m**	**2 – 2.5 m**	**2.5 – 3 m**
Present	Devils	4.35±0.09	3.38±0.13	3.16±0.14	3.18±0.14	3.22±0.14	3.21±0.14
	Mainland 1	4.81±0.05	4.27±0.11	4.12±0.12	4.00±0.13	3.64±0.14	3.26±0.15
	Raspberry	4.93±0.03	4.68±0.07	4.40±0.09	3.79±0.12	4.08±0.11	3.82±0.12
	Stockton 3	4.60±0.08	3.66±0.13	3.33±0.13	3.13±0.13	2.94±0.13	3.11±0.13
	Stockton 7	4.83±0.05	4.58±0.08	4.22±0.11	3.93±0.12	3.66±0.13	3.41±0.13
	South Twin	4.21±0.09	3.72±0.12	3.59±0.12	3.59±0.11	3.51±0.12	3.51±0.11
	Outer 1	4.66±0.05	4.06±0.09	3.66±0.11	3.40±0.11	3.51±0.11	3.23±0.11
	Outer 2	4.74±0.07	4.21±0.12	3.86±0.15	3.96±0.14	3.74±0.15	3.66±0.15
	Outer 3	4.66±0.05	4.36±0.07	4.09±0.08	3.97±0.09	4.11±0.08	4.03±0.09
	Oak 1	4.11±0.10	2.94±0.14	2.39±0.13	2.20±0.12	2.30±0.13	2.27±0.13
	Mean	4.59±0.02	4.00±0.04	3.71±0.04	3.53±0.04	3.49±0.04	3.36±0.04
Absent	Mainland 2	4.43±0.08	3.53±0.11	3.23±0.12	3.28±0.12	3.43±0.12	3.50±0.12
	Stockton 1	4.68±0.07	4.09±0.11	4.09±0.11	3.94±0.11	3.88±0.12	3.61±0.12
	Stockton 2	4.51±0.08	3.40±0.13	3.21±0.13	3.11±0.13	2.94±0.14	2.98±0.12
	Stockton 4	4.19±0.10	2.97±0.13	2.71±0.12	2.41±0.12	2.26±0.11	2.28±0.11
	Stockton 5	4.55±0.08	3.68±0.12	3.16±0.13	3.01±0.13	2.95±0.13	2.81±0.13
	Stockton 6	4.55±0.07	3.73±0.11	3.39±0.12	3.28±0.13	2.96±0.12	2.77±0.12
	Oak 2	3.33±0.09	2.36±0.11	2.09±0.10	2.26±0.11	2.31±0.10	2.38±0.11
	Ironwood	4.68±0.06	3.81±0.11	3.33±0.11	3.08±0.11	3.06±0.12	3.06±0.12
	Mean	4.36±0.03	3.45±0.04	3.15±0.05	3.04±0.04	2.97±0.05	2.92±0.04
All	Mean	4.49±0.02	3.75±0.03	3.45±0.03	3.30±0.03	3.25±0.03	3.16±0.03
Mean Difference (Present – Absent)		**0.23**	**0.55**	**0.56**	**0.49**	**0.52**	**0.44**

Table 4. Mean (± SE) visual obstruction score estimated using a modified cover pole from a random direction at a distance of 15 m from a height of 1 m for locations where snowshoe hare fecal pellets were present and absent. Obstruction was scored from 1 (0-20% covered) to 5 (81-100% covered). Bold values represent significantly different median values (Mann-Whitney U test, P≤0.05). Values within ( ) represent effect size calculated using pooled SDs. Positive effect size scores represent higher 'Present' scores, while negative value represent higher 'Absent' scores

Grid	N	Pellet Presence	0 – 0.5 m	0.5 – 1 m	1 – 1.5 m	1.5 – 2 m	2 – 2.5 m	2.5 – 3 m
Devils	89	Present	**4.10±0.14** (-0.50)	**3.11±0.17** (-0.38)	2.97±0.18 (-0.25)	3.18±0.18 (0.005)	3.22±0.18 (0.006)	3.30±0.18 (0.13)
	70	Absent	**4.67±0.11**	**3.73±0.19**	3.40±0.20	3.17±0.21	3.21±0.21	3.09±0.21
South Twin	24	Present	4.33±0.25 (0.13)	4.13±0.27 (0.32)	3.83±0.30 (0.20)	3.63±0.31 (0.03)	3.54±0.29 (0.02)	3.75±0.28 (0.19)
	136	Absent	4.18±0.10	3.65±0.13	3.54±0.13	3.58±0.12	3.51±0.13	3.47±0.13
Raspberry	18	Present	5.00±0.00 (0.19)	4.78±0.17 (0.12)	4.44±0.30 (0.04)	4.22±0.33 (0.33)	4.44±0.30 (0.31)	3.89±0.40 (0.05)
	142	Absent	4.92±0.04	4.67±0.08	4.39±0.10	3.74±0.13	4.03±0.11	3.81±0.12
Outer 1	4	Present	4.5±0.29 (-0.24)	3.25±1.03 (-0.71)	3.00±0.71 (-0.48)	3.00±0.58 (-0.30)	3.25±1.03 (-0.18)	3.50±0.87 (-0.27)
	156	Absent	4.67±0.05	4.08±0.09	3.67±0.11	3.41±0.11	3.51±0.11	3.22±0.11
Outer 2	6	Present	**4.17±0.40** (-1.04)	**3.17±0.60** (-1.06)	3.50±0.56 (-0.29)	3.50±0.43 (-0.41)	3.17±0.48 (-0.47)	3.33±0.33 (-0.27)
	74	Absent	**4.78±0.06**	**4.30±0.12**	3.89±0.16	4.00±0.14	3.78±0.15	3.69±0.16
Outer 3	3	Present	4.33±0.33 (-0.52)	4.33±0.67 (-0.03)	3.67±0.33 (-0.40)	3.67±0.33 (-0.28)	3.67±0.33 (-0.47)	3.67±0.33 (-0.33)
	157	Absent	4.67±0.05	4.36±0.07	4.10±0.09	3.97±0.09	4.12±0.08	4.03±0.09
Stockton 3	10	Present	4.30±0.47 (-0.33)	3.50±0.45 (-0.11)	3.00±0.52 (-0.21)	3.10±0.53 (-0.02)	2.90±0.46 (-0.03)	3.20±0.61 (0.06)
	148	Absent	4.62±0.07	3.67±0.13	3.35±0.14	3.13±0.13	2.95±0.14	3.10±0.13
Stockton 7	8	Present	4.88±0.13 (0.08)	4.75±0.25 (0.18)	4.88±0.13 (0.52)	4.13±0.58 (0.14)	4.63±0.26 (0.63)	4.50±0.27 (0.08)
	152	Absent	4.83±0.05	4.57±0.08	4.18±0.11	3.91±0.12	3.61±0.13	3.36±0.14

Table 5. Carnivore summary information from an ongoing remote camera project conducted by the University of Wisconsin – Madison, Northland College, National Park Services, and the Apostle Islands National Lakeshore (Allen *et al.*, 2017). Gray lines indicate locations where snowshoe hare pellets were found. Values listed under species name are relative abundances (detections per 100 camera nights), where RA = (D / TN) x 100, where D is the number of detections and TN is camera nights. Camera information is based on the camera nearest to the center of pellet and visual obstruction grids

Location	Hares/ha	Carnivore richness	Black Bear	Bobcat	Coyote	Gray Fox	Fisher	Gray Wolf	Marten	Raccoon	Red Fox	Weasel	Total Carnivore Abundance	Distance (m) to camera
Devils	0.98	1	0	0	0	0	0	0	0	0	0	0.28	0.28	210
South Twin	0.137	1	0	0	0	0	0	0	0	0	1.41	0	1.41	400
Raspberry	0.11	2	0	0	13.2	0	0	0	0	0	1.12	0	14.32	570
Stockton 7	0.058	4	6.09	0.87	3.48	0	0	0.43	0	0	0	0	10.87	620
Stockton 3	0.054	2	1.36	0	4.08	0	0	0	0	0	0	0	5.44	1230
Outer 2	0.054	2	0.54	0	0	0	0	0	0	0	0.18	0	0.72	400
Outer 1	0.036	2	0.28	0	0	0.14	0	0	0	0	0	0	0.42	220
Outer 3	0.018	1	0	0	0	0	0	0	0.14	0	0	0	0.14	490
Mainland 1	0.014	5	9.25	0	8.67	0	0	2.89	0	0.58	0.58	0	21.97	1350
Oak 1	0.007	3	5.53	0.5	0	1.51	0	0	0	0	0	0	7.54	380
Ironwood	-	1	1.05	0	0	0	0	0	0	0	0	0	1.05	500
Oak 2	-	3	1.56	0	0	0.22	0.22	0	0	0	0	0	2.00	440
Stockton 1	-	2	2.97	0	0	0	0	0	0.99	0	0	0	3.96	850
Stockton 2	-	4	0.74	0.37	1.47	0	0	0	0	0	0.37	0	2.95	610
Stockton 4	-	3	3.29	0	0	0	0	0	1.65	0	1.23	0	6.17	330
Stockton 5	-	2	10.87	0	0	2.17	0	0	0	0	0	0	13.04	590
Stockton 6	-	4	2.47	0.35	1.06	0	0	0	0.71	0	0	0	4.59	470

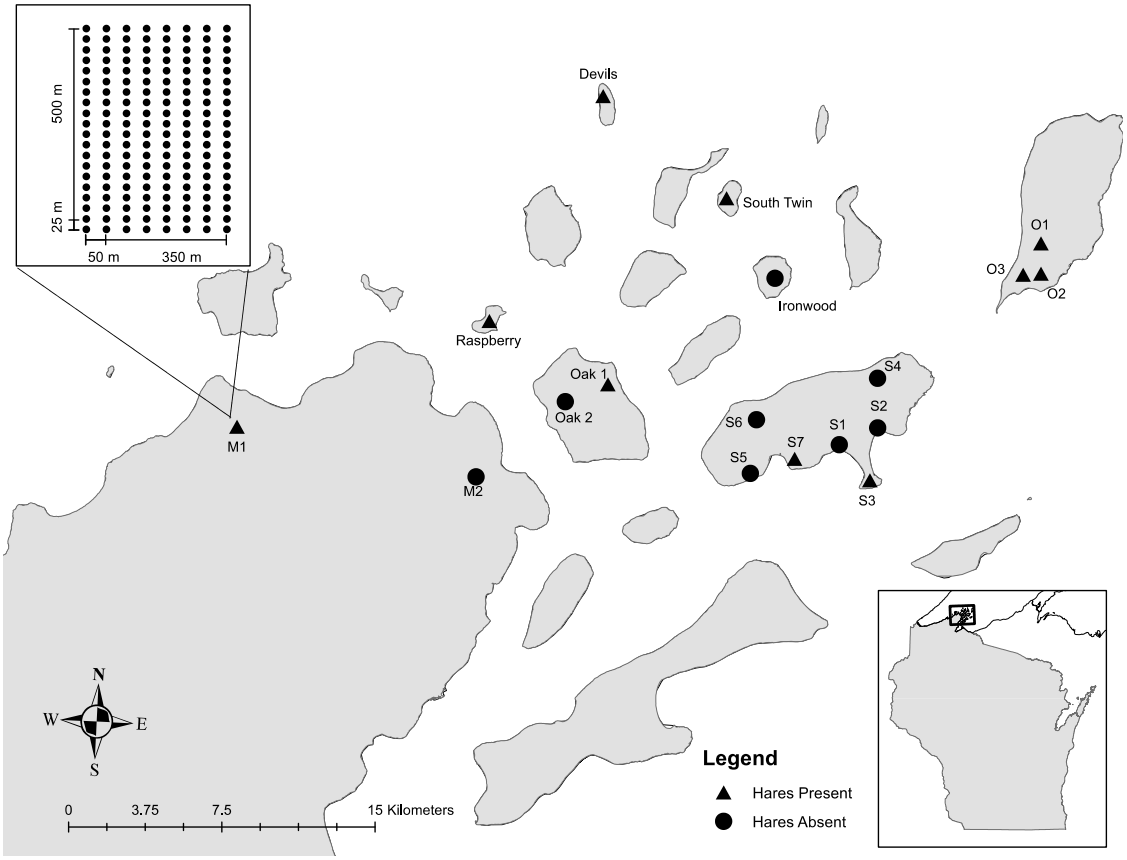

Figure 1. Snowshoe hare and visual obstruction sampling locations on the Apostle Islands and Bayfield Peninsula, Wisconsin. We sampled 18 grids, encompassing 7 islands and the mainland. Islands sampled included Devils Island, Ironwood Island, Oak Island (Oak 1-2), Outer Island (O1-O3), Raspberry Island, South Twin Island, and Stockton Island (S1-S7). Two locations were sampled on Bayfield County owned land (M1, M2). An example sampling grid, showing transect spacing is represented in the top left corner. Grids (500 m x 350 m) were composed of 8 transects spaced 50 m apart. Transects were composed of 20 sampling points, with 25 m spacing between points. Grids where snowshoe hare fecal pellets were found are represented by a triangle, whereas circles represent grids where pellets where not found

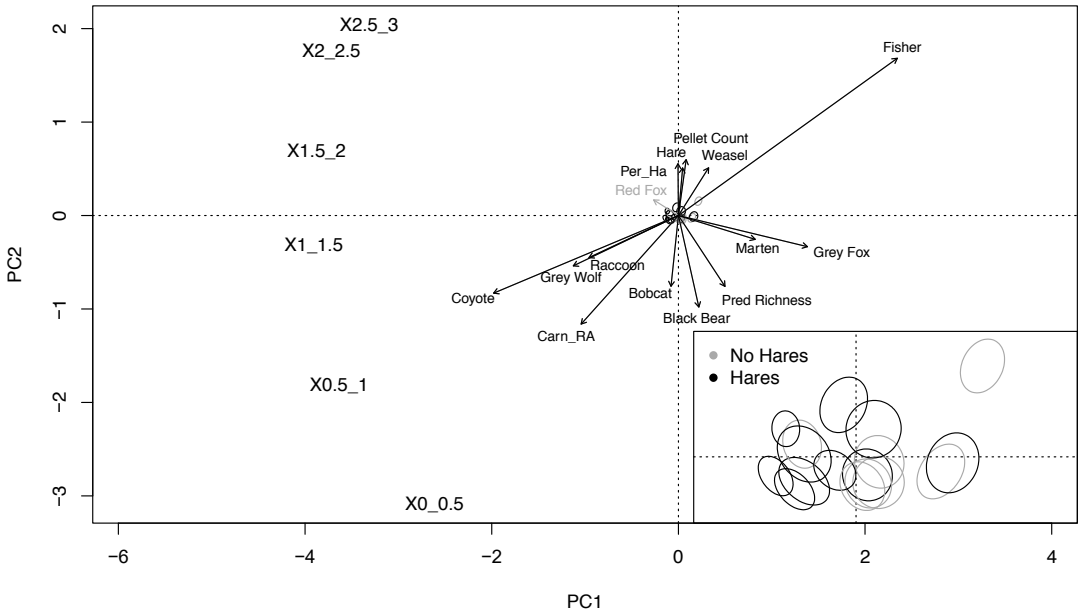

Figure 2. PCA (Scaling = 2) of visual obstruction values (1 – 5) for all height 0.5 m increments (X0_0.5 – X2.5_3). Mainland 2 points were not included as camera data was unavailable. The proportion explained by the first 2 axes was 76.71% (PC1=60.15%, PC2=16.57%). Inset in the lower corner is of enlarged ordiellipses of standard error of each grid to show grouping. Black ellipses represent grids with snowshoe hares present, whereas gray represents the absence of hares. Environmental variables (snowshoe hare abundance (Per_Ha), number of pellets found in pellet plots (Pellet Count), carnivore richness (Pred Richness), total carnivore relative abundance (Carn_RA) and carnivore relative abundances (represented by species name), and snowshoe hare relative abundance based on camera survey (Hare)) were overlaid using Envfit to examine relationships. Locations are represented by se ellipses for clarity. Black represents locations where snowshoe hare fecal pellets were present, whereas gray represents locations where they were absent. Black environmental vectors represent significant (P<0.05) correlations

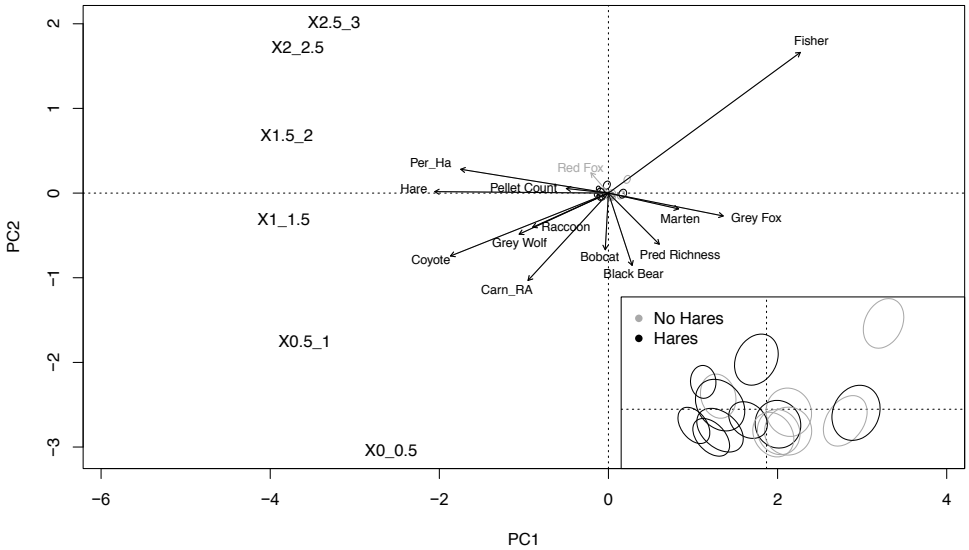

Figure 3. PCA (Scaling = 2) of visual obstruction values (1 – 5) for all height 0.5 m increments (X0_0.5 – X2.5_3). Mainland 2 points were not included as camera data was unavailable and Devils Island points were removed after skewing the results shown in figure 1. The proportion explained by the first 2 axes was 76.60% (PC1=60.09%, PC2=16.51%). Inset in the lower corner is of enlarged ordiellipses of standard error of each grid to show grouping. Black ellipses represent grids with snowshoe hares present, whereas gray represents the absence of hares. Environmental variables (snowshoe hare abundance (Per_Ha), number of pellets found in pellet plots (Pellet Count), carnivore richness (Pred Richness), total carnivore relative abundance (Carn_RA) and carnivore relative abundances (represented by species name) and snowshoe hare relative abundance based on camera survey (Hare)) were overlaid using Envfit to examine relationships. Locations are represented by se ellipses for clarity. Black represents locations where snowshoe hare fecal pellets were present, whereas gray represents locations where they were absent. Black environmental vectors represent significant (P<0.05) correlations

Chapter III

Extended Literature Review

Snowshoe Hare

Snowshoe hare (*Lepus americanus*) are a wide ranging lagomorph with a distribution that primarily coincides with the treeline in northern Canada and Alaska, down into the Rocky and Appalachian Mountains and through the Great Lakes region (Murray, 2000). Distribution at both extremes of their ranges seem to be largely a function of habitat and predation (Murray, 2000). While snowshoe hares have such a large distribution, they are a climate sensitive species with a southern range limit moving northward, likely due to changing climate conditions (Diefenbach *et al.*, 2016; Sultaire *et al.*, 2016; Burt *et al.*, 2017). Hares act as an important prey species for numerous predators, including the threatened Canadian lynx (*Lynx canadensis*), across their range (Hodges, 2000). Their close association with lynx, along with their climate sensitivity have caused the species to receive a large amount of research attention.

Hodges (2000) largely covers natural history, summarizing the findings from compiled studies. Here I briefly mention some aspects covered. Snowshoe hares are primarily herbivorous, consuming many plant species, twigs, bark, and many nonwoody species. However hares scavenge on carrion, primarily in winter months, which may be due to decreases in food and nutrient availability (Peers *et al.*, 2018). Hares may have up to four litters during the summer season, ranging from one to 14 young, called leverets. Breeding tends to be synchronous, which leads to distinct litter grouping. First litters tend to be smaller than the later litters. Dispersal studies have been limited, although in Wisconsin 7.8% of tracked hares dispersed or were found dead far enough away to suggest possible dispersal, but it has been argued that rates may be higher in smaller habitat patches. Natal dispersal distances ranged greatly, from 23 m to greater

than 16 km (Gillis and Krebs, 1999). Home ranges have been found to range from 0.5 – 6.1 hectares. Males were found to have a larger mean home range size of 2.8 hectares, compared to 1.4 hectares for females (Ferron and Ouellet, 1992).

Much of the research regarding snowshoe hares has focused on documenting and explaining their cyclical population trends. In the northern portions of their range, hares have well documented population cycles of about 10 years, although the cyclical trend is less pronounced and often debated in southern populations (Hodges, 2000). Potential factors that could have produced the cycles included overgrazing and therefore a food shortage, predation mortality, and parasites and diseases (Krebs *et al.*, 2018). Main causes are now mainly pointing to either food, or predators as the controlling agent.

Krebs *et al.* (2018) summarizes several hypotheses that have been tested over the years, including: 1.) winter food shortage 2.) changes in food quality and increases in secondary compound production 3.) heavy predation 4.) both food and predators. There is limited evidence of food quantity or quantity being limited (Krebs *et al.*, 2001a), although the addition of food has been shown to increase hare densities (Krebs *et al.*, 1986;Krebs *et al.*, 1995). In response to secondary compounds, resin has been shown to decrease protein digestibility, but this is unlikely to cause the decline in hare populations (Sinclair *et al.*, 1988). Predation has been shown to account for over 90% of hare mortality (Sievert and Keith, 1985; Cox *et al.*, 1997). Predatory influence on hares extends past direct mortality, including non-lethal indirect effects that negatively impact snowshoe hares, which I discuss later in the predation section. Krebs *et al.* (1995) were also able to show hare densities doubled in the absence of predators, however when adding food and removing predators the results were additive and was the only scenario that stopped the cyclical trend, indicating a three-trophic level interaction (Krebs *et al.*, 2001a). Krebs

et al. (2018) believe that the causation for the cycles across the northern region is direct mortality and indirect chronic stress on breeding females.

Another area that has been heavily researched is their molting between brown and white fur in relation to changing climate conditions. The molting process is initiated by photoperiod, not snow cover, therefore hares are facing an increasing number of days where they are mismatched from their surroundings (*i.e.,* brown hair and snow / white hair and no snow) (Mills *et al.*, 2013). Plasticity of molt characteristics had been thought to be a potential coping mechanism, however only limited plasticity was documented for the spring molt (Zimova et al., 2014). Additionally, mismatched hares did not modify their predatory avoidance behavior, indicating mismatched individuals were more at risk of predation (Zimova et al., 2014). Mismatched individuals were later shown to experience weekly survival decreases up to 7%, which could contribute to population declines with the further changing climate (Zimova *et al.*, 2016).

Predation

Throughout their range, snowshoe hare are an important prey species and are preyed upon by numerous predators including Canadian lynx (*Lynx canadensis*), coyotes (*Canis latrans*), bobcat (*Lynx rufus*), gray fox (*Urocyon cinereoargenteus*), red fox (*Vulpes vulpes*), Great Horned Owls (*Bubo virginianus*), and Goshawks (*Accipiter gentilis*) (O'Donoghue et al., 1998; Hodges, 2000). While lynx and hare relationships are often discussed, lynx are uncommon in portions of the southern extent of snowshoe hare's range and therefore coyotes are known to be one of the most important predators of hares (Sievert and Keith, 1985; Theberge and Wedeles, 1989; Cox *et al.*, 1997; O'Donoghue *et al.*, 1998;). Avian predatory pressure is also influential on hare populations. Avian predation is believed to limit hares from colonizing above the treeline

(Barta *et al.*, 1989). Avian predation also accounts for a large portion of snowshoe hare mortality in Wisconsin (Sievert and Keith, 1985). Studies indicate that most hares in southern populations die as a result of predators (Hodges, 2000).

Having an abundance of predators, hares have been shown to have high mortality rates. In Wisconsin near their southern boundary, predation accounted for over 90% of hare mortality (Sievert and Keith, 1985; Cox *et al.*, 1997). Survival probability of hares from birth to 1 year has been found to be 0.16 and adult yearly survival ranging from 0.33 to 0.58 (Brand *et al.*, 1975). Krebs *et al.* (1995) were also able to show snowshoe hare densities doubled in the absence of predators.

With decreasing snow duration, hares are seeing an increasing amount of days having a camouflage mismatch with their environment (brown fur with snow ground cover, or white fur with no snow cover). When mismatched, studies have shown increased predation rates, with hares having a 7% lower weekly survival rate when completely mismatched (Zimova *et al.*, 2016). Other studies have shown that when mismatched, hares don't change their predator avoidance techniques which likely explains higher mortality rates (Zimova *et al.*, 2014). For example, hares don't change hiding locations to where they blend in better or increase their flight initiation distances (Zimova *et al.*, 2014).

Predatory influence on hares extends past direct mortality. Predation risk may have indirect effects which negatively impact snowshoe hares, such as increased stress which has been shown to lower reproductive output (Sheriff *et al.*, 2009). Female hares that were stressed with a dog, representing a mammalian predator, produced smaller and lighter young than control females (Sheriff *et al.*, 2009). Female hares, stressed only during gestation, were also found to have lower survival rates themselves, and produced less young that made it to weaning age

(MacLeod *et al.*, 2018). The elevated stress levels of the dam has also been shown to be echoed into their offspring, which could lead to further lasting effects (Sheriff *et al.*, 2010).

Habitat

Habitat is a crucial component of any wildlife species. Snowshoe hares rely on high levels of cover, as protection from predators and the weather, as well as for winter browse (Buehler and Keith, 1982). While typically associated with the boreal forests of Alaska and Canada, snowshoe hares inhabit a wide variety of cover types given the broad extent of their range. The most commonly supported trends in habitat usage by hares is that hare use is correlated with understory cover (Hodges, 2000). Understory density appears to be the most important component in determining habitat usage, rather than species composition (Litvaitis *et al.*, 1985; Ferron & Ouellet, 1992). Overstory cover is also sometimes found to be correlated with habitat use (Hodges, 2000). However, in areas of heavy tree cover, shading may inhibit understory growth, indicating there may be an optimum level of cover (Adams, 1959).

In Carreker's (1985) suitability index, he recommends measuring cover up to 3 m, as heavy cover 3 m above the ground provides protection from potential avian predators, while cover below 1 m provides concealment from potential terrestrial predators (Wolff, 1980). Areas able to provide 90% visual obstruction during the winter are considered optimal, whereas values below 40% provide no suitable habitat during the winter months (Wolfe *et al.*, 1982; Carreker, 1985). Hares will occupy areas providing optimal habitat, dispersing into the less suitable areas as hare density increases (Wolff, 1980) This was further supported as Wirsing *et al.* (2002) found the greatest number of hares where the habitat featured a dense understory, but found areas without a dense understory virtually empty.

Hares may also impact and alter forest stands and in turn degrade their habitat. Hare browsing has been found to limit seedling survival and therefor caused tree recruitment to plummet after introduction of hares on Kent Island in New Brunswick (Peterson *et al.*, 2005). In northern Wisconsin and the Upper Peninsula of Michigan, hemlock regeneration was limited by snowshoe hares in deer exclosures (Alverson *et al.*, 2019). However, trees may combat heavy browsing pressure. After heavy browsing by hares, some species produce advantageous sprouts that contain higher terpene and phenolic resins concentrations that act as hare repellents (Bryant, 1981).

Pellet Surveys

Snowshoe hare populations have typically been estimated using fecal pellet surveys or mark-recapture live trapping. Traditional estimates came from mark-recapture studies, which are labor intensive and may induce unnecessary stress on animals. This approach was later used to develop a quicker estimation method, fecal pellet surveys. This technique generally involves counting the number of snowshoe hare pellets found within a set number of quadrants coupled with a regression equation, developed from mark-recapture studies of the same population, used to obtain a population estimate (Krebs *et al.*, 1987; Krebs *et al.*, 2001b).

The best methodology for this approach is often debated. Different size and shape quadrants have been found to yield different estimates (Mckelvey *et al.*, 2002; Murray *et al.*, 2002; Hodges and Mills, 2008). Krebs *et al.* (1987, 2001b) originally used small (0.155-m^2) rectangular quadrants for sampling, and this configuration is also recommended by other researchers (Mills *et al.*, 2005; Hodges and Mills, 2008). The use of large (1 m^2) circles has also been recommended, as this configuration has been found to be the most efficient logistically and statistically by some (Mckelvey *et al.*, 2002; Murray *et al.*, 2002). On the contrast, Hodges and

Mills (Hodges and Mills, 2008) found the smaller rectangular plots to take less time to sample, therefore allowing larger sample sizes for the same sampling effort as larger plots. Additionally, they question the ability of the large circles to sample under elevated downed wood, thickets, or along the edge of large trees, where rectangles might have a better ability at sampling these locations (Hodges and Mills, 2008).

While a relatively local equation has been developed in Minnesota (McCann *et al.*, 2008), they used large circular plots to count pellets, which may not perform well in our study area (Hodges and Mills, 2008). The Yukon regression equation developed by Krebs *et al.* (2001b) using small rectangular plots has been shown to perform similarly to locally developed equations (Murray *et al.*, 2002; Mills *et al.*, 2005). When using small rectangular plots, it is recommended that sample sizes should range between 50-100 per site, as small sample sizes result in poor estimates and precision, and larger sample sizes have decreasing returns in increased precession and accuracy (Hodges and Mills, 2008). When possible, it is recommended to clear plots prior to the start of the study so pellet counts aren't reflecting accumulating pellets that remain for more than a year and converting uncleared plots to cleared plots by aging pellets is inaccurate (Prugh and Krebs, 2004; Murray *et al.*, 2005). However, this is less practical in short-term studies such as ours, as you can't begin collecting data until the second year.

In using uncleared plots, we must just keep in mind the limitations and potential biases of our data. Uncleared plots will lack the ability to show rapid declines in hare populations if pellets last greater than a year, as the time frame being sampled is unclear (Prugh and Krebs, 2004). Uncleared plots will also likely yield higher pellet counts, and therefor higher, less accurate population estimates than previously cleared plots (Prugh & Krebs, 2004; Murray *et al.*, 2005, Hodges and Mills, 2008). While pellet surveys, previously cleared or uncleared, have their

limitations, they allow areas to quickly be evaluated in terms of low, medium, or high hare densities prior to labor intense mark-recapture studies (Mills *et al.*, 2005).

Apostle Islands

The Apostle islands archipelago make up the northernmost tip of Wisconsin, consisting of 22 islands in Lake Superior. All but Madeline Island are a part of the Apostle Islands National Lakeshore, which also includes a section of the mainland and was established in 1970 with the purpose "to conserve and develop for the benefit, inspiration, education, recreational use, and enjoyment of the public certain significant islands and shoreline of the United States" (Busch, 2008).

Judziewicz and Koch (1993) conducted a vegetation survey, detailing island specific summaries. Islands' vegetational communities vary across the archipelago as a result of microclimatic differences, their maritime situation and varying disturbance histories (Judziewicz and Koch, 1993). For example, far northern islands, such as Devils and Outer Islands, tend to have cooler climates and get hit by prevailing storm winds blowing across Lake Superior (Judziewicz and Koch, 1993). Temperatures also vary greatly due to microclimatic effects, with central locations of larger, higher islands having higher temperatures than at lake level and ravines draining cold air (Judziewicz and Koch, 1993). Disturbance histories include fire, logging, quarries, and homesteading, however lighthouses were constructed on five islands and their "reservations" of uncut forest remain on Devils, Raspberry, and Outer Islands showing the original vegetation (Judziewicz and Koch, 1993). Second growth now covers the majority of the islands (Judziewicz and Koch, 1993).

Relevant previous research has been conducted on the black bear populations inhabiting the islands. Black bear density was found to be the highest in Wisconsin and among the highest

in North America, and genetic variation suggested immigration from the mainland (Belant *et al.*, 2005; Wilton *et al.*, 2015). Black bears are also the only winter-inactive species found, which are capable of swimming the distances to the islands (Belant and Van Stappen, 2002). However, ice cover duration is declining by approximately three days per decade, which may limit immigration by other species to the islands from the mainland in the future (Howk, 2009).

More recent research has been focused on documenting the carnivore guide found across the archipelago. Remote camera traps were dispersed in a systematic grid across 19 of the 21 islands and the mainland within the National Lakeshore to document what is inhabits the area (Allen *et al.*, 2017). In this study, they were able to document higher richness (including all but two native carnivores), abundance, and occupancy than expected (Allen *et al.*, 2017)(Allen *et al.*, 2018a). This included documenting the states only endangered mammal, American marten (Allen *et al.*, 2018b). While this camera survey was targeting carnivores, prey species appeared to be outnumbered by carnivore species, which raises questions regarding the sustainability of carnivore populations (Allen *et al.*, 2017). Small mammal trapping also identified a limited subset of potential prey species (Smith and Maragi, 2004; Smith and Fawver, 2005). The recent findings on the diverse carnivore community found across the Apostle Islands archipelago calls for a better understanding of ecological dynamics, including small mammals which may act as a prey base (Allen *et al.*, 2017; Allen *et al.*, 2018a).

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