SEASONAL INFLUENCES ON HABITAT USE BY SNOWSHOE HARES: IMPLICATIONS FOR CANADA LYNX IN NORTHERN MAINE

By
Sheryn J. Olson
B. S. Zoology, University of South Florida, 1977

A THESIS
Submitted in Partial Fulfillment of the Requirements for the Degree of Master of Science (in Wildlife Ecology)

The Graduate School
The University of Maine
May 2015

Advisory Committee:

Daniel J. Harrison, Professor and Chair, Department of Wildlife, Fisheries, and Conservation Biology, and Cooperating Professor of Sustainable Forestry, Advisor

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On behalf of the Graduate Committee for Sheryn J. Olson, I affirm that this manuscript is the final and accepted thesis. Signatures of all committee members are on file with the Graduate School at the University of Maine, 42 Stodder Hall, Orono, Maine.

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SEASONAL INFLUENCES ON HABITAT USE BY SNOWSHOE HARES: IMPLICATIONS FOR CANADA LYNX IN NORTHERN MAINE

By Sheryn J. Olson

Thesis Advisor: Dr. Daniel J. Harrison

An Abstract of the Thesis Presented
In Partial Fulfillment of the Requirements for the
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Snowshoe hares (*Lepus americanus*) respond to seasonal changes in vegetation in the northern and western portions of their range. During winter, hares use dense conifer stands that may provide thermal and predatory refugia, then during summer move to areas with more herbaceous food and cover. These movements influence hare demographics, with greater survival rates corresponding to seasonal use of dense, primarily coniferous stands. Different harvesting practices in commercial forests produce vegetative communities that may support differing hare densities among forest stand-types between seasons, but seasonal use of habitat had not been documented in northern Maine on a large spatial and temporal scale. In response to spatio-temporal availability of hares, the U.S. federally threatened Canada lynx (*Lynx canadensis*) may shift their resource selection. Though lynx may be relatively less specialized on snowshoe hares in mid- and southwestern regions of their range, their degree of dietary specialization had not been quantified in Maine.

In Chapter One, I investigated whether snowshoe hare pellet densities were different between two seasons across three forest stand-types: regenerating (RG) coniferous-dominated (19-39 years post-harvest), selection harvested (SEL) mixed coniferous-deciduous (8-18 years), and mature (42-80 years). I then determined what vegetation
characteristics most strongly influenced hare densities between seasons across 26 forest stands. I evaluated 17 candidate models using generalized linear mixed models and standard model selection techniques.

Hare densities, indexed by pellet densities, were measured semi-annually in 41 stands from 2005–2012. Densities were significantly higher during leaf-off (winter) than leaf-on (summer) periods in RG stands, but not in mature or SEL stands. Pellet densities were greater in RG than other stand-types during both seasons, and unexpectedly, significantly higher during the leaf-on season. These results suggest greater winter survival or movement to RG from summer to winter, and relatively higher summer survival and juvenile recruitment in RG. Seasonal differences in pellet densities across 26 stands were most strongly influenced by conifer sapling density [68% relative importance weight (RIW)] and total sapling density (11% RIW). During the leaf-off season when snow may interact with vegetation, the strongest influence on pellet densities was percent understory coverage of all conifer foliage (RIW 88.9%).

In Chapter Two I examined whether lynx shift their food habits at the southeastern limit of their range. I documented food habits using scats genetically confirmed as lynx during a summer-lower (2007-2012, 0.92 hares/ha, n=199 scats) and a winter-higher hare density period (2001-2006, 1.98 hares/ha, n=125). The summer-low had greater dietary breadth than winter-higher hare density period ($F_{4,322}=0.0068$, 1000 randomizations). Frequency of occurrence of hares in food item categories declined during summer-low (75.2%, n=230 food item categories) compared to winter-high hare density period (92.1%, n=127). I suggest increased relative availability and accessibility of rodents and birds promotes diversification of lynx diets during the summer-low. Greater use of hares
during both seasons and across periods of changing hare density indicated lynx specialize on snowshoe hares at the southeastern limit of their geographic range, although lynx broaden their dietary niche when relative availability of alternative prey increases.
PREFACE

Canada lynx, hereafter lynx, were declared federally Threatened on March 24th, 2000 (U.S. Fish and Wildlife Service 2000), and have long been recognized to have a co-evolved relationship with snowshoe hares and the snow-covered landscapes of the boreal and sub-boreal forests of north America (McFarlane 1905, Seton 1909, Elton and Nicholson 1942). In March, 2009 the U.S. Fish and Wildlife Service designated critical habitat for Canada lynx in 13 states (declared “final” in 2014), including Maine (U.S. Fish and Wildlife Service 2009;2014). Maine is approximately 90% forested, and the 26,218 km² of northern Maine that was designated as critical lynx habitat is 92% privately owned and managed principally for wood products. Land owners who practice forestry to promote sustainably sourced timber products through the Forest Stewardship Council® or the Sustainable Forestry Initiative, have an incentive to monitor threatened and endangered species.

Lynx are considered specialist predators of snowshoe hares and depend upon hares for their survival. Lynx may require > 0.5 hares/ha across the landscape to persist (Ruggiero et al. 2000, Steury and Murray 2004, Simons-Legaard et al. 2013). In Maine, the probability of occurrence by a resident individual lynx in a home range increased with both a higher percentage of mature conifer forest and greater landscape-scale snowshoe hare density (average = 0.74 hares/ha). Further, lynx did not occupy areas with landscape-scale snowshoe hare density < 0.5 hares/ha (Simons-Legaard et al. 2013). Seasonal differences in hare density across different habitats may influence lynx reproduction and survival of kittens into winter because female lynx with kittens contract their home ranges during summers (Vashon et al. 2008a) and during the April-May denning season (Mallett 2014), and may consequently have fewer snowshoe hares
available to them while provisioning kittens. Low hare densities in Alberta, Canada resulted in kitten mortality of 65-95% (Brand and Keith 1979). Thus, relative densities of snowshoe hares among different forest stand treatments and the configuration of those forest patches may affect landscape and stand-scale habitat quality for lynx in the transitional northern hardwood-southern boreal region known as the Acadian Forest (Seymour and Hunter 1992).

Although landscape-scale abundance of snowshoe hares can affect lynx occurrence (Simons-Legaard et al. 2013), relative abundance of hares among different habitats and between seasons likely influences movement (Fuller and Harrison 2010) and reproductive performance of individual lynx, such as yearling fecundity and recruitment (Brand and Keith 1979, Moen et al. 2008). Lynx respond to relative densities of snowshoe hare among different habitats and in different seasons, preferring dense forest stands compared to open areas in Yukon, Canada, (Mowat and Slough 2003), Washington (Koehler et al. 2008), and Montana (Squires et al. 2010). Female lynx may be affected most when they are denning, because they contracted their home ranges when using dens in Alaska (Kesterson 1988), the Yukon, Canada (Mowat and Slough 1998), Minnesota (Burdett et al. 2007), and in Maine (Vashon et al. 2008a, Mallett 2014). Female lynx with kittens may need to either have locally available snowshoe hares when they are foraging near their dens, or broaden their diets if hares are at low density.

Hares may be less important to lynx at the southern extent of their range (Apps 2000, O'Donoghue et al. 2001, Roth et al. 2007), during cyclic low hare density periods (Brand et al. 1976, Koehler 1990, Staples 1995, O'Donoghue et al. 1998, Mowat and Slough 2003), and during snow-free periods (van Zyll de Jong 1966, Parker et al. 1983, Staples...
Seasonal prey shifting from larger snowshoe hares to smaller, less energetically efficient prey such as red squirrels or voles may influence lynx reproductive success. If lynx in Acadian Forests of Maine exhibit seasonal changes in food habits during periods of relatively lower hare densities, habitat management for alternative prey may be important. For example, red squirrels require conifer stands with trees mature enough to produce cones (Holloway and Malcolm 2006) and may not reach highest densities in regenerating conifer stands where hares are most abundant. In contrast, if lynx in Acadian Forests are dietary specialists upon snowshoe hares throughout the year and during high and relatively lower hare density periods, providing adequate high quality snowshoe hare habitat at a landscape scale to ensure lynx persistence will need to be a high priority for land managers attempting to promote lynx habitat near the southeastern edge of the species' geographic range.

I investigated how snowshoe hares respond to seasonal influences of vegetation characteristics among different forest stands, and documented seasonal food habits of lynx in Acadian Forests of northern Maine with three objectives. I sought to: 1) determine and compare the magnitude of changes in hare density between seasons across three forest stand-types that had different silvicultural legacies (Chapter 1, Objective 1); 2) examine how vegetative structure and species composition affected hare pellet densities between seasons across a gradient of forest stands (Chapter 1, Objective 2); and 3) document the extent to which lynx may shift their food habits away from snowshoe hares when other prey is seasonally available, and when hares are at relatively low versus high densities (Chapter 2).
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we can influence their future. I had the notable opportunity to spend time in the north Maine woods with Dan, Bill and Bob, and learned more from those days walking and snowshoeing through the forests with them than I could from years of reading journal articles and consulting field guides! Jennifer Vashon at MDIFW generously shared lynx data, and her knowledge of lynx and snowshoe hare ecology. Our conversations and Jennifer’s perceptive questions led me to understand lynx ecology in ways I could not have from reading the literature. The quietest member of my committee was Mark McCollough and I can count the number of words I’ve heard him say throughout my graduate program. But each question, each phrase was so insightful and pointed that I was considering his thoughts for many months. I hope to attain a level of proficiency and professionalism with undiminished enthusiasm for the ecological systems of our planet that my committee members have demonstrated.

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CHAPTER 1

SEASONAL CHANGES OF SNOWSHOE HARE PELLET DENSITIES AMONG MANAGED FOREST STANDS IN NORTHERN MAINE

ABSTRACT

Commercial forest management within the transitional Acadian Forest region produces diverse forest stands, some with characteristics of spruce-fir boreal forests and others with mixed deciduous-coniferous composition. Snowshoe hares (*Lepus americanus*) have been documented to move seasonally between dense conifer stands that may provide thermal and predatory refugia during winter, and adjacent areas that provide herbaceous food and cover during summer. These movements influence hare demographics, with greater survival rates corresponding to seasonal use of stands with different vegetative communities. Snowshoe hares in Maine comprise an important prey base for a rich community of avian and mammalian predators, especially the U.S. federally threatened Canada lynx (*Lynx canadensis*), but seasonal hare use of forest stands has not been examined on large spatial and temporal scales in the Acadian Forest region.

I first determined whether seasonal (leaf-off vs. leaf-on) change in hare fecal-pellet density differed across three stand-types; Mature (MT), Selection harvest (SEL), and Regenerating conifer (RG), located within a 2,516 km² study area. I used semi-annual pellet counts from 2005–2012 (16 seasons) conducted in 41 forest stands within the three stand-types, to develop a generalized linear mixed model. I then assessed what vegetation structure and species composition best explained seasonal differences in hare pellet
densities across a gradient of 26 stands, during three winter and three summer seasons from 2010–2013.

Seasonal change in the density of hare pellets was significantly greater in RG stands than in MT or SEL stands. Contrary to expectations for the leaf-on season, pellet densities in RG stands were $3.1 \times > SEL$ and $9.3 \times > MT$ stand-types, suggesting that RG stands do not just serve as winter refugia, but are superior habitat for snowshoe hares throughout the year. RG stands had greater winter and summer pellet densities relative to SEL and MT stands, suggesting that RG stands provided more favorable conditions for survival or recruitment of hares. The greater rate of increase in summer to winter pellet densities observed in RG stands relative to other stand-types indicates that hares may also move into RG stands from adjacent stands during winter.

Across 26 stands that were not grouped into stand-types, conifer sapling density had the most support relative to 16 other structure and species composition models affecting hare pellet density differences between seasons, with 68% of the relative variable importance weight (RIW), followed by total sapling density (11% RIW), percent understory coverage (8.1%), percent understory conifer coverage (6.5%), and deciduous tree density (4.6%). The importance of dense understory coverage was evident during leaf-off seasons. Using a leaf-off subset of the data, I demonstrated that snow interacting with percent coverage of understory conifer vegetation (RIW=88.9%) positively influenced hare pellet densities more than 12 other models ($\Delta AIC_c > 4.2$) that assessed vegetation interactions with snow depth. Dense coniferous-dominated stands 19–39 years old with a multi-structured coniferous community supported the highest densities of snowshoe hares during both summer and winter within the Acadian Forest region.
INTRODUCTION

Observers of snowshoe hares (*Lepus americanus*) have long recognized that individual hares use different habitats seasonally. Wallace Grange (1932:4) remarked of Wisconsin snowshoe hares:

"There is no doubt a great variation in the attractiveness of certain of the forest habitats during the different seasons. It is evident that swamps and clumps of upland conifers are of increased importance in winter, and that some aspen woods that are deserted in winter are inhabited in summer; but beyond this rather vague statement we have no very tangible conclusions."

There is now evidence that hares (*Lepus* spp.) monitored with telemetry do shift their home ranges seasonally, selecting dense conifer or mixed coniferous-deciduous forest stands in winter, and more open areas with dense herbaceous understory during summer (Wolff 1980, Hearn et al. 1987, Hulbert et al. 1996, Dahl 2005, St. Laurent et al. 2008, Griffin and Mills 2009, Ivan et al. 2014). Additionally, seasonal habitat choices by hares directly influence vital rates in the southern portion of their range (Dolbeer and Clark 1975, Pietz and Tester 1983, Griffin and Mills 2007, Griffin and Mills 2009). Juveniles dispersing through open areas encountered high predation rates, the major factor attributed to dampened amplitude of hare population cycles in Utah and Colorado (Dolbeer and Clark 1975). Higher winter survival was associated with hares shifting their winter habitat use to dense coniferous stands in Montana, where those stands were considered source areas (Griffin and Mills 2009). In contrast, hares exhibited declining populations in dense scrub patches within a highly fragmented landscape in Idaho; metapopulation processes were proposed to maintain population stability via immigration.
to dense areas of vegetation (Wirsing et al. 2002). Thus, individual snowshoe hare movement and habitat use by season affects population level dynamics, such as over-winter survival rates of adults, and can result in large differences in relative hare densities among forest stands with different vegetative characteristics (Wirsing et al. 2002, Griffin and Mills 2009).

Snowshoe hare demography is associated with the ecology of the U.S. federally threatened Canada lynx (*Lynx canadensis*). During periods of low snowshoe hare densities, lynx dispersal distances increase, home range sizes may increase, social structure may degrade, and fecundity declines (Nellis et al. 1972, Brand and Keith 1979, Koehler and Brittell 1990, Poole 1994, Slough and Mowat 1996, O'Donoghue et al. 1997, Apps 2000, Mowat et al. 2000, O'Donoghue et al. 2001). Recruitment of lynx kittens ceased at hare densities of 0.4–1.3 hares/ha in Alaska, Yukon and Northwest Territories, Canada (Poole 1994, Mowat et al. 1996, Slough and Mowat 1996). Reduced litter sizes of lynx were observed in Maine (Vashon et al. 2012) during periods of lower hare density (Harrison et al. 2011) (Figure E.4). In the Acadian Forest Region (Seymour and Hunter 1992), lynx population dynamics may be affected by changing seasonal distributions of hares responding to phenological changes in vegetation.

In Maine, stand level hare densities appear greatest in dense forests, especially conifer-dominated stands where sapling densities can reach >10,000/ha (Fuller and Harrison 2005, Homyack et al. 2007). These conclusions, however, were based on leaf-off season (November 1–April 30) hare densities (Lachowski 1997, Fuller and Harrison 2005, Robinson 2006, Homyack et al. 2007, Scott 2009, Fuller and Harrison 2013). Seasonal dynamics contributing to stand-level differences in hare densities have not been
characterized on a large spatio-temporal scale in the transitional mixed coniferous-deciduous Acadian Forest region that includes the commercially managed forests of northern Maine.

My goal was to characterize how forest stands with different harvest treatments influenced seasonal change in densities of snowshoe hares in northern Maine. Studies investigating aspects of snowshoe hare ecology commonly use annual fecal pellet counts (Murray et al. 2002, McCann et al. 2008, Berg and Gese 2010, Thornton et al. 2012) and pellets from previously un-cleared plots (Newbury and Simon 2005, Hodges et al. 2009, Berg and Gese 2010, Sullivan et al. 2010, Lewis et al. 2011), despite that pooling data across seasons or years can lead to misleading inferences about temporal variability in habitat use (Schooley 1994). Research designs using a long term data set of semi-annual pellet counts are rare (but see Sullivan et al. 2007). Semi-annual counts were conducted in northern Maine beginning in 2001 (Homyack et al. 2006), which provided an opportunity to compare how use of stands by hares changes between the leaf-on seasons from May 1 – October 31 (termed summer) and leaf-off seasons from November 1 – April 30 (termed winter), and to evaluate the vegetative and structural characteristics of stands associated with those changes.

My first objective compared seasonal changes in hare pellet densities across three forest stand types: regenerating coniferous-dominated (19-39 years post-harvest), selection harvested mixed coniferous-deciduous (8-18 years post-harvest), and mature conifer and mixed (42-80 years post-harvest). Disproportionate seasonal changes in pellet densities across stand types could indicate seasonal movement of hares, or relatively greater survival and reproduction of resident hares within different stand types.
Importantly, stands with insufficient cover in either season may be functioning as areas of high snowshoe hare mortality, as was documented elsewhere (Dolbeer and Clark 1975, Sievert and Keith 1985, Griffin and Mills 2009). I hypothesized that hare pellet densities would exhibit greater change from summer to winter in 19-39 year old regenerating conifer stands relative to other forest stand-types, resulting from hares moving into those stands with greater cover. Additionally, I hypothesized that selection harvest stands would exhibit a greater seasonal change in pellet densities than mature stand types, because selection harvest stands have a diverse, multi-storied vegetative community (Fuller et al. 2004, Robinson 2006, Campbell et al. 2007, Bataineh et al. 2013, Fuller and Harrison 2013), that could provide relatively more food resources during leaf-on seasons and more near-ground conifer cover during leaf-off seasons.

In a second objective, I examined which components of vegetation structure and species composition influenced snowshoe hare use of seasonal resources, as measured by fecal pellet densities. Structure has been described as more important than species composition as a driver of habitat selection by snowshoe hares in Maine and southeastern Quebec, Canada (Litvaitis et al. 1985, Ferron and Ouellet 1992, Potvin et al. 2005). Hence, I predicted that vegetation structure would influence seasonal change in pellet densities more than composition of the vegetative community. I expected that structural variables including sapling densities, canopy cover, and lateral cover (visual obstruction) would contribute to large seasonal differences in pellet densities. Further, I expected that pellet densities would be greatest during both seasons where the understory density was greatest because hares may use dense cover as a resource for resting (Ferron and Ouellet 1992, Wirsing et al. 2002, Beaudoin et al. 2004, Osburn and Cramer 2013, Feierabend
and Kielland 2014), or as a thermal refuge (Sheriff et al. 2009c). Species composition affects structure, however, and conifer-dominated forest stands at a young seral stage typically reach higher sapling densities than stands with more deciduous components within Acadian Forests. Thus, I expected metrics that describe conifer components (percentage of understory conifer coverage, conifer sapling densities) would influence seasonal changes in hare densities more strongly than other vegetation attributes. Because deciduous vegetation provides little cover in winter, but might provide ephemeral cover from leaves, as well as leafy food resources during summer, I expected variables describing deciduous vegetation to also significantly affect seasonal shifts in hare density. In winter I considered the effects of snow, as an important abiotic factor, interacting with vegetation on a subset of winter-specific pellet densities. I expected that snow interacting with greater canopy cover and greater conifer sapling density would positively affect pellet densities during winter, while snow interacting with deciduous vegetation and less overhead canopy cover would negatively affect pellet densities.

METHODS

Study Area

My study area spanned 15 townships (Figure 1.1) of privately owned forestland managed for saw timber, pulp wood products, and wood biomass in northern Maine (Maine Forest Service 2009). The extent of the study area that encompassed my 30 forest stands (circa 2012) was ~2,516 km². Ownership included private Timberland Investment Management Organizations (TIMO), family-owned companies, investor organizations, and Real Estate Investment Trusts (REIT) (McWilliams et al. 2005). Elevations range from 290-686 m and average annual temperature was 13.3°C, with average temperatures
for July of 17.5°C and for January of 3.0°C. Average annual precipitation was 95.6 cm, of which 167.4 cm was snow (National Oceanic and Atmospheric Administration, 2000–2008).

The study area is in the Acadian Forest Region, an ecological transition zone between the southernmost extent of the boreal forest and northernmost extent of the temperate deciduous forest (Seymour and Hunter 1992). Much of the study area consists of the “Spruce-Fir Wet Flat” community type (Maine Natural Areas Program 2010). Forest management prescriptions and their harvest legacies, coupled with stand-replacing disturbances, created dense forest stands dominated by primarily balsam fir (Abies balsamea), red (Picea rubens) or black (P. mariana) spruce, with minor components of white spruce (P. glauca), northern white pine (Pinus strobus), northern white cedar (Thuja occidentalis), larch (Larix laricina), and eastern hemlock (Tsuga canadensis). These conifer-dominated stands resemble boreal forests and resulted from clear-cut logging, followed by herbicide treatment (e.g., glyphosate) to suppress competing deciduous regeneration (Seymour et al. 2002). Other stands that were never herbicide treated occurred on slopes or at higher elevations and featured sugar maple (Acer saccharum), yellow, paper and gray birch (Betula alleghaniensis, B. papyrifera, B. populifolia) respectively, striped, mountain and sugar maple (Acer pensylvanicum, A. spicatum, A. saccharum) respectively, American beech (Fagus grandifolia), with occasional balsam fir, ash species (Fraxinus spp.), aspen (Populus tremuloides and P. grandidentata), pin cherry (Prunus pensylvanica), raspberry (Rubus idaeus), and alder (Alnus incana).
Figure 1.1. Location and extent of the 2,516 km$^2$ study area and stand locations in Piscataquis and Aroostook Counties, Maine, USA. Depicted are locations of 29 stands surveyed for hare pellets and vegetation in 2012. Stand-types were regenerating conifer-dominated, post-herbicide treatment, represented by light circles ($n = 15$), selection-harvest mixed coniferous-deciduous, triangles ($n = 9$), mature conifer spruce-dominated stands, squares, and mature mixed coniferous-deciduous, dark circle. Mature stands combined into one mature category ($n = 5$). The number of stands sampled varied each season because of harvest activity that occurred during the study period (2005–2013).
Stand Configuration and Hare Pellet Surveys

Beginning in 2001, hare pellet survey plots were established in forest stands to represent six management legacies throughout northern Maine, with a total of 52 stands established by 2013 (Table A.1). Eleven stands that were surveyed prior to 2005 were excluded from this study because they were harvested. For objective one, I evaluated three stand-types composed of the remaining 41 stands that were surveyed starting in fall 2005 and ending in spring 2012 (Table A.2).

For objective two, I evaluated which vegetation characteristics best explain seasonal differences in pellet density. For those analyses, I used 26 stands over a three year period (2010-2013, 6 seasons) to avoid the possibility of successional processes affecting vegetative communities. By 2010, the number of samples for objective two was 26 stands, as 15 of the 41 stands used for objective one had been harvested (Table A.3).

The three stand-types considered were mature conifer and mature mixed coniferous-deciduous stands (MT), regenerating conifer-dominated stands (RG), and partial harvest stands of mixed coniferous-deciduous cover type that were categorized as selection harvest (SEL) or overstory removal (OVR). Mature stands (MT, \( n=13 \)) were established and cleared of pellets in 2007 and surveyed beginning in 2008 (Scott 2009). I combined two mature stand-types mature conifer and mature mixed coniferous-deciduous into a single mature stand (MT) type because of similar structural characteristics such as diameter at breast height (DBH) and a sparse understory. Forest Inventory Assessment data estimated mature conifer-dominated stand age at \(~80\) years among a broader matrix in northern Maine (E. Simons-Legaard, personal communication), and all mature stands had not been harvested for at least 42 years prior to 2012. Regenerating conifer stands
(RG, \( n = 15 \)) were clear-cut an average of 32.3 years prior to 2012 (range 27-39), then herbicide treated and average of 8.6 years post-harvest (range 4-21) to suppress deciduous growth and to release naturally regenerating spruce and fir. Resulting stands were densely stocked with balsam fir with minor components of white pine, and red and black spruce. Partial harvest (~50% of basal area removed) stands were harvested an average of 16.8 years before 2012 (range 16-18, \( n = 11 \)) and included one shelterwood retention stand, two overstory removal stands, and eight selection harvest stands (Table A.2). These stands included conifer and deciduous components, and were established to represent partial harvest practices throughout the study area (Robinson 2006). I used 11 SEL stands for objective one (Table A.2), and 7 for objective two (Table A.3).

Sampled stands were separated by > 0.6 km to maintain independence, given home range sizes of hares in Maine (Litvaitis 1984). Each stand was at least 335 m x 500 m (16.75 ha), including a 70 m buffer to minimize edge effects for hares (St. Georges et al. 1995, Newbury and Simon 2005). Stand areas including their buffers ranged from 16.8-47.5 ha. Most stands had four transects 65 m apart, each with seven 1.5 m² pellet plots, which were spaced 60 m apart for a total of 28 plots per stand (Figure C.1). However, stand configuration varied to ensure intra-stand consistency in stand type and harvest treatment, which resulted in 24–43 plots/stand that were spaced along 4-9 transects. To address objective one, 89% (36/41) of stands had 28 plots, and for objective two 85% (22/26) of the stands had 28 plots. Pellet plots were 1.5 m² in a “long-thin” configuration recommended to capture microsite gradients of topography and vegetation (Hodges and Mills 2008). Though circular plots performed better than rectangular plots to model hare densities below 0.5 hares/ha in Idaho, where 0.155 m² rectangular plots were compared to
one m² circular plots (Murray et al. 2002), the area of plots in Maine were ten times larger than the area of rectangular plots sampled in Idaho. In a typical stand, the 28 pellet plots that were surveyed totaled 42 m². Leaf-on (summer) pellets counts were conducted during late September-early October and leaf-off (winter) pellet counts occurred during May-early June. Field crews counted, then cleared all pellets in each randomly oriented rectangular plot (5 x 0.3 m) using a 30 cm dowel as a guide.

Vegetation Surveys

To assess how vegetation structure and composition affected seasonal differences in hare pellet densities, I measured vegetation in 20 plots/stand during summers 2011 and 2012, and in 10 plots/stand during winter 2012. Fewer plots were surveyed during winter to ensure that I could sample each stand during a single day and that I could complete all stands during winter 2012. I quantified overhead cover, snow depth, basal area (BA), lateral cover (visual obstruction), and sapling and tree counts in four categories: conifer, deciduous, dead, and live. All saplings were defined as <7.6 cm diameter, >1.5 m tall, and trees >7.6 cm diameter. At each of the 20 plots, I point-sampled summer vegetation in 10 m² plots.

Standing at each plot’s center, technicians took overhead canopy-cover (cc) measurements using a spherical densiometer, averaged from four cardinal directions along a random azimuth and measured at 1.3 m above ground. We measured average snow depth (cm) based on two measurements/plot taken 2.5 m from plot center; the first in a randomly chosen direction and the second 180° from the first. We measured basal area (BA) with a 2-factor metric prism (BA m²/ha) for saplings and trees. Life size standing and bedded deer silhouettes painted with black and white checker-board squares
have been used to assess relative cover values (Griffith and Youtie 1988), but black and white squares may be more visible through vegetation than a vertebrate that has cryptic coloring, and sizes of squares are arbitrary. To assess lateral cover more accurately, crews evaluated lateral cover (LC) with a silhouette of life-sized photographs of a brown hare in summer and white in winter, silkscreened (Dynamic Seven, Inc., Titusville, FL) onto corrugated plastic (Coroplast™) (Figure C.2). A field technician rotated the hare 360° until another technician, facing away, signaled to drop the hare at center plot. Crews estimated coverage of the silhouette with 2 ocular measurements 180° from each other, 5 m distant at 0.5 m above ground; photos were taken for later confirmation of field estimates. I defined LC categories as: 0%, 1-5%, 6-25%, 26-50%, 51-75%, 76-95%, 95-99%, or 100% obscured. We counted trees and saplings surrounding each plot’s center in a 20 m², or 10 m² circle when trees were very dense (>10,000 trees/ha), then standardized to count/0.1 ha for analysis.

Vegetation survey plots were offset 50 cm from pellet plot centers to avoid disturbances to vegetation that may have occurred from counting and clearing pellets (Figure C.3A). I sampled four layers (strata) of vegetation with a GRS densitometer™: ground to 7 cm high, 7 cm–50 cm, 50 cm–150 cm (understory), and overhead; at 18 points/stratum, 20 plots/stand (Figure C.3B), and totaling 360 points/stratum for each stand. I then calculated percent of a vegetation category/stand/stratum; for example, if 53 of 360 points were conifer branches or tree boles, that stand had 14.7% conifer coverage at a given stratum. The stratum at 50–150 cm high was available to snowshoe hares year-round and was used in models as a predictor variable termed “understory” for this study; in winter, that height corresponded with vegetation that was ~17–117 cm above snow-
level, when snow depth averaged 32.6 cm ($n=26$ stands) during winters 2012–2013. Average snow depth among stand-types ranged from 28.1 cm in RG stands to 44.8 cm in MT stands. Vegetation and ground cover were consolidated into each of 3 categories: % total coverage, % conifer understory, and % deciduous/shrub understory.

**Statistical Analyses**

For both objectives, I evaluated the efficacy of using hare rather than pellet densities as a response to seasons (Appendix B), because hare density can be more directly used as a management tool. Although winter pellet densities predict hare densities well in Maine (adj. $r^2=0.87$) (Homyack et al. 2006), I found that summer pellet densities had less precision to predict hare densities when calibrated with hares live-trapped in June ($r^2 = 0.428$, $F_{(1,6)} = 4.49$, $P = 0.078$, predicted residual sum of squares (PRESS) = -0.03, Figure B.1A). Thus, I chose to use pellet density, not hare density to evaluate changes in seasonal habitat use by hares. Rather than use the rate - pellet counts per unit time per unit area - as the response variable, I used direct pellet counts within each stand and incorporated temporal and spatial variability into specifications of the models.

When a count dataset includes a large proportion of zeros, it can have a highly skewed distribution that may be overdispersed (i.e., as the mean increases, the variance increases), and a negative binomial generalized linear mixed model (GLMM) with a log link has been shown to perform well with overdispersed count data (Boyce et al. 2001, VerHoef and Boveng 2007, Richards 2008, Linden and Mantyniemi 2011, Linder and Lawler 2012, Saffari et al. 2012). Preliminary analyses of the datasets for both objectives confirmed that the response variable, pellet counts, conformed to a negative binomial distribution. Further, I used standard inference techniques to assess the fit of a global
model as a negative binomial GLMM relative to four other model frameworks, (Appendix D) and found the negative binomial model had the most support. All models were thus specified as a negative binomial GLMM that uses a log-link function with an overdispersion parameter. During this study, area sampled for pellets and time between counts varied, necessitating spatial and temporal adjustments in statistical models. I used a standardized area covariate to adjust for different areas (m$^2$) sampled for pellets and an offset to adjust for differing time available for pellet accumulation; model algorithms do not calculate effect sizes for offsets. I defined each year as a contiguous leaf-off + leaf-on season to specify random year variation. Models were fit using R ver. 2.15.2 (2012-10-26) for objective one, and R version 3.0.2 (2013-09-25) for objective two (R Core Team 2013); R library packages used for both objectives are listed in Appendix D, Table D.1.

Objective One: Seasonal Change in Snowshoe Hare Pellet Densities across Three Forest Stand Types

To assess the extent that pellet densities changed between seasons across three stand-types, I compared two seasons, leaf-off (Nov.-Apr.) and leaf-on (May-Oct.), using 41 stands as sample units: Regenerating Conifer (RG, $n = 15$ stands); Partial Harvest by Selection Cut (SEL, $n = 11$); and Mature-Mixed and Mature Conifer-Dominated (MT, $n = 15$). These stands were repeatedly measured for a total of 16 leaf-on and leaf-off seasons over 8 years (Table A.3). Number of stands/year varied because stands that were harvested were removed from the study. Table 1.1 lists variables used to assess whether pellet density changes between seasons occurred differentially across stand types. Preliminary analysis of the pellet count response variable revealed skew (Figure D.1), inherent non-normality (Figure D.2A), and a graphical approach (Bolker et al. 2011)
revealed an overdispersed distribution (Figure D.2B); therefore, I specified a negative binomial model structure in which season interacted with stand-type to evaluate seasonal differences in pellets across stand-types. Area (m\(^2\)) sampled for pellets was standardized. I aggregated plots to stand level as a grouped variable. The negative binomial distribution has a Poisson mean defined by a probability distribution function with a gamma distribution (Boyce et al. 2001:500) and adds an overdispersion parameter, \(\omega\):

\[
\text{pellets} \sim \text{nbinom} (\mu_b, \sigma^2 = \frac{\mu + \mu^2}{\varphi})
\]

\[
\alpha_{\text{stand}} \sim N(\mu, \sigma^2), \quad \alpha_{\text{year}} \sim N(\mu, \sigma^2)
\]

\[
\ln(\mu_{\text{pellets}}) = (\beta_{\text{stand-type}} \times \beta_{\text{season}}) + \alpha_{\text{stand}} + \alpha_{\text{year}} + \omega + \epsilon
\]

I used the model’s PREDICT function to graph estimates of pellet densities between seasons, and across stand-types, after back-transforming the log-link function of the GLMM. I obtained each beta coefficient’s 95% credible interval with 10,000 Markov-chain Monte Carlo iterations from the model’s variance-covariance matrix, using R package glmmMCMC (Bolker 2012).
Table 1.1. Parameters used in generalized linear mixed-effects models (GLMMs) to evaluate seasonal changes in use of forest stand-types by snowshoe hare in northern Maine, 2005-2012.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Factor levels</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Response variable</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pellet Counts</td>
<td></td>
<td>Counts in stand for each season</td>
</tr>
<tr>
<td><strong>Predictor variables</strong></td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Fixed effects</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forest Stand Type</td>
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<td>Mature, Regenerating conifer, Selection harvest</td>
</tr>
<tr>
<td>Season</td>
<td>2</td>
<td>Leaf-off (winter), Leaf-on (summer)</td>
</tr>
<tr>
<td><strong>Random effect</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Years</td>
<td>8</td>
<td>2005 – 2012</td>
</tr>
<tr>
<td><strong>Covariates</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Days of accumulation</td>
<td></td>
<td>offset variable = ln(No. days of accumulation)</td>
</tr>
<tr>
<td>Stand area (^a)</td>
<td></td>
<td>mean area sampled/stand = 44.2 m(^2)/stand</td>
</tr>
</tbody>
</table>

\(^a\) Stand area was standardized \([\text{area in stand}_i – \text{mean area of all stands}]/\text{sd area}\).
Objective Two: Stand-scale Vegetation Influences on Seasonal Change in Snowshoe Hare Pellet Densities

I evaluated how vegetation influenced the extent of seasonal changes in hare density with the same statistical approach as for objective one, except that I used a data set of 26 unique stands, monitored for pellets over six seasons in three years (2010 leaf-on–2013 leaf-off) (Table D.2), and I specified vegetation covariates (described in Table 1.2) in models to address a priori hypotheses (Table C.1). I assumed that successional processes over a three year period were minimal, as was demonstrated for regenerating-conifer stands in my study area (Scott 2009:82). I used 26 stands because 15 of the 41 stands used in objective one were harvested by 2010, and vegetation measurements were taken in 2011-2012. Stand types were not used for comparisons, rather, gradients of vegetation among all the stands were considered as predictor variables to assess pellet density differences between seasons. I re-assessed the distribution of the 3-year pellet count response variable for skewness (Figure D.3) and overdispersion and found that it again fit a negative binomial distribution (Figure D.4). Although pellet counts were conducted for six seasons, three each during both the leaf-on and leaf-off periods, I had only one set of vegetation metrics for each leaf-on and leaf-off season. I repeatedly matched records from the one year’s dataset of leaf-on vegetation metrics to records from each of the three unique years of leaf-on pellet count records, and similarly, matched the one year of data of leaf-off vegetation metrics to each of the records from three years of leaf-off pellet counts.
Table 1.2. Variable names, descriptions and units, used to assess effects of vegetation structure and composition on seasonal changes in snowshoe hare fecal pellet densities across 26 forest stands with different harvesting legacies in northern Maine, 2010-2013.

<table>
<thead>
<tr>
<th>Variable name</th>
<th>Variable description</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>season</td>
<td>leaf-off, Nov 1-Apr 30 (wtr)</td>
<td>factor</td>
</tr>
<tr>
<td></td>
<td>leaf-on, May 1-Oct 31 (smr)</td>
<td></td>
</tr>
<tr>
<td>hareyr</td>
<td>three year:season repeated measures</td>
<td>factor</td>
</tr>
<tr>
<td></td>
<td>2010smr - 2011wtr</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2011smr - 2012wtr</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2012smr - 2013wtr</td>
<td></td>
</tr>
<tr>
<td>UndCov a</td>
<td>under story from 0.5 m to 1.5 m</td>
<td>percent</td>
</tr>
<tr>
<td>LC</td>
<td>lateral cover of hare silhouette</td>
<td>ordinal</td>
</tr>
<tr>
<td>CC</td>
<td>canopy cover, densiometer</td>
<td>percent</td>
</tr>
<tr>
<td>totl.splgs</td>
<td>all saplings &lt; 7.6 cm DBH, &gt;1.5 m</td>
<td>count</td>
</tr>
<tr>
<td>totl.trees</td>
<td>all trees &gt; 7.6 cm at DBH</td>
<td>count</td>
</tr>
<tr>
<td>BAsplgs b</td>
<td>basal area saplings &lt; 7.6 cm at DBH</td>
<td>count</td>
</tr>
<tr>
<td>BAtrees</td>
<td>basal area all trees &gt;7.6 cm at DBH</td>
<td>count</td>
</tr>
<tr>
<td>snow</td>
<td>snow depth by conifer interaction</td>
<td>cm</td>
</tr>
<tr>
<td></td>
<td>snow depth by deciduous interaction</td>
<td>cm</td>
</tr>
<tr>
<td>dec.splgs</td>
<td>angiosperm (deciduous) saplings</td>
<td>count</td>
</tr>
<tr>
<td>con.splgs</td>
<td>gymnosperm (coniferous) saplings</td>
<td>count</td>
</tr>
<tr>
<td>UndDec d</td>
<td>All live &amp; dead understory deciduous trees, saplings, woody shrubs, branches</td>
<td>percent</td>
</tr>
<tr>
<td>UndCon d</td>
<td>All live &amp; dead understory conifer trees, saplings, branches</td>
<td>percent</td>
</tr>
<tr>
<td>con.trees</td>
<td>total coniferous trees</td>
<td>count</td>
</tr>
<tr>
<td>dec.trees</td>
<td>total deciduous trees</td>
<td>count</td>
</tr>
</tbody>
</table>

a understory coverage included all vegetation living and dead.
b basal area measured with a variable radius 2-factor metric prism at center plot.
c counts were standardized to 0.1 ha.
d UndCon (coniferous) and UndDec (deciduous) included all living and dead branches, foliage, and tree boles of all sizes in the 0.5 m to 1.5 m height stratum.
To evaluate the influence of structure on seasonal changes in pellet densities, I specified candidate variables that I expected would vary most with seasons: lateral cover (LC), percent overhead canopy cover (CC), cm snow depth (snow), tree density, basal area (BA), and % understory coverage; all variables and their descriptions are listed in Table 1.2. I used midpoints of the ranges for LC rather than coded categories to preserve 0% and 100% obscured values: 0.0, 3.0, 15.5, 38, 63, 85.5, 97.5, and 100. After determining the two LC measurements that we obtained in the field had similar distributions, I chose one to use as a covariate in models to preserve the ordinal categories, rather than averaging them together. Tree density does not vary by season, but I expected it to interact with snow near tree boles, especially where trees or saplings were densest. The vegetation stratum at 0.5–1.5 meters, defined as “understory” included all shrub, tree and sapling branches and boles, living and dead. I used three % understory coverage/stand variables: % coverage of all vegetation to describe structure, and two to describe species composition, % conifer and % deciduous (Table 1.2). Tree and sapling density was scaled to an area surrounding each plot, 1000 m², or 0.1 ha. Predictor variables used as counts were square-root transformed prior to modeling to reduce skew of the distributions (Table D.3) (Zuur et al. 2007:488). I calculated variance inflation factors (VIF) to screen for multicollinear variables and I specified models with covariates that had VIF’s ≤ 4.0 (Table D.4), and Pearson r ≤ 0.56 (Figure D.5, D.6).

I addressed the multicollinearity of structural variables by determining relative influences of basal area and densities of trees and saplings to explain the extent of change in pellet densities between seasons and across stands (Table D.5). The best performing model using AICc inference was total sapling density with 92% relative importance
weight of evidence (RIW) (Burnham et al. 2011). Basal area of trees had a minor amount of explanatory value, with 5% RIW, and basal area of saplings and tree density had no relative importance. Thus, I used tree basal area and total sapling density to specify models describing structure, and I excluded other structural variables.

I developed 16 alternative multiple candidate models (Chamberlin 1965) depicting my a priori hypotheses regarding which vegetative and structural attributes could best explain extent of change in seasonal use of stands by hares (Table C.1), and two null models. I compared structural diversity to species composition to determine if structure was more important to snowshoe hare use of stands than species by specifying global structure and species composition models. Conifer-dominated stands can reach greater structural densities than deciduous or mixed stands, so I then hypothesized which species compositional components provided superior seasonal resources among all stands. I ranked relative strengths of vegetation habitat models and their influence on pellet densities among forest stands with AICc. In an AICc ranking, null models may better describe the data than predictor covariates, so I specified two null models: one with season (m.null.ssn), standardized area, the random covariate, “hareyr”, and the offset “ln.days”, and a second without season (m.null). Models designated “full” (structure.all and speciesComp.all) had a maximum of 12 parameters including seasonal interactions, so no models were saturated. I assessed relative strength of evidence for null and alternative models by ranking them with second order Akaike Information Criteria (AICc) (Burnham and Anderson 2004). I considered a parameter to have some ecologically relevant strength of evidence when that parameter had a relative importance weight > 5%. 

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and was included in a model with a ΔAICc value < 6 (Burnham and Anderson 2002:70, Richards 2005, Richards 2008).

During leaf-off seasons, I expected that snow depth interacting with conifer vegetation, especially dense saplings, would provide superior cover for hares relative to deciduous, and conversely, that areas dominated by deciduous trees and saplings would be poor cover in winter. I restricted the dataset to the three leaf-off (winter) seasons and specified 13 candidate models and one null model to determine which vegetative characteristics most affected hare pellet densities in winter, when interacting with snow depth. These models did not include “hareyr” but included year as a random covariate.

RESULTS

Extent of Seasonal Change in Snowshoe Hare Pellet Densities across Three Forest Stand Types

We sampled 41 stands for 16 seasons, to total 13,509 plots within 459 stand-seasons. Number of plots/stand averaged 29.7 (SE ± 0.3, range 22-43, mode = 28) and number of stands sampled each season ranged from 26-38 (x = 28.75 ± 0.1, mode = 26). We conducted semi-annual pellet surveys within RG, SEL and MT stand-types from 2005-2012.

In RG stands, seasonal change in hare pellet density was greater than observed in SEL and MT stands. Based on overlapping 95% credible intervals (CI), pellet density in SEL and MT stand types did not differ between the leaf-off and leaf-on seasons (Figure 1.2); however, the RG stand type exhibited a significant increase in pellet density from summer to winter based on non-overlapping CI (Figure 1.2). Additionally, RG stands exhibited more inter-stand variability. Pellet densities increased 115.2% in RG, 44% in
SEL and 72.4% in MT stand-types from the leaf-on to leaf-off seasons (Table 1.3), as expected from increased pellet production when hares shift to their ligneous winter diets. Unexpectedly, during the leaf-on season, estimated stand-level pellet densities (pellets/ha/month) were greater in RG (2795.1 < 4487.4 < 6168.7) than in SEL (956.4 < 1463.7 < 2281.7) or MT (291.2 < 483.1 < 779.2) stand-types (Table 1.3).
Figure 1.2. Estimates generated with a generalized linear mixed model of the difference in seasonal pellet densities (Pellets/ha/month) across mature mixed, selection harvest mixed, and regenerating conifer stand types in northern Maine (2005-2012). The regenerating conifer stand-type had greater seasonal pellet differences and greater inter-stand variation. Each season’s sample size $n$ is a repeated measure of 41 stands among all stands and years ($n = 459$ stand-years). Year is included in models as a random variable. Smr is leaf-on (summer) and Wtr is leaf-off (winter). Closed squares represent summer, open squares winter and lines define 95% credible intervals.
Table 1.3. Model estimates of snowshoe hare pellet densities in three forest stand types between seasons, 95% credible intervals were estimated using a Markov-chain Monte Carlo process, and the percentage increase of pellet densities from summer to winter. Estimates are from 41 stands sampled semi-annually from 2005–2012 in northern Maine.

<table>
<thead>
<tr>
<th>Stand type</th>
<th>Season</th>
<th>Pellets/ha/month</th>
<th>Credible intervals</th>
<th>% Increase summer to winter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mature conifer and mature mixed b</td>
<td>summer</td>
<td>483.1</td>
<td>291.2</td>
<td>779.2</td>
</tr>
<tr>
<td></td>
<td>winter</td>
<td>832.7</td>
<td>490.2</td>
<td>1280.6</td>
</tr>
<tr>
<td>Selection harvest mixed</td>
<td>summer</td>
<td>1463.7</td>
<td>956.4</td>
<td>2281.7</td>
</tr>
<tr>
<td></td>
<td>winter</td>
<td>2108.1</td>
<td>1209.5</td>
<td>3266.1</td>
</tr>
<tr>
<td>Regenerating conifer</td>
<td>summer</td>
<td>4487.4</td>
<td>2795.1</td>
<td>6168.7</td>
</tr>
<tr>
<td></td>
<td>winter</td>
<td>9658.9</td>
<td>6472.5</td>
<td>15067.9</td>
</tr>
</tbody>
</table>

a Seasons are termed summer (leaf-on, May 1–October 30) and winter (leaf-off, November 1–April 30).

b Mixed refers to mixed coniferous-deciduous cover types.
Effects of Vegetation Structure and Composition on Seasonal Change in Snowshoe Hare Pellet Densities

Vegetative characteristics were considered along a continuum across all stands, rather than grouping stands into types. During six seasons in 2010-2013, 26 unique stands were repeatedly sampled for snowshoe hare pellets semi-annually to total 2,197 plots over 81 stand-seasons (Table D.1). We measured vegetation during summers 2011 and 2012 on 520 plots in the 26 stands. Among 16 candidate models describing effects of vegetation characteristics on seasonal change in hare pellet density, one single-variable model containing conifer sapling density was most informative (ΔAICc ≤ 2, relative importance weight [RIW] 68.4%, Table 1.4). Additionally, 4 other models had moderate support based on ΔAICc ≤ 6, and RIW > 4% (Table 1.4). Species composition played a role in model performance; conifer sapling densities (RIW 68.4%), % living and dead understory conifer stems (RIW 6.5%), and deciduous tree counts (RIW 4.6%) ranked 1, 4, 5 respectively, among the 16 models considered (Table 1.4). Structural variables contributing most to differences in seasonal pellet deposition were total sapling densities (RIW 11.3%) and % understory coverage of all vegetation (RIW 8.1%); those models ranked 2nd and 3rd. Because the top 5 models were univariate models, RIW of the predictor variables were based directly on model outputs for each variable. In contrast, there was neither support for models based upon lateral cover, overhead canopy cover, percent understory deciduous cover, and season affecting canopy cover in deciduous areas (3-way interaction), nor was there support for the 2 multivariate models that were considered.
Table 1.4. The relative support for 16 *a priori* generalized linear mixed models developed to describe the effects of vegetative structure and species composition on seasonal changes in snowshoe hare pellet densities during leaf-on 2010–leaf-off 2013, in Maine, USA. Number of parameters (*K*), model log likelihood (LL), Akaike's Information Criterion value adjusted for small sample size (AIC<sub>c</sub>), model likelihood differences (ΔAIC<sub>c</sub>), and Akaike weight (*w<sub>i</sub>*) are presented for each model.

<table>
<thead>
<tr>
<th>Models&lt;sup&gt;a&lt;/sup&gt;</th>
<th><em>K</em></th>
<th>LL</th>
<th>AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>ΔAIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th><em>w&lt;sub&gt;i&lt;/sub&gt;</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>conifer saplings</td>
<td>8</td>
<td>-4187.8</td>
<td>8400.1</td>
<td>0</td>
<td>0.684</td>
</tr>
<tr>
<td>total saplings</td>
<td>8</td>
<td>-4194.5</td>
<td>8413.5</td>
<td>13.4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>% understory coverage</td>
<td>8</td>
<td>-4190.2</td>
<td>8404.4</td>
<td>4.7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>% understory conifer</td>
<td>8</td>
<td>-4190.5</td>
<td>8405.5</td>
<td>5.4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>deciduous trees</td>
<td>8</td>
<td>-4194.5</td>
<td>8413.5</td>
<td>13.7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>BA trees</td>
<td>8</td>
<td>-4194.6</td>
<td>8413.7</td>
<td>13.4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>null.ssn&lt;sup&gt;b&lt;/sup&gt;</td>
<td>6</td>
<td>-4197.7</td>
<td>8411.9</td>
<td>11.8</td>
<td>0.002</td>
</tr>
<tr>
<td>conifer trees</td>
<td>8</td>
<td>-4194.4</td>
<td>8416.8</td>
<td>16.7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>% canopy cover</td>
<td>8</td>
<td>-4196.2</td>
<td>8416.9</td>
<td>16.8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>con.splgs + con.trees + % und.con</td>
<td>12</td>
<td>-4184.4</td>
<td>8416.8</td>
<td>16.7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>% understory deciduous</td>
<td>8</td>
<td>-4196.2</td>
<td>8416.9</td>
<td>16.8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>lateral cover</td>
<td>8</td>
<td>-4196.6</td>
<td>8417.7</td>
<td>17.6</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>deciduous saplings</td>
<td>8</td>
<td>-4197.5</td>
<td>8419.4</td>
<td>19.3</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>dec.splgs + dec.trees + % und.dec</td>
<td>12</td>
<td>-4189.3</td>
<td>8426.6</td>
<td>26.6</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>canopy cover × deciduous</td>
<td>12</td>
<td>-4193.4</td>
<td>8434.8</td>
<td>34.7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>structure.all&lt;sup&gt;c&lt;/sup&gt;</td>
<td>16</td>
<td>-4176.8</td>
<td>8446.0</td>
<td>45.9</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>null (no season)&lt;sup&gt;d&lt;/sup&gt;</td>
<td>5</td>
<td>-4234.9</td>
<td>8482.7</td>
<td>82.6</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>species_comp.all&lt;sup&gt;e&lt;/sup&gt;</td>
<td>18</td>
<td>-4178.3</td>
<td>8490.4</td>
<td>90.3</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

<sup>a</sup> general linear mixed models, except null, had season as an interacting covariate.

<sup>b</sup> season by (area.std + offset(ln.days) + hareyr).

<sup>c</sup> % UndCov + LC + CC + BAtrees + total saplings.

<sup>d</sup> area.std + offset(ln.days) + hareyr.

<sup>e</sup> deciduous trees + conifer trees + % deciduous understory + % conifer understory +
deciduous saplings + conifer saplings.
Conifer sapling densities best explained seasonal differences in pellet densities of hares across our 26 stands. Covariates from four of the top five models had a positive winter effect and negative summer effect on pellet density differences by seasons: conifer sapling density, total sapling density, % understory, and % conifer understory (Table 1.5). The probability of the covariate interaction with seasons or the covariate and an additive effect with seasons is estimated as an approximated Wald $|z|$ value. An additive effect could be considered the annual effect of the covariate alone, because combining both seasons encompassed the entire year.

The magnitude and direction of vegetation effect sizes on pellet densities between seasons for the top five models can be plotted as regression coefficients (Figure 1.3). When the regression coefficient of a parameter in a model crosses zero (i.e. $\beta_1 = 0$), the effect of that parameter ($\beta_1 \times (X_0)$, is negligible, $(0) \times (X_0) = 0$. The outer bars represent +/-95% confidence intervals. Figure 1.3 illustrates that conifer saplings had a positive influence in winter, and negative influence in summer, and that total saplings had a similar, but less pronounced effect. Deciduous tree density had little support (RIW 4.6%) relative to other models; however deciduous trees negatively affected leaf-off pellet densities and positively affected leaf-on densities.

Across all stands, conifer sapling densities contributed the most to seasonal hare pellet density change, with relative importance weight (RIW) of 68.4%. The predictive graph (Figure E.1) estimates pellet densities and derives from an equation generated by the GLMM negative binomial model that describes season X conifer sapling density:

$$\ln(\tilde{y}_i) = \beta_0(smnr \text{ intercept} \times \sqrt{\text{con saplings}}) + \beta_1(\text{season} = \text{winter}) + \beta_2(\sqrt{\text{con saplings}}) + \beta_3(\text{winter by} \sqrt{\text{con saplings}})$$
Table 1.5. Effects of vegetation covariates from the top five candidate models that describe seasonal changes in snowshoe hare pellet densities during leaf-on 2010 to leaf-off 2013, in Maine, USA. Generalized linear mixed models, number of parameters ($K$), model differences ($\Delta\text{AIC}_c$), and Akaike Information Criteria for small sample size weights ($w_i$). Interactive and additive effects of winter relative to summer with the covariate’s influence on pellet density differences in 26 stands. The significance of the covariates is derived from approximated Wald $|z|$ values.

<table>
<thead>
<tr>
<th>Models $^a$</th>
<th>$K$</th>
<th>$\Delta\text{AIC}_c$</th>
<th>$w_i$</th>
<th>Summer to winter change</th>
<th>Interactive</th>
<th>Additive $^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>conifer saplings</td>
<td>8</td>
<td>0</td>
<td>0.684</td>
<td>+***</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>total saplings</td>
<td>8</td>
<td>3.6</td>
<td>0.113</td>
<td>+***</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>% understory coverage</td>
<td>8</td>
<td>4.3</td>
<td>0.081</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>% understory conifer</td>
<td>8</td>
<td>4.7</td>
<td>0.065</td>
<td>+**</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>deciduous trees</td>
<td>8</td>
<td>5.4</td>
<td>0.046</td>
<td>-**</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

$a$ generalized linear mixed models included season as an interacting covariate and year as a random covariate.

$b$ Significance: Probability (Wald $|z|$) $\leq 0.001$ '***', 0.001 '***', 0.01 '*', 0.05 '*', 0.1 '.':
Figure 1.3. Coefficients from generalized linear mixed model regressions for the log effect sizes of vegetation parameters (Xᵢ) on pellet density in each season in forest stands assessed in northern Maine, 2010-2013. Each X:season denotes an interaction of that season with a given Xᵢ variable. A. Winter effect of the covariates interacting with winter (Xᵢ:wtr) on pellet density, holding summer density constant. B. Summer effect of the covariate (Xᵢ) interacting with summer (Xᵢ:smr) on pellet density, holding winter density constant. Years 2010–2013 represent three summer and three winter seasons during which 26 unique stands were repeatedly measured. Thin bars represent 95% confidence intervals.
The predicted \( \hat{y}_i \) are pellet counts that can be scaled to pellets/ha/month. This equation depicts two curves, one for each season that illustrates the difference of pellet densities between seasons as a function of conifer sapling density. The model produces the following equation:

\[
\ln(\text{pellets}_i) = -4.9(\text{summer intercept} \times \sqrt{\text{con saplings}}) + 0.237(\text{winter}) + -0.0009(\sqrt{\text{con saplings}}) + .0167(\text{winter} \times \sqrt{\text{con saplings}})
\]

As conifer sapling density increases, pellet densities increase in winter, while summer pellet densities remain flat relative to winter (Figure E.1A), which contributes to the large difference between seasons. Leaf-on pellet densities also increase with higher sapling densities, but over a restricted range of pellet densities relative to leaf-off seasons (Figure E.1B).

**Snow Interaction with Vegetation Influences on Snowshoe Hare**

**Pellet Densities**

I evaluated whether snow interacts with dense understory vegetation to enhance thermal and predator refugia for hares during winter. A Sheffé test revealed snow depths were different among stand types \((F_{3,253} = 2.64, \text{ MSE} = 137.9, P \leq 0.001)\) thus confirming that deciduous vegetation, more prevalent in SEL stands we sampled, may interact with snow depth differently than coniferous vegetation, which was more prevalent in RG stands. Among 26 stands, average snow depth was 32.6±0.8 cm, so that the understory vegetation layer was ~17–117 cm high in winter. To assess how snow depth interacted with vegetation to affect winter use of stands by hares, I used only the leaf-off seasons of the three year data set that included 751 pellet plots surveyed within 26 stands during
2011-2013. I specified 13 candidate models that related vegetation characteristics to pellet density.

Percentage of understory conifer coverage interacting with snow depth was the most strongly supported model (RIW = 88.8%) and the interaction of snow depth and percent understory coverage on winter pellet density had minor (RIW = 10.8%) support (Table 1.6); both of the variables influencing pellet densities positively. Further, there was no support (RIW < 0.001) for more complex interaction models (Snow X % Understory Deciduous X CC, Snow X % Understory Conifer X CC) and the null model (snow depth alone) also had no support. Although conifer sapling density had the greatest effect on the difference in pellet densities between seasons, the interaction of conifer saplings and snow depth, with RIW 0.2% and \( \Delta AIC_c > 12.4 \), did not correspond to higher pellet densities across stands during the winter season, relative to understory conifer coverage.
Table 1.6. Model selection results evaluating the interacting effects of snow depth with vegetation parameters on snowshoe hare winter pellet densities in northern Maine. Number of parameters ($K$), model likelihood (logLik), Akaike’s Information Criterion value adjusted for small sample size ($AIC_c$), change in $AIC_c$ value from the top model ($\Delta AIC_c$), and Akaike weight ($w_i$) for stand-level models are presented. Models predicted pellet counts/stand ($42 \text{ m}^2$) for three winter seasons, 2010–2012, $n = 26$ stands/season, with 257 subsampled plots in stands sampled each year. Snow depth (cm) was an interaction term with all other covariates in each model.

<table>
<thead>
<tr>
<th>Models a</th>
<th>$K$</th>
<th>logLik</th>
<th>$AIC_c$</th>
<th>$\Delta AIC_c$</th>
<th>$w_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>% understory conifer coverage b</td>
<td>8</td>
<td>-1797.8</td>
<td>3620.1</td>
<td>0.0</td>
<td>0.888</td>
</tr>
<tr>
<td>% understory coverage c</td>
<td>8</td>
<td>-1799.9</td>
<td>3624.4</td>
<td>4.2</td>
<td>0.108</td>
</tr>
<tr>
<td>conifer saplings</td>
<td>8</td>
<td>-1804.0</td>
<td>3632.6</td>
<td>12.4</td>
<td>0.002</td>
</tr>
<tr>
<td>basal area trees</td>
<td>8</td>
<td>-1804.2</td>
<td>3632.9</td>
<td>12.8</td>
<td>0.002</td>
</tr>
<tr>
<td>deciduous trees</td>
<td>8</td>
<td>-1804.8</td>
<td>3634.1</td>
<td>14.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>total saplings</td>
<td>8</td>
<td>-1806.3</td>
<td>3637.1</td>
<td>17.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>snow depth (null)</td>
<td>6</td>
<td>-1810.5</td>
<td>3637.4</td>
<td>17.3</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>% understory conifer X CC</td>
<td>12</td>
<td>-1797.5</td>
<td>3643.0</td>
<td>22.8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>% overhead canopy coverage (CC)</td>
<td>8</td>
<td>-1809.7</td>
<td>3643.9</td>
<td>23.7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>conifer trees</td>
<td>8</td>
<td>-1809.8</td>
<td>3644.0</td>
<td>23.9</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>lateral cover (LC)</td>
<td>8</td>
<td>-1810.0</td>
<td>3644.5</td>
<td>24.3</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>deciduous saplings</td>
<td>8</td>
<td>-1810.7</td>
<td>3644.6</td>
<td>24.4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>% understory deciduous</td>
<td>8</td>
<td>-1810.3</td>
<td>3645.1</td>
<td>24.9</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>% understory deciduous X CC</td>
<td>12</td>
<td>-1808.8</td>
<td>3665.6</td>
<td>45.4</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

a generalized linear mixed models had snow depth (cm) as an interacting covariate and year as a random covariate.

b understory comprised conifer trees and saplings, both live and dead, and their foliage.

c understory comprised all live and dead vegetation in the stratum of 0.5–1.5 m, taken from summer ground level. Leaf-off stratum was 0.1–1.1 m high.
DISCUSSION

Extent of Seasonal Change in Snowshoe Hare Pellet Densities Across Three Forest Stand Types

My study assessed effects of vegetation on seasonal change in snowshoe hare pellet density among different forest stand types in Maine. Contrary to reports that hares move away from dense, primarily coniferous stands, during the leaf-on season in Maine (O'Donoghue 1983, Litvaitis 1985), and elsewhere (Grange 1932, Wolff 1980, Griffin and Mills 2009, Berg and Gese 2010), I observed that seasonal shifts by hares did not occur to areas with higher deciduous and herbaceous understories in summer as represented by selection harvest (SEL) and mature (MT) stands. At the stand level, snowshoe hare pellet densities were higher in regenerating conifer (RG) stands during both the leaf-on and leaf-off seasons relative to MT and SEL stands. The vegetative characteristic that most contributed to seasonal change in pellet densities was density of conifer saplings, and in winter, % understory of all conifer coverage (i.e. saplings, low limbs, and trees) was most strongly associated with high hare pellet densities.

My findings of higher winter pellet densities in RG relative to other stand types are consistent with previous research in northern Maine conducted during winter (Lachowski 1997, Fuller and Harrison 2005, Robinson 2006, Homyack et al. 2007, Scott 2009, Fuller and Harrison 2013). The high leaf-on (summer) densities in RG stands was unexpected, however, and was contrary to my working hypothesis that the dense conifer vegetation would shade summer undergrowth, precluding growth of adequate food resources, and induce hares to move out from RG stands during summer. This indicates RG stands provided adequate food and cover resources during leaf-on seasons to promote high year-
round use by hares. That RG stands in northern Maine could be functioning as source areas for hare populations was supported by two patterns: only regenerating conifer-dominated (RG) stands exhibited a significant difference in pellet densities between seasons, and there were greater hare pellet densities in the leaf-on season in RG compared to selection harvest SEL and mature MT. The relatively large increase in pellet densities of hares from summer to winter in RG stands suggested higher rates of juvenile recruitment into winter and higher rates of adult overwinter survival. The higher relative pellet densities documented during leaf-on season in RG stands would be consistent with both higher over-winter survival and less summer mortality and suggests that RG stands may be functioning as source habitats (Levins 1970, Lidicker 1975). Stands providing hares with dense cover have also been documented to serve as source habitats for hares in the western USA (Griffin and Mills 2009, Ivan et al. 2014). Research on the relative vital rates of hares across RG, MT, and SEL stands is encouraged to test the assertion that RG stands serve as source habitats and MT and SEL stand types as sink (Pulliam 1988) habitats.

Hare use of different seasonal habitats has been demonstrated to affect overwinter survival, and overwinter survival of adult hares, combined with immigration into superior winter habitat, most strongly affected fecundity and consequent population growth in Idaho (Wirsing et al. 2002) and Montana (Griffin and Mills 2009). Although higher hare densities were associated with dense early-seral lodgepole pine in Colorado, vital rates (over-winter survival and juvenile recruitment) were not related to attributes of the densest stands (Ivan et al. 2014), indicating that immigration to those dense stands contributed to high densities. Relative to two other stand types in my study area.
however, RG stands supported higher hare densities throughout the year. My results suggest that fecundity, juvenile survival, and over-winter survival are greater in 25-39 year post-harvest conifer-dominated stands, relative to MT and SEL stands in northern Maine.

My comparative results across the 3 stand-types suggest that hares may be immigrating into RG stands in autumn, but not emigrating from them in spring. While at a stand level the RG stand type may provide adequate resources year-round to hares, there are likely sub-stand components that contribute to higher hare densities in summer than in other stand-types. Rather than seasonal shifts of hare home ranges, diel movements by hares into RG stands during the leaf-off period could have contributed to both higher pellet densities in winter and the significant seasonal difference in RG stands. Snowshoe hares monitored with telemetry migrated between dense conifer winter and summer home ranges, hares moved further and had larger home ranges during winter, in Montana (Griffin and Mills 2009), Yukon Territories, Canada (Hodges 2000a) and in Alaska (Feierabend and Kielland 2014). Distances between capture and mortality recovery locations in Alaska averaged 2.5 times greater in winter (825 m) than in summer (321 m), and 82% of recoveries were within 500 m (Feierabend and Kielland 2014). In Wyoming, where habitat type differences are more distinct than in Maine, snowshoe hare sign was observed in the surrounding "matrix" of sagebrush-wheatgrass and riparian willow-meadow communities in summer, but not winter (Berg and Gese 2010).

Integration of individual movement patterns can be important to make inferences about habitat preference, even if available versus used habitat is sampled and known (Sievert and Keith 1985, Beyer et al. 2010, Gaillard et al. 2010). Yet, the significantly higher
pellet density increase from summer to winter in RG stands suggests immigration into those stands in autumn may have augmented juvenile recruitment, as was observed in Colorado (Ivan et al. 2014).

The significant decrease in pellet densities that I observed from winter to summer only in the RG stand-type could result from a combination of lower pellet production during summer from herbaceous food resources, over-summer mortality, localized and daily movements away from dense conifer patches to adjacent areas surrounding the RG stands, or from emigration away those stands during summer. A combination of these processes occurred to a greater degree in the RG stands relative to the SEI. and MT stand-types, indicating that micro-habitat use by hares may differ in the RG relative to other stand-types (Fuller and Harrison 2013). The stands in my study area were 7.2-38 ha excluding the 70 m buffer, and were not established to encompass an individual snowshoe hare’s home range, but to encompass a forest cover type larger than the typical home range area of hares in Maine. Throughout the distribution of the snowshoe hare, home ranges average 2–4 ha and range from 1–13 ha (Wolff 1980, Ferron and Ouellet 1992, Hodges 2000b, Beaudoin et al. 2004). The size of areas used for feeding periods in Quebec ranged from 0.5-5.6 ha and home ranges were 0.5 – 6.1 ha. In contrast to evidence from western and boreal forest hares, in Quebec, hares had larger summer (5.3 ha) than winter (2.9 ha) home ranges (Beaudoin et al. 2004). Though our stands may encompass some individual hares’ home ranges, there are also individual hares that use portions of a given stand, and could be using those portions differently between seasons.

Hares are capable of daily movements that exceed the distances of our stands, the smallest of which were 360 m in length. Snowshoe hares exhibited inter-habitat diel
movements twice per day on average, over distances of 0.2-1 km in Alaska (Feierabend and Kielland 2014). In response to forest management prescriptions that created 60 m wide strips in eastern Canada, hares had a larger proportion (52%) of daily movements > 330 m in strips, than in uncut blocks of residual forests (35%) and home ranges were larger (112 ha) in strips, than in uncut residual blocks where home ranges were 39 ha (St. Laurent et al. 2008). Gap dynamics created an optimal configuration of the “foodscape” (Searle et al. 2007) at a scale relevant to hares and hares used gaps for foraging that had 4 times more browse available, returning to dense conifer patches to rest or to feed on harvested branches (Hodson et al. 2010). I hypothesized that hares shifted their home ranges from dense conifer sapling patches in winter to more herbaceous, less closed cover areas in summer, yet seasonal home range shifts are unnecessary if gaps or edges with superior forage are within the 200 m to 1,000 m daily travel distances of hares. My result that summer had significantly fewer pellet densities than winter within the RG stands suggests that hares could exhibit diel movements in summer from our RG stands of 7–38 ha to forage adjacent to RG stands during summer, but not within them, then spend more time within RG stands during winters. Monitoring hare movements in RG stands would reveal daily and seasonal use of micro-habitats and monitoring the relative survival and recruitment by hares across RG, SEL and MT types would also be enlightening to elucidate the processes contributing to higher use of RG stands by hares during both seasons.

Regenerating conifer-dominated stands had greater inter-stand variability of pellet densities than other stand-types, and greater variation in winter than summer (Figure 1.2). Conifers in some of the older stands in the RG stand-type had undergone self-thinning
and crown recession (Scott 2009: Figure 2.2) and may have had characteristics of more mature stand types in patches. One of the RG stands was 39 years post-harvest in 2012 (Table A.1), and one atypical stand could contribute to the variability of the stand-type group, though factors other than age, such as soil characteristics and harvest techniques, contribute to stand structure and composition (Scott 2009). A factor that likely contributed to both intra- and inter-stand heterogeneity is the aerial application of herbicide that occurred between 4 and 21 years post-harvest, which resulted in a variable persistence of understory angiosperms. If some RG stands had a relatively greater percentage of deciduous cover, then winter mortality of hares in those stands could increase, but summer conditions may be favorable.

RG stands may provide optimal resource configurations relative to other stand-types. Hares with optimal distribution and configuration of resources should experience better proximate contributions to fitness (Hodson et al. 2010), such as better regulation of critical temperature with thermal refugia and available food resources (Sheriff et al. 2009b), maintenance of body condition (Hodges et al. 2006), less indirect predation pressure (Boonstra et al. 1998, Sheriff et al. 2009a), and ultimately higher fecundity (Sheriff et al. 2010). In boreal forests a bimodal distribution of highest snowshoe hare pellet densities was associated with peaks at stand ages of 40-50 years and >180 years post-disturbance, when small gap dynamics was important (Hodson et al. 2011). RG stands had small (< 0.01 ha) gaps from old skid trails with compacted soil that suppressed tree regeneration and provided light penetration to allow patches of herbaceous ground cover such as *Rhododendron canadense, Vaccinium spp.*, *Rubus spp.*, *Lupinus polyphyllus*, and ferns and grasses, components of hare summer food resources
(Seccombe-Hett and Turkington 2008). The diversity and configuration of plant species within RG stands in northern Maine could be key to providing hare source habitat throughout the year, and combined with an examination of hare demographics, is an area that could benefit from future research.

Though lower winter pellet densities in mature mixed and selection harvest mixed wood stands may result from greater over-winter mortality, lower pellet production may occur in these stands because hares have more digestible browse available in winter, relative to RG stands. I expected that all stands would have greater pellet production in winter than summer resulting from winter hare diets that contain more lignin, as was observed in Yukon Territories, Canada (Hodges and Sinclair 2003). If food resources were equally available, hares would select similar species of food resources in all stands, and if hare densities were equal in all stand-types, pellet production should have increased proportionately in winter. Pellet densities did increase from summer to winter in all stand-types (Table 1.3), but the significantly greater seasonal difference in RG stands was in marked contrast to the seasonal changes observed in MT and SEL stands.

Individual hares move among patches of dissimilar vegetation as they feed and this food resource use, more so than predator pressure, influences relative stand-scale densities (Hodges and Sinclair 2003;2005). Maple and alder were more common in SEL and MT than RG stands (Table E.1), and the relative digestibility of food resources chosen by hares in winter is unknown for snowshoe hares in Maine, (e.g. balsam fir needles vs. alder shoots). However, as generalist herbivores, hares select plant species to balance plant secondary compounds (e.g. phenols) with protein and energy content, rather than selecting greater low-value quantity (Adams 1959, Rodgers and Sinclair 1997,
Seccombe-Hett and Turkington 2008, Ellsworth et al. 2013). Plant species have a wide range of digestibility for hares that cause variable pellet production, but hares select plant species and portions of plants with higher digestibility, and do so in winter when their diets contain relatively more lignin (Wolfe et al. 1982). Hares in Yukon Territories, Canada, in winter preferred plant species that had 40% digestibility, while non-preferred plant species had 20% digestibility (Sinclair et al. 1988). In winter, hares select more twigs < 4mm diameter relative to availability (Smith et al. 1988, Rodgers and Sinclair 1997) because of their digestibility, avoid winter browse that has > 45% fiber (Seccombe-Hett and Turkington 2008), and choose as few as three plant species (Zimmer 2004). In Maine, Litvaitis (1985) observed that hares consumed four species in leaf-off seasons more than their availability: red spruce, paper birch, red and striped maple. On Mt. Desert Island, Maine, hares preferred six out of 23 species more than their availability (Saeki 1991). Thus, across the study area, hares will likely use the same few plant species, but in differing quantities based on availability. If preferred plant species were differentially available among the stand-types, their pellet production could be affected. However, apparent food resource scarcity that might induce hares to shift their food habits was not observed in my study area, as I and other colleagues observed little visual evidence of over-browsing during three winter seasons (2011-2013). Research to determine whether hares’ choose the same species of plants equally in all of our study stands would reveal if pellet production varies among the stand-types.
Effects of Vegetation Structure and Composition on Seasonal Change in Snowshoe Hare Pellet Densities

In a second objective of this study I examined which vegetation structure and composition most affected seasonal differences in pellet densities across a continuum of 26 stands over six seasons. One single parameter, conifer sapling density, was seasonally influential (Table 1.4), although some elements besides conifer saplings contributed to seasonal differences of pellet densities. Total sapling counts (conifer, deciduous, and dead) contributed to seasonal changes in pellet densities, and deciduous saplings in winter affected hare use negatively (Figure 1.2). Conifer sapling densities and total sapling densities contributed to the largest difference between seasons and suggest that these variables are likely the largest determinants to the relative quality of winter and summer habitat.

During winter, I expected that snow would interact with lateral cover, conifer understory, and with conifer saplings, but not deciduous vegetation, to enhance thermal cover and obstruct hares from predators (Table C.1, hypothesis 3). I also expected lateral cover during winters as well as summers to be important for hares because understory shrub density and horizontal cover were correlated with high pellet densities throughout the southern extent of the snowshoe hare range distribution (Fuller and Heisey 1986, Koehler 1991, Sullivan et al. 2010, Lewis et al. 2011, Berg et al. 2012, Thornton et al. 2013). In Maine (Litvaitis et al. 1985) and in Utah (Wolfe et al. 1982) horizontal cover above 60% was associated with higher pellet counts, and in Utah, when mean % obscurity per transect < 40%, no pellets were detected. Contrary to my expectations, lateral cover did not explain variation in hare pellet density between seasons, and lateral
cover did not interact with snow to increase pellet densities during winter. Those results confirm earlier work in Maine (Robinson 2006, Scott 2009), suggesting that lateral cover, or visual obstruction measured from 5 m distant at a height of 0-0.5 m is not a reliable predictor of hare density.

Deciduous tree density had a minor influence on seasonal difference in pellet density, and that variable had a seasonal effect that was reversed from the effects of other vegetative parameters (coefficients in Figure 1.3). Deciduous trees negatively influenced pellet counts in both winters and summers, but the effect was stronger during winter (Figure E.2). The observation that less ground cover corresponds to fewer snowshoe hare pellets has long been recognized (Adams 1959, Wolff 1980, Wolfe et al. 1982), and was recently reported at a sub-stand scale for northern Maine (Fuller and Harrison 2013). As canopy cover from leaves of deciduous trees increases in summer, undergrowth is shaded and understory stem growth is suppressed, which reduces cover and forage for hares.

Though I expected an inverse relation of snow depth and deciduous components and a direct relation of snow and conifer saplings with pellet densities, only % understory conifer coverage interacting with snow had strong support among the alternative hypotheses. The importance of understory coverage to hares, and especially the contribution from conifers to the understory as predictors of absolute pellet density is consistent with work in other areas near the southern extent of snowshoe hares’ distribution (Fuller and Heisey 1986, Koehler 1991, Sullivan et al. 2010, Lewis et al. 2011, Berg et al. 2012, Thornton et al. 2013). In south-central British Columbia, Canada, hare use of five types of pre-commercially thinned stands was related to horizontal cover and shrub volume (Sullivan et al. 2010). In Washington, hare track and pellet counts were
positively associated with tree and shrub densities less than 2.5 cm diameter (Koehler 1990). Sites preferentially colonized by snowshoe hares in Idaho had more vertical and horizontal cover relative to all other stand level variables (Thornton et al. 2013). Conifers are able to provide more structure than deciduous vegetation at the stratum I measured (0.5-1.5 m high), but in both seasons, more structure is better. In Maine, previous work documented that hares used areas with densest understory structure more than expected, regardless of whether the understory species composition was conifer, or deciduous (Litvaitis et al. 1985). Live conifer + deciduous saplings previously predicted hare densities in winter better than other vegetation measures used in Maine, including basal area of trees, lateral cover/visual obstruction, canopy cover, and sapling density (Litvaitis et al. 1985, Robinson 2006, Scott 2009, Fuller and Harrison 2013). Though conifer sapling density in this study was most strongly associated with the magnitude of seasonal change in pellet densities, the highest pellet densities in winter were associated with conifer understory coverage interacting with snow. The additional structure to conifer saplings provided by a multi-layer conifer understory, including tree branches and boles, was important in winter. These areas of dense conifer saplings and a higher % conifer understory are more prevalent in the regenerating-conifer dominated stand-type.

In regenerating conifer stands, where pellet densities were highest in both summer and winter, winter density of snowshoe hares at a stand scale averaged 0.97±0.10 SE (n = 15-18 stands) hares/ha during 2010-2014, relative to 0.29 ± 0.06 hares/ha in mature and selection harvest stand-types combined (Figure E.3). Average winter hare density among all of the stands was 0.67 ± 0.26 hares/ha (n = 29 stands) in four stand-types monitored from 2010-2014, years that bracket the 2011–2013 winter seasons used for objective two
of this study (Figure E.3). This was a stand-scale investigation, and to accurately depict landscape-scale hare abundance it is necessary to calibrate known stand-scale hare densities to land cover-types at a broader scale. Yet this study is the first to assess the importance of leaf-on influence on hare densities at the stand-scale in Maine, and revealed that regenerating conifer-dominated stands had higher hare densities in summers. Further, in winter, it was evident that multi-structured conifer vegetation, rather than sapling densities as was previously thought, was most associated with higher hare densities. More research is needed to elucidate how differing configurations and distributions of regenerating conifer stand-types across the landscape affect stand-scale hare densities in northern Maine.

SUMMARY AND MANAGEMENT IMPLICATIONS

My results indicate that regenerating conifer-dominated stands support higher relative winter and summer snowshoe hare densities and that conifer sapling density along with % conifer coverage in the understory structure in winter are the factors most strongly associated with increased hare density. At a stand scale of 7-40 ha, these results indicate that regenerating conifer-dominated stands 25-39 years of age provided superior habitat for hares during both the leaf-off and leaf-on seasons, where both leaf-on season recruitment and over-winter survival of hares may be greater compared to the other stand types considered. The regenerating conifer stands may also be areas of increased winter immigration. Across all stands, a multi-layered structure composed of conifer saplings, stems and branches were associated with higher winter hare densities. The abundance of this stand type is projected to decrease in northern Maine by 2032 (Simons 2009), which could affect landscape-scale densities of hares and reduce habitat quality for U.S.
federally threatened Canada lynx (Simons et al. 2013). Forest practices that promote stand types with high conifer sapling densities and multi-structural conifer components will enhance snowshoe hare habitat, and consequently, habitat for Canada lynx in Maine.

LITERATURE CITED


CHAPTER 2

FOOD HABITS OF LYNX ACROSS PERIODS OF HIGH AND LOW HARE DENSITY IN NORTHERN MAINE, 2001-2012

ABSTRACT

In the southern portions of their range, and in the northern boreal regions when snowshoe hares are at a cyclic low, Canada lynx (*Lynx canadensis*) exhibit a functional dietary response, shifting from prey specialists of snowshoe hares to a more generalized diet. Lynx may shift to prey species that are more available in summer than winter, such as subnivean small mammals, or migratory and ground nesting birds. Although lynx populations respond negatively to snowshoe hare declines, seasonal responses are not well understood at the southeastern limit of their geographic range of lynx and hares, and may affect lynx viability. To evaluate the dietary plasticity of lynx near that limit, I tested whether diet breadth increased between 2 periods when I expected: 1) lynx to be most specialized on hares, in winters during a period of higher hare density (2001-2006); and 2) lynx to be most generalized, in summer during a period of lower hare density (2007-2012). Additionally, I evaluated the extent to which hares are represented in the diet of lynx between those 2 periods to determine the extent that lynx specialize on hares near their southeastern extent of their geographic range.

I documented seasonal foods habits of lynx using scats collected during 2001-2012, which included 199 scats from a summer-lower hare density period and 125 from a winter-higher hare density period. All scats were genetically confirmed as being deposited by lynx. There was an increase in dietary breadth (*F*$_{4,322} = 0.0068$, 1000 randomizations), from the winter-higher hare density period (3.0%, n=125 scats) to the summer-lower hare density period (16.9%, n=199 scats) and reduced frequency of
Occurrence of hares during the summer-low (75.2%, n=230 prey item categories) compared to the winter-high hare period (92.1%, n=127 prey item categories). I suggest increased relative availability and accessibility of rodents and birds during the summer as a major reason for the diversification of lynx diets during that time, but high reliance on snowshoe hares throughout seasons and across periods of changing hare density indicate that, contrary to conclusion of Roth et al. (2007), lynx specialize on snowshoe hares near their southeastern limit in Maine. These results indicate that hares were the primary component of lynx diets in both seasons, and during periods of higher and lower hare density in the Acadian Forest region near the southeastern range limit for lynx and hares.

**INTRODUCTION**

Canada lynx (*Lynx canadensis*) are U.S. federally threatened and depend upon snowshoe hares (*Lepus americanus*) for up to 97% of their diet (Apps 2000). Lynx use of alternative prey varies seasonally, and increases when hare densities decline. When hare densities in the northern boreal region of their distribution are cyclically low, lynx exhibit prey-shifts and increase use of red and flying squirrels, birds, and carrion (Brand et al. 1976, O'Donoghue et al. 1998, Apps 2000). Seasonal prey shifts occur during summer when access to alternative prey species increases, such as in Nova Scotia, where 93% of winter but 70% of summer scats contained snowshoe hare (Parker et al. 1983). Similarly, hares comprised 85% of winter, but 58% of summer lynx diets on the Gaspé peninsula, Québec, Canada (Fortin and Huot 1995).

Lynx exhibit a numerical response to declines in hare densities, with kitten survival declining (Elton and Nicholson 1942, Brand et al. 1976, Mowat et al. 1996, Slough and Mowat 1996, O'Donoghue et al. 1997, Mowat et al. 2000, Hone et al. 2007). Snowshoe hares are 1.2 - 1.6 kg, larger than alternative prey such as red or flying squirrels (~0.2-
0.35 kg), or red-backed voles (*Myodes gapperi*) at 0.025 kg. Seasonal availability of adequate prey can affect lynx kitten recruitment (Brand and Keith 1979). When using dens, female lynx in Alaska (Kesterson 1988), in Yukon Territories, Canada (Mowat and Slough 1998), in Minnesota (Burdett et al. 2007), and in Maine (Vashon et al. 2008a, Mallett 2014) contracted their home ranges. Thus, female lynx with kittens may need to either have locally available snowshoe hares when they are foraging near their dens, or broaden their diets if hare populations fall below some critical threshold while provisioning kittens.

Lynx in Maine seem to forage where snowshoe hares are more accessible, rather than most abundant (Fuller et al. 2007). During summer, prey species other than hares are accessible, such as small mammals that emerge from hibernation or torpor, some from the subnivium, migrating passerine birds, and ground-nesting birds. Prey species potentially available to lynx in Acadian Forests are ruffed grouse (*Bonasa umbellus*) and spruce grouse (*Falcipennis canadensis*), passerine birds, ground nesting Anatidae, woodchucks (*Marmota monax*), muskrats (*Ondatra zibethicus*), beaver (*Castor canadensis*), red squirrels (*Tamiasciurus hudsonicus*), northern flying squirrels (*Glaucomys sabrinus*), eastern chipmunks (*Tamias striatus*), woodland jumping mice (*Napeozapus insignis*), red-backed voles (*Myodes gapperi*), other voles (*Microtus* spp.), deer and white footed mice (*Peromyscus maniculatus, P. leucopus*), and shrew species such as masked and smoky shrews (*Sorex cinereus, S. fumeus*), pygmy shrews (*Microsorex hoyi*), and the larger short-tailed shrew (*Blarina brevicauda*). Many of these potential prey have different structural and compositional habitat associations than snowshoe hares (Monthey and Soutiere 1985, Fuller et al. 2004, Fisher et al. 2005, Homyack et al. 2005, Vanderwel et al. 2009). If lynx exhibit enough dietary plasticity to
use alternate prey as a substantial portion of their diet, forest stands with vegetative structure that support various prey species and seasonal alternative prey may provide viable lynx habitat in the Acadian Forest region.

It has been suggested that alternative prey would be more important to lynx in the southern extent of their range (O'Donoghue et al. 2001, Steury and Murray 2004, Roth et al. 2007, Murray et al. 2008), given that typical hare densities are similar to densities in northern boreal forests when hares reach a cyclic low. Red squirrels increased in lynx diets to 20-44% of prey biomass during low hare density periods, relative to 0-4% during high hare density periods in Yukon Territories, Canada (O'Donoghue et al. 1998, Apps 2000). During low hare densities in Alberta, Canada, alternative food resources such as carrion, red squirrel, ruffed grouse and other birds increased in lynx diets (Brand et al. 1976). On a broad geographic scale, stable isotope ratios from lynx hair samples had stronger red squirrel than hare signatures from southern and eastern parts of the lynx range (Minnesota – 63% hare, Ontario – 68% hare, but not Quebec – 95% hare), leading Roth et al. (2007) to conclude that lynx are “facultative” predators and that it is “important to manage habitat for alternative prey” near the southern limits of the geographic range of lynx (Roth et al. 2007:2741). At the southern extent of the lynx and hare range, modeling of climatic factors resulted in northward recession of both the hare and red squirrel distribution (Peers et al. 2014). Thus, lynx may need to rely on prey other than snowshoe hares to persist near the present southern extent of their range in the face of impending climate change, if they are capable of broadening their dietary niche and if alternative prey can meet their energetic requirements.

My goal was to evaluate the range of dietary plasticity of lynx near the southeastern limit of their range in the Acadian Forests of Maine by documenting food habits when
they could be expected be most specialized, specifically during winter and during a relatively higher hare density period, compared to their food habits when they would be expected to be most generalized, during summer when hares were at a lower density. I expected that during a period defined as lower hare density ($\bar{x} \leq 0.92$ hares/ha, 2007-2013) (Harrison et al. 2014) lynx would display greater diet breadth, and use alternative prey to snowshoe hares compared to a higher hare density period observed during 2001-2006 (Scott 2009) when hares averaged 1.98 hares/ha in regenerating conifer-dominated forest stands. Regenerating conifer forest stands have represented the highest stand-level hare densities among all stand types surveyed in northern Maine from 2005-2014 (Harrison et al. 2014:Figure 4-1). To define different hare-density periods, I used one stand-type, the regenerating conifer-dominated (RG) stands. However, stand-level hare densities in four stand-types, including the RG stand type, were lower than in RG stands, and averaged 0.67 hares/ha (SE ±0.26, $n = 29$) from 2010-2014 (Figure E.3).

I evaluated evidence of prey switching to determine whether lynx, as a more generalist predator, would require habitats that support prey other than those supporting high snowshoe hare densities and accessibility (Fuller and Harrison 2010). I further evaluated evidence to support or refute the hypothesis that lynx at the southeastern extent of their range have a broader dietary niche and habitat associations than in boreal forest regions of Canada and Alaska (Roth et al. 2007).

**METHODS**

**Materials**

The Maine Department of Inland Fisheries and Wildlife (MDIFW) collected lynx feces (scat) during winter backtracking and telemetry surveys in 33 townships throughout northern Maine during 2001-2008 (Vashon et al. 2012:Fig. 2.3). Additionally, researchers
from our lab collected scat while backtracking lynx during winters 2002 and 2003 in northern Maine (Fuller et al. 2007). Few lynx scats had been collected in Maine during summer or low hare-density periods, as most research was conducted during winter months, and scats are difficult to detect under vegetation. For this investigation, I used a trained scat detection dog and handler, an efficient, non-invasive technique for carnivore scat collection (Wasser et al. 2004, MacKay et al. 2008). I contracted with the Conservation Canines Program at the University of Washington’s Center for Conservation Biology (CCB). Prior to the field session, CCB personnel trained a dog to detect scat from known male and female lynx that were collected while back tracking radio-collared lynx in Maine. In July 2011, we surveyed 94.6 km along unimproved dirt and overgrown skid trails, and within forest stands up to 150 m from road edges. We sampled within 10 northern Maine townships (Figure 2.1) in and surrounding the four-township study area where MDIFW had focused a radio telemetry study on Canada lynx in Aroostook County, Maine (Organ et al. 2008:Fig. 1).

I chose areas to survey based upon telemetry locations of radio-collared lynx (n= 10 lynx) collected during the previous two years (2009-2010; Vashon et al. 2012:Fig. 4.2). Telemetry clusters have been successfully used to detect and evaluate kill sites and determine predation rates in puma (Anderson and Lindzey 2003, Knopff et al. 2009), Eurasian lynx (Lynx lynx: Krofel et al. 2013), and bobcats (Lynx rufus: Svoboda et al. 2013), though not to detect scats. We searched areas that met three criteria where I expected a high probability of detecting lynx scat: greatest telemetry density of lynx locations, lynx home range boundaries, and adjoining borders of different individual lynx home ranges.
Figure 2.1. Study areas in Maine where Canada lynx scat was collected, 2001-2012. Critical lynx habitat is stippled (U.S. Fish and Wildlife Service 2014). A. MDIFW detected lynx in the townships outlined during 2001 – 2009 (Adapted from Vashon et al. 2012: Figure 2.3) and collected winter scats during those surveys. I sampled the townships outlined with a dotted line, inset B. Locations of scat survey routes sampled with a detection dog trained on Maine lynx scat during July 2011, Aroostook County, Maine. Circles mark scat locations, lines are researcher’s track logs that total 94.6 km.
Each scat was geo-referenced (Figure 2.1) with ESRI™ ArcPad on a GPS-enabled handheld computer and collected in a labeled whirl-pak® bag prepared with silicon desiccant beads. Approximately one-half of the scats were swabbed for genetic identification in the field the day they were collected, and the remainder were dried and processed upon our return to the laboratory.

**Genetic Identification**

I prepared duplicate samples from each scat to send to the University of Washington’s (UW) genetics laboratory for species identification to confirm species of origin for scats collected with the aid of the detection dog. Scats were swabbed with phosphate buffered saline, swabs were placed in 2 mL tubes with 0.5cc of Qiagen™ ATL lysis buffer, stored at 4°C, and shipped overnight in dry ice. I sent 14 additional scat samples for genetic identification that MDIFW researchers collected opportunistically while radio-tracking known lynx, but had been uncertain as to species of origin at the time of collection. Ten samples previously collected while backtracking known radio-collared lynx on snow were included to be analyzed as blind positive controls. An additional 27 scats collected from 2003–2007 during MDIFW’s backtracking and radio telemetry studies were genetically analyzed at the US Forest Service Rocky Mountain Research Station, Missoula, Montana (Schwartz and Pilgrim 2009; unpublished report).

DNA was extracted with a modified version of Qiagen DNeasy Tissue Kit™. To control for contamination, negative extract controls were included in each batch. Extracted DNA samples were stored at 4°C until polymerase chain reactions (PCR) were completed and then were frozen at -20°C for long term storage. Qiagen’s Multiplex PCR kit with fluorescent-labeled primers was used for PCR reactions, and multiplex PCR reactions of two fragments for the lynx-specific species and the gender identification
assays were run for each sample. Both fragments in the lynx-specific assay were run together in one multiplexed PCR reaction, and both gender assays, Amelogenin and sex-determining region Y (SRY), were also run together in one PCR reaction. PCR reactions were run on an Applied Biosystems® ABI 3100 Genetic Analyzer (ThermoFisher Scientific, Waltham, Massachusetts, USA), and fragment sizes were analyzed using GeneMarker software. DNA sequencing reactions were performed at UW’s High Throughput Genomics Center in Seattle, WA, USA, on an ABI 3730XL sequencer. DNA sequences were recorded and sent back to the University of Washington for further analyses. The University of Washington designed lynx-specific species primers of small fragment lengths, 150bp and 263bp, to ensure that only lynx DNA would amplify, and to increase amplification success in degraded scat samples (Foran et al. 1997). Of all samples confirmed as lynx, only 10% were confirmed as female, and 19% male, so I did not pursue an assessment of differential use of prey by gender.

**Diet Analysis**

Scats were soaked in water for ≥ 48 hours, washed through Humboldt Mfg. 20 and 60 gauge brass mesh screens with running water, then dried in 50°C ovens for 24–48 hours. Two to four different observers verified prey remains in each scat using a dissecting microscope (20x magnification) based on bone fragments, feather quills, teeth, and hair dimensions. Medullary banding patterns of individual hairs detectable at 100x magnification with a compound microscope were used to identify mammalian prey items to genus, whenever possible. Hair, dental morphology, and skull keys were used to identify most mammals to species (Moore et al. 1974, Jones and Manning 1992, Knecht 2012:137), or to family (Soricidae), or order (Chiroptera).
Diet Composition

I defined five categories of food items in lynx scats: snowshoe hare; bird; white-tailed deer (*Odocoileus virginianus*); and two mammal categories, intermediate and small. All birds were combined into a single category because tissues were not distinctive enough to allow further taxonomic precision. I defined intermediate mammals as ≥ 70 g, the smallest of which was flying squirrel (*Glaucomys* spp.) and small mammals as ≤ 42 g, the largest of which were undetermined to species, but likely represented red-backed voles (*Myodes gapperi*) that weigh between 6–42 g (Reid 2006).

I considered the summer-lower hare density period as corresponding to leaf-on months of May 1–October 30 during the years 2007-2012. Correspondingly, I considered the winter-higher hare density period as the leaf-off months of November 1–April 30 during 2001-2006, though no scats were collected during April. Hare densities in both periods were estimated from stand-level winter hare pellet counts in regenerating conifer-dominated stands (Homyack et al. 2006). The low hare density period averaged 0.92 hares/ha annually across 15 regenerating conifer stands per year (Harrison et al. 2014) and a relatively higher hare density period from 2001-2006 when hares density averaged 1.98/ha across a varying number of 4-17 (\( \bar{x} = 11, \text{mode} = 15 \)) regenerating conifer stands (Scott 2009).

I used two metrics of prey item categories to address different objectives. To test the breadth of prey items between two periods I compared the number of scats in each period that contained multiple and a single prey item. Because I had no information on available prey densities, and there were low numbers in some cells of the contingency table, I chose not to use a niche breadth index such as the Shannon-Wiener diversity index. I also quantified lynx diets in each season-hare density period using frequency of occurrence...
(FO), a metric to better quantify relative frequencies of prey consumed than percent occurrence of prey item/scat, when there are multiple prey items in each scat (Ackerman et al. 1984, Murdoch et al. 2010). I calculated frequency of occurrence as: 100 × number of occurrences of a given prey item/total number of all prey items within each season-hare period. Though volumetric and gravimetric methods of diet analysis could yield more accurate assessments of relative use of prey items (Kelly 1991), scat collection from free-ranging mammals excludes these methodologies, because intervals between meals varies considerably and is unknown.

I tested the two-sided hypothesis that diet breadth of lynx was equal during the summer-lower hare density and the winter-higher hare density periods using counts of scats with multiple food item categories per scat and those containing only a single food item using Fisher’s exact test from R statistical package “exact2x2” (Ruxton and Neuhauser 2010). To determine if distributions of foods consumed by lynx differed between season-periods, I also used an ANOVA with individual scats blocked. This analysis similarly addressed the question of diet breadth as did the Fisher’s exact test, but the ANOVA was a more conservative test that retained information in all the food categories, while adjusting for non-independence of multiple prey items in scats. Some food items were sparsely represented in scats; therefore I used a randomization ANOVA that allowed inferences without having to make assumptions about the distribution of the error structure (Kutner et al. 2005:712). I used outputs from an ANOVA repeated with 1000 randomized permutations of season-periods and prey items, to average the F-statistics.

To facilitate comparisons with previous food habits studies for lynx I used Frequency of Occurrence (FO) of prey item categories for the remaining analyses. If there was an
overall difference between season-periods detected by the ANOVA, I tested which of the five prey-item categories contributed to the difference. Within each prey item category, I used chi-square tests of proportions of summer-lower vs. winter-higher hare density \( P \)-values, randomized with 2000 Monte Carlo iterations, then adjusted for family-wise error rates by applying a sequential Holm-Bonferroni correction at the 5% level. I used R version 3.1.0 (2014-04-10) to perform statistical procedures (R Core Team 2013).

RESULTS

From 2001 through 2012, we collected a total of 388 scats throughout northern Maine. Researchers in our lab collected 42 winter scats verified as being deposited by lynx during a backtracking study of radio-collared lynx in 2002-2003. We collected 226 probable lynx scats in July 2011 with the aid of the scat detection dog-handler team, and I collected 11 scats suspected as lynx without the aid of the dog. The Maine Department of Inland Fisheries and Wildlife (MDIFW) provided 98 winter and 2 summer scats suspected as deposited by lynx that were collected during snow-tracking studies of lynx during 2001-2008. Most of the MDIFW collection had been previously verified as lynx by the Genetics Laboratory located at the US Forest Service, Rocky Mountain Research Station, Missoula, MT. I sent 23 scats of unknown species origin to the UW genetics lab that were opportunistically collected during 2011 and 2012.

Of the 270 scat samples I sent to UW for identification, DNA amplification rate was 97% (254/270). Of the scats collected with the aid of the CCB dog, 82.7% (187/226) were genetically confirmed as lynx. This rate may be a low estimate of the ability of the dog to accurately detect lynx scats, given that DNA from 15 of the 226 samples (6.6%) either did not amplify or was inconclusively identified (Table 2.1). There were 334 scats that were verified as lynx, including those previously genetically confirmed as lynx by
another lab. Overall, 324 scats that were verified as being deposited by lynx (199 lower period-summer, 125 higher period-winter), were subsequently analyzed for prey content.

There were 230 food item categories in 199 scats from the summer-lower hare density period and 127 food item categories in 125 scats from the winter-higher density period (Table 2.1). Individual scats (n = 324) included up to 3 prey items including hares; 36 (11.1%) contained multiple prey items. Diet breadth was more pronounced during the summer-lower hare density period (2007-2012), with 16.08% (32/199) of scats containing multiple prey items, and 3.20% (4/125) with multiple prey during the winter-higher density period from 2001-2007 (Fisher’s exact $P = 0.0002$, odds ratio 5.77, n = 324). A more conservative randomized ANOVA that I used to assess percent occurrence of prey item categories in scats also detected that diet breadth was greater during the summer-low period ($F_{4,322} = 0.0068$, 1000 randomizations).
Table 2.1. Source of scats collected in northern Maine during 2001-2012, year(s) collected, number of samples genetically analyzed at the University of Washington, and results of genetic identification. DNA amplification was successful for 97% of the samples analyzed (n = 270).

<table>
<thead>
<tr>
<th>Source</th>
<th>Years collected</th>
<th>Samples sent</th>
<th>% Genetic identification (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>MDIFW^c</td>
<td>2001-2009</td>
<td>14</td>
<td>Lynx 85.7 (12) Coyote 14.3 (2)</td>
</tr>
<tr>
<td>Known samples^d</td>
<td>2002-2003</td>
<td>10</td>
<td>100.0 (10)</td>
</tr>
<tr>
<td>Detection dog^e</td>
<td>2011</td>
<td>226</td>
<td>Lynx 82.7 (187) Coyote 10.7 (24) Other^a 3.5 (8) ND^o 3.1 (7)</td>
</tr>
<tr>
<td>Opportunistic^f</td>
<td>2011-2012</td>
<td>20</td>
<td>Lynx 55.0 (11) Coyote 40.0 (8) Other^a 5.0 (1)</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>270</td>
<td>81.5 (220) 12.6 (34) 3.0 (8) 3.0 (8)</td>
</tr>
</tbody>
</table>

^a Other carnivore species or possibly lynx. Bands had low signal strength or samples matched only one of three possible lynx base pair fragments.

^b No Data; DNA did not amplify.

^c Maine Department of Inland Fisheries and Wildlife.

^d Collected by University of Maine researchers backtracking radio-collared lynx.

^e The dog and handler were provided by University of Washington’s Center for Conservation Biology and trained to detect Maine lynx.

^f Opportunistically collected by field crews.
Of the five categories of food items, snowshoe hares and deer occurred more frequently during the winter-higher than during the summer-lower hare density period (Figure 2.2). Frequency of occurrence of hares was greater during the higher-winter (92.13%, 117/127) vs. the summer-lower hare-density period (75.2% FO, 173/230), \( P_H = 0.003 \), Table 2.2). Deer was rare, comprising 1.1% of the 357 food item categories identified across both seasons.

Small and intermediate-mammals and birds all occurred more frequently during the summer-lower period (Figure 2.2), which was expected because of increased availability of these foods during the snow-free leaf-on period. Birds occurred more frequently during the summer-lower 13.9% (32/230) compared to winter-higher period (4.7%, 6/117, \( P_H = 0.018 \)). Bird species were difficult to identify, though we detected grouse feet and a gray jay skull \((Perisoreus canadensis)\). Small mammals were 6.9% (15/230) of the prey items in scats during the summer-low and 0% \((n=127)\) during the winter-high period \( P_H = 0.020 \). Small mammals comprised deer or white footed mice, jumping mice, meadow or red-backed voles, shrews and a bat \((Chiroptera)\). There were no differences in frequency of occurrence between summer-lower and winter-higher hare density periods for intermediate mammals \((3.9% \text{ of summer-low, } 9/230, \ 0.8% \text{ of winter-high, } 1/127, \ P_H = 0.188)\), and deer \((0.4% \text{ of summer-low, } 4.4% \text{ of winter-high, } P_H = 0.134)\). Use of intermediate mammals by lynx was similar between seasons and periods \((3.9% \text{ of summer-low, } 0.8% \text{ of winter-high, } P_H = 0.188)\). Species identified in the intermediate-mammal category \((\geq 70 \text{ g})\) included muskrat, an eastern chipmunk, red and flying squirrels.
Figure 2.2. Frequency of occurrence of food items in lynx scats collected in northern Maine, 2001-2012, during summer-lower hare density ($n = 230$ food item categories) and winter-higher hare density ($n = 127$ food item categories) periods. Categories include: snowshoe hares (*Lepus americanus*); birds; small mammals ≤42 g (voles, mice, shrews, and a bat); and intermediate mammals ≥70 g (red squirrels, flying squirrels, muskrats and a chipmunk). Frequency of occurrence = (100 × number of occurrences of a given food item)/total number of food items in each season-period. Scats from the lower hare density period (2007-2012) were collected during summer, and scats from the higher hare density period (2001-2006) were collected during winter.
Table 2.2. Frequency of occurrence (FO) of 5 food categories in Canada lynx scats collected during a period of winter-higher hare density (2001-2006) and a period of summer-lower hare density (2007-2012) in northern Maine, USA.

<table>
<thead>
<tr>
<th>Season-hare density period</th>
<th>No. of scats</th>
<th>No. of food items</th>
<th>Hares</th>
<th>No.</th>
<th>FO</th>
<th>Birds</th>
<th>No.</th>
<th>FO</th>
<th>Small(^a) mammals</th>
<th>No.</th>
<th>FO</th>
<th>Intermediate mammals</th>
<th>No.</th>
<th>FO</th>
<th>Deer</th>
<th>No.</th>
<th>FO</th>
</tr>
</thead>
<tbody>
<tr>
<td>Summer-low</td>
<td>199</td>
<td>230</td>
<td>173</td>
<td>75.2</td>
<td>32</td>
<td>13.9</td>
<td>15</td>
<td>6.5</td>
<td>9</td>
<td>3.9</td>
<td>73</td>
<td>92.1</td>
<td>82</td>
<td>73</td>
<td>1</td>
<td>0.4</td>
<td></td>
</tr>
<tr>
<td>Winter-high</td>
<td>125</td>
<td>127</td>
<td>117</td>
<td>92.1</td>
<td>6</td>
<td>4.7</td>
<td>0</td>
<td>0.0</td>
<td>1</td>
<td>0.8</td>
<td>77</td>
<td>75.2</td>
<td>75</td>
<td>77</td>
<td>3</td>
<td>2.4</td>
<td></td>
</tr>
<tr>
<td>p (^c)</td>
<td>0.003</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.018</td>
<td></td>
<td></td>
<td>0.020</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Totals</td>
<td>324</td>
<td>357</td>
<td>290</td>
<td>81.2</td>
<td>38</td>
<td>10.6</td>
<td>15</td>
<td>4.2</td>
<td>10</td>
<td>2.8</td>
<td>63</td>
<td>81.2</td>
<td>81</td>
<td>63</td>
<td>4</td>
<td>1.1</td>
<td></td>
</tr>
</tbody>
</table>

\(^a\) Mice (*Peromyscus* spp.), voles (*Myodes gapperi* and *Microtus* spp.) and prey items from Chiroptera and Insectivora (bat, short-tailed shrew), < 42 g.

\(^b\) Muskrat (*Ondatra zibethicus*), red and flying squirrels, chipmunk, ≥ 70 g.

\(^c\) Simulated P-value (2000 iterations) with Holm-Bonferroni correction at \(\alpha = 0.05\), to test season-hare density period difference in proportions of the FO.
DISCUSSION

Near the southern extent of the geographic range of Canada lynx, stable isotope ratios from lynx pelts suggest that that lynx may shift their relative use of prey from snowshoe hares to red squirrels compared to within the core of their boreal forest range (Roth et al. 2007). This evidence has led authors to assert that lynx can occupy a broader dietary niche at low hare densities near the southern extent of their range (Roth et al. 2007, Murray et al. 2008) and has been used as a basis for modeling potential range shifts by lynx in response to changing climate and availability of alternate prey (Peers et al. 2014). It has been further suggested that lynx at the southern edges of their range may need to broaden their dietary niche as they experience increased competition for food resources with carnivores such as bobcat, coyote and fisher, species that could respond to shifting climatic conditions (Peers et al. 2013). During winter seasons and higher hare density years, snowshoe hares represented 92.1% FO of prey items consumed and during summer seasons in lower hare density years, hares represented 75.2% FO of prey items. Thus, my data indicate that lynx near the southeastern extent of their range in Maine rely extensively on hares both when I expected lynx to be most specialized, as well as when I expected lynx to be most generalized.

My results suggest that lynx are hare specialists throughout their geographic range are further supported by research conducted near the southern extent of lynx range in Washington (Koehler 1990:79.3 PO, n=29), Wyoming (Dowd and Gese 2012:85.2 PO, n=24), Montana (Squires and Ruggiero 2007:96 PO, n=86), Minnesota (Hanson and Moen 2008), and Quebec (Roth et al. 2007). Canada lynx seem to be dietary specialists throughout the southern edge of their distribution, despite hare densities of only 0.02 – 1.0 hares/ha (Apps 2000, Hodges 2000a, Murray et al. 2002, McCann et al. 2008, Ivan et
al. 2014). Although lynx expanded their dietary breadth during the summer-lower period, hares were still >75% of prey items. The caloric contribution of hares may be greater than 75%, as hares are a larger prey item than species that comprised most of the other items in the summer-lower period, birds at 13.9% and small mammals at 6.5%. This suggests that survival of kittens could depend upon availability of snowshoe hares.

The importance of snowshoe hares to survival of lynx kittens through the summer season has been documented in the boreal forest: in Alberta, postpartum mortality of kittens was associated with declines in hare densities (Brand et al. 1976, Brand and Keith 1979). A paucity of research throughout the geographic range of lynx documenting their summer food habits compromises interpretations of the ability of the species to broaden their dietary niche, when relative availability of alternative prey increases. My study is the first to use genetically verified lynx scats that were collected in summer, during a period of relatively lower hare density and revealed that lynx are hare specialists in Maine during both summer and winter periods and when hares were at lower versus higher relative availability. Availability of prey biomass in summer seasons is critical to lynx kitten recruitment, and snowshoe hares that provide adequate caloric value were the majority of prey consumed in Maine by lynx.

The prey shifts that contributed to increased dietary diversity of lynx during the summer-lower hare density period were represented by lower frequency of occurrence of hares and increased occurrence of small mammals and birds. Frequency of occurrence of intermediate mammals also increased in summer diets, but not as drastically as small mammals, which are protected from lynx under snow for approximately 5 months/year in the northern Maine study area. Small mammals represented 6.5% of prey items during the summer-lower hare density period, and, at 20 – 42 grams, could not have approached
the caloric value of hares at an average of 1.4 kg. Birds represented 13.9% of prey items in summer, and the largest bird species most available are likely the ruffed grouse (Bonasa umbellus) and spruce grouse (Falcipennis canadensis) that weigh 400 – 750 g. The bird category of food items also included passerine birds, so that as a category, similarly to small mammals, provided less caloric value to lynx than hares. Frequency of occurrence in scats likely underestimates the caloric value and ecological importance of hares, as hares were the largest of the prey items observed with the exception of deer (4 of 324 scats) and muskrats (2 of 324 scats). During this study, I detected no regularly consumed prey that could provide lynx with equivalent energetic requirements to hares. Though red squirrels have been suggested as viable alternate prey for lynx (Murray et al. 2008), and have been detected in empirical studies of lynx food habits (Fortin and Huot 1995, O’Donoghue et al. 1997, O’Donoghue et al. 2001, Roth et al. 2007). occurrence of red squirrels was ≤ 1.7 % during both seasons and hare density periods. This research corroborates the most extensive study that was conducted in the southeastern portion of the lynx range (Parker et al. 1983), where an examination of 441 summer scats from lynx on Cape Breton Island, Canada revealed 70% FO of hare and 4% FO of red squirrel (Hanson and Moen 2008). Lynx in Maine and in other areas at the southern edge of their range (Koehler 1990, Squires and Ruggiero 2007. Dowd and Gese 2012), seem to be reliant on snowshoe hares rather than red squirrels. In the face of possible range contractions that changing climatic conditions may impose upon lynx, it is doubtful that lynx could persist upon red squirrels if the snowshoe hare experiences range contraction (Peers et al. 2014). Additionally, climate change may induce abiotic changes that favor the predator community of generalists, such as fisher, bobcat and coyotes, all
possible direct and indirect competitors of the specialist lynx (Dowd and Gese 2012, Peers et al. 2013, Dowd et al. 2014).

As climate change induces northern shifts in suitable resource gradients for lynx, it has been suggested that lynx can display the phenotypic plasticity necessary to shift to prey such as red squirrels (Peers et al. 2014). This was based on results from Yukon Territories, Canada, where 58-72% of the biomass of lynx diets were red squirrel when hares reached low densities (O'Donoghue et al. 1997), and on stable ratios indicating relatively higher red squirrel than hare signatures in southern lynx populations (Roth et al. 2007). For example, in the Kootenay valley, British Columbia, Canada, hare density at a stand scale was approximately 0.01–0.47 hares/ha over a two year period, where 30% of 137 lynx kills (n = 10 lynx) observed during snow tracking were red squirrels, and 52% were hares (Apps 2000). It is notable that during the summer season and during years of lower hare density (0.92 hares/ha in high quality hare habitat) when lynx could be expected to exhibit the broadest dietary breadth, hares still dominated the diet (Table 2.2). Although lynx have the capability to use alternative prey, yearling lynx fecundity declines, litter sizes decrease, kitten mortality increases (Brand et al. 1976, Brand and Keith 1979), juvenile recruitment declines (Poole 1994, Mowat et al. 1996) and emigration increases (Slough and Mowat 1996, Mowat et al. 2000) concurrent with decreased proportion of hare in lynx diets. If lynx can broaden their dietary niche to include prey other than hares at the southern extent of their range, they may not do so until hare densities decline to levels similar to the hare densities that were reported in boreal forests.
MANAGEMENT IMPLICATIONS

Lynx in northern Maine are dietary specialists and are likely to occupy habitat with biotic features that favor snowshoe hares such as dense early-seral forest cover (Scott 2009, Simons-Legaard et al. 2013) and abiotic resource gradients that may reduce competition with sympatric carnivores, such as higher altitude, deep snow cover, and snow consistency (Stenseth et al. 2004, Peers et al. 2012). Dense conifer-dominated regenerating habitat is succeeding to later seral stages, and harvesting practices are producing less acreage of regenerating conifer-dominated 10-40 years old in Maine, (Simons-Legaard et al. 2013). Hence, in Maine effects of climate change on the abiotic community and the predator community, combined with reduced available habitat for snowshoe hares, could influence lynx demographics and ultimately the future geographic range of both hares and lynx. At the southeastern edge of their range where lynx occupancy has been associated with dense early seral-stage forest types, land managers that attempt to promote stands with dense conifer sapling densities and complex conifer understories at the stand (see Chapter 1) and sub-stand scale (Fuller and Harrison 2013), will enhance foraging opportunities for lynx, and may enhance the probability of landscape-scale occurrence of lynx (Simons-Legaard et al. 2013).

LITERATURE CITED


APPENDIX A

Characteristics and silvicultural histories of the study stands where pellet densities of snowshoe hares were quantified and vegetation was sampled in northern Maine, 2001–2013.
Table A.1. Stand ID, vegetation-harvest type, location, harvest history, years since harvest as of 2012, and years monitored for stands where snowshoe hare pellet densities were monitored in northern Maine, 2001-2013. Vegetation-harvest types include regenerating herbicide-treated conifer 18–39 years post-clearcutting (RG), selection harvest (SEL), shelterwood (SHW), overstory removal (OVR), mature mixed (MMX), and mature conifer (MSW; Mature Softwood) stands. Stands identified in **Bold** were used to address Chapter 1, Objective 1 based on data collected during 2005-2012 (Table A.2) and Table A.3 lists stands used for Chapter 1, Objective 2. Stands not bolded were harvested before, or established after the 2005-2012 study period used for Chapter 1, and thus were excluded from all analyses.

<table>
<thead>
<tr>
<th>Stand ID monitored</th>
<th>Type</th>
<th>Township</th>
<th>Management history</th>
<th>Years since harvest</th>
</tr>
</thead>
<tbody>
<tr>
<td>CLREG1 RG</td>
<td>T11R13</td>
<td>1976</td>
<td>1997</td>
<td>36</td>
</tr>
<tr>
<td>CLREG2 RG</td>
<td>T11R13</td>
<td>1976</td>
<td>1994</td>
<td>36</td>
</tr>
<tr>
<td>CLREG3 RG</td>
<td>T11R10</td>
<td>1984</td>
<td>1991</td>
<td>28</td>
</tr>
<tr>
<td>CLREG4 RG</td>
<td>T11R10</td>
<td>1984</td>
<td>1989</td>
<td>28</td>
</tr>
<tr>
<td>JH01C RG</td>
<td>T4R11</td>
<td>1978</td>
<td>1988</td>
<td>34</td>
</tr>
<tr>
<td>JH02C RG</td>
<td>T4R11</td>
<td>1978</td>
<td>1983</td>
<td>34</td>
</tr>
<tr>
<td>JH03C RG</td>
<td>T4R11</td>
<td>1975</td>
<td>1984</td>
<td>37</td>
</tr>
<tr>
<td>JH04C RG</td>
<td>T5R11</td>
<td>1983</td>
<td>1988</td>
<td>29</td>
</tr>
<tr>
<td>JH05C RG</td>
<td>T4R11</td>
<td>1975</td>
<td>1985</td>
<td>37</td>
</tr>
<tr>
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<td>T5R11</td>
<td>1973</td>
<td>1982</td>
<td>39</td>
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<tr>
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<td>T4R11</td>
<td>1978</td>
<td>1988</td>
<td>34</td>
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<tr>
<td>SM4C RG</td>
<td>T11R12</td>
<td>1983</td>
<td>1987</td>
<td>29</td>
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<tr>
<td>SM4D RG</td>
<td>T11R11</td>
<td>1985</td>
<td>1992</td>
<td>27</td>
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<tr>
<td>TLRG1 RG</td>
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<td>1994</td>
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<td>20</td>
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<td>1991</td>
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</tr>
<tr>
<td>TLRG3 RG</td>
<td>T3R12</td>
<td>1992</td>
<td>2005</td>
<td>18</td>
</tr>
</tbody>
</table>

Selection Harvest

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a Harvest and herbicide dates established by landowner maps, discussions with forest managers (Mullen 2003, Robinson 2006, Homyack et al. 2007, Stephen Dunham, University of Maine and Scott Joachim, Katahdin Forest Management personal communication 2012), and confirmed or adjusted using harvest history information for Northern Maine, 1970-2007, derived from LandSat and MSS imagery (Simons-Legaard and Legaard, unpublished data, University of Maine). (Table adapted from Robinson 2006:15 and Scott 2009:11).

b All mature stands had not been harvested for at least 42 years prior to 2012, when records were first kept. MSW stands were approximately 80 years old. (E. Simons-Legaard, School of Forest Resources, University of Maine, personal communication).
Table A.2. Vegetation-harvest type, stand ID, number of pellet plots, area sampled (m²) for pellets, and years monitored for stands used to model seasonal differences in hare pellet densities across three stand-types in Chapter 1, Objective 1. Mature stands were monitored for pellets beginning in 2008. Otherwise, variation in numbers of years monitored resulted from some stands being harvested by landowners during the study; after harvesting stands were excluded from further monitoring and analyses.

<table>
<thead>
<tr>
<th>Stand Type</th>
<th>Stand ID</th>
<th>No. plots</th>
<th>m² sampled per stand</th>
<th>No. years monitored for hare pellets</th>
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Table A.2. Continued.

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Table A.3. Vegetation-harvest type, stand ID, and number of years monitored for 26 stands used to model effects of vegetation on seasonal differences in hare pellet densities in Chapter 1, Objective 2. Vegetation in northern Maine was measured in 20 plots during summer 2011 and in 10 plots during winter 2012.

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$^a$ MSW9 and MSW10 were established and cleared of pellets Fall, 2011; first count occurred Spring, 2012.
APPENDIX B

The reliability of annual and summer pellet surveys to predict densities of snowshoe hares in northern Maine.
INTRODUCTION

My goal was to compare hare densities across seasons in Chapter 1, which necessitated the use of the same response variable for each season (i.e., either pellet densities or hare densities), to make comparisons among forest stand treatments between seasons. Although Homyack et al. (2006) verified the utility of overwinter pellet counts conducted in May-June to predict June densities of hares in Maine, the reliability of over-summer pellet counts conducted in September-October to predict hare densities was previously undetermined. Using hare trapping data from May-June, I explored the feasibility of using over-summer counts conducted in late September-mid October to predict May-June hare densities. I further evaluated our ability to predict May-June densities of hares from annual counts of hare pellets. The annual counts were pooled from our semi-annual pellet counts. My objective was to assess the feasibility of using the more direct variable of hare density rather than an index to density. pellet counts, as a response variable when evaluating seasonal effects on habitat choices by hares in Chapter 1.

Pellet counts are a reliable index for hare densities, and predict hare densities well when pellet densities have been validated with a direct capture-mark-recapture effort (Krebs et al. 2001, Mills et al. 2005, Homyack et al. 2006, Hodges et al. 2009), but often lack accuracy and precision, especially if counts are conducted only once annually (Mills et al. 2005, Murray et al. 2005). Hare densities can be more accurately predicted from pellet densities when mark-recapture (MR) studies describe the degree to which hare densities estimated from capture rates are correlated with pellet counts in the same area during the same time period (Litvaitis 1985, Krebs et al. 2001, Murray et al. 2002, Mills
et al. 2005, Murray et al. 2005, Homyack et al. 2006, Hodges and Mills 2008, Berg and Gese 2010). In northern Maine, the accuracy of predicting May-June density of hares based on winter counts of pellets was validated using counts from October-April regressed against hare densities estimated in May-June during 2001 and 2002 (Homyack 2003). Those data were subsequently combined with previous hare pellet counts and MR data collected during 1983-1984 in eastern and western Maine (Litvaitis 1985) to develop a regression equation to predict hares/ha based on pellet deposition rates (pellets/ha/month) during the winter period (Homyack et al. 2006). Although that publication reported a correlation coefficient of $R = 0.65$ (n=8), for leaf-on (i.e., summer) data, that dataset was not comparable to the winter regression that combined two datasets (n=16), and the utility of using summer or annual pellet counts (i.e., pooled across semi-annual counts) to predict estimated densities of hares was not evaluated.

METHODS

**Summer Pellet Density and June MNA Hare Estimates**

The Wildlife Department at the University of Maine, in collaboration with the Maine Department of Inland Fisheries and Wildlife, conducted semi-annual fecal pellet counts in spring (May-June, leaf-on season) and in autumn (Sept-Oct, leaf-off season), 2001–present, to assess snowshoe hare density in northern Maine (see Chapter 1 for study area description). I used pellet count data collected during 2001-2002, corresponding to hare trapping conducted during June 2001 and June 2002 to assess the over-winter hare population. Hare density was calculated from the minimum number alive (MNA) of hares trapped, with juveniles excluded (Homyack 2003). Pellet counts were conducted at summer’s end, during September-early October in eight different forest stands in 2001.
and 2002. Pellet counts were averaged across 84 plots in each of the eight stands. During May-June, 2001-2002, these eight stands were live trapped for snowshoe hares and their density estimated from mark-recapture (Homyack et al. 2006).

The response variable of hares/ha was calculated from Minimum Number of Hares Alive (MNA) in each of eight stands that were trapped from 13 to 18 nights, divided by the stand specific effective trapping area (SSETA) (Homyack 2003). Thirty-five traps were positioned approximately 50 m apart in each stand.

\[
\frac{\text{MNA}}{\text{SSETA}} = \frac{\text{initially captured hares} - \text{recaptured, marked hares}}{(\text{stand trap grid area}) + (\text{buffer of 1/2 average recapture distance for the stand})}
\]

The regression model produces the equation to predict summer hare density:

\[
\frac{(\text{MNA/ SSETA})}{\text{using summer pellet counts}}: \hat{y} = \beta_0 + \beta_1 x
\]

Where \(y = \text{June hares} \) hectare and \(x = \text{summer pellet counts/ hectare/month} \)

Initial statistical diagnostic plots revealed residuals for the summer counts were normally distributed (Shapiro-Wilk \(W = 0.898, P = 0.28\), and a Breusch-Pagan test (BP = 1.8838, \(df = 1, P = 0.17\)) revealed constant variance, meeting assumptions of linear models (IID).

To assess relative accuracy of several models, the response variable (hares/ha) was transformed with a square root, then a 4\(^{th}\) root, and a log\(_e\)\(y\). The winter predictive model was linear, so I chose the linear summer model with no transformations for equivalent comparisons.

**Annual Pellet Density and June MNA Hare Estimates**

Annual pellet counts were combined from May-June and September-October counts, in eight forest stands 2001 and 2002. As with the summer analysis, this annual analysis uses the same eight stands that were trapped for hares in May through June, 2001 and
2002 by Homyack et al. (2006). Pellet counts were averaged across 84 sub-plots for each of the eight stands which yielded eight replicate means. The response variable, hares ha\(^{-1}\), was calculated from Minimum Number of Hares Alive (MNA) in each of eight stands that were trapped from 13 to 18 nights, divided by the stand specific effective trapping area. Leverets less than eight months old were excluded from the MNA calculations (Homyack 2003:31) which should underestimate hare densities relative to pellet densities for the summer season. I used linear regression to assess ability of annual pellet counts to predict annual hare densities.

RESULTS

Summer Pellet Density and June MNA Hare Estimates

A scatter-plot of summer pellet density as a function of MNA hares/ha shows greater variability at lower pellet counts, and a positive trend (Figure B.1A). That variability is reflected by the fit of the linear regression model to predict hare density from summer pellet densities \((r^2 = 0.428, F_{(1,6)} = 4.49, P = 0.078)\), in which 57.2% of the total variation in hare densities was unexplained. A model that transformed the response variable (log\(\gamma\)) explained only slightly more of the variability than the linear summer model (Table B.1), \((\text{adj} \ r^2 = 0.45, F_{(1,6)} = 6.64, P \leq 0.042)\). The equation derived from the transformed summer hares/ha as a function of summer pellets model is:

\[
y = \log_{10} \text{hares/ha} = 0.0013 \text{ (summer pellets/ha/month)} + 1.34
\]
Table B.1. Season that snowshoe hare pellet counts were conducted during 2001-2002, predictive equations for hare densities from pellet counts, \( r^2 \) values, number of stands where both pellet counts and mark-recapture estimate of hare density were available, and sources for pellets in Maine and Idaho. The Maine dataset is derived from hare trapping conducted in June (Homyack et al. 2006) and I used end-of-summer pellet counts for the summer equation.

<table>
<thead>
<tr>
<th>Pellet count season</th>
<th>Predictive equation</th>
<th>( r^2 )</th>
<th>( n )</th>
<th>Study area(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annual</td>
<td>( y_{am} = 0.2726 + 0.00006x )</td>
<td>0.88</td>
<td>8</td>
<td>north-central Maine</td>
</tr>
<tr>
<td>Winter</td>
<td>( y_{wtr} = 0.2810 + 0.00008x )</td>
<td>0.89</td>
<td>8</td>
<td>north-central Maine</td>
</tr>
<tr>
<td>Summer</td>
<td>( y_{smr} = 0.9543 + 0.0002x )</td>
<td>0.43</td>
<td>8</td>
<td>north-central Maine</td>
</tr>
<tr>
<td>Winter</td>
<td>( y_{wtr} = 0.15979 + 0.00010x )</td>
<td>0.87(^a)</td>
<td>16</td>
<td>north-central, southeast, southwest Maine(^b)</td>
</tr>
<tr>
<td>Annual</td>
<td>( y = 1.423 \times (2.077 - e^{-0.562x}) )</td>
<td>0.79(^c)</td>
<td>24</td>
<td>northern Idaho</td>
</tr>
</tbody>
</table>

\(^a\) adjusted \( r^2 \).
\(^b\) (Homyack et al. 2006).
\(^c\) I calculated \( r^2 \) from the reported \( r \) value (Murray et al. 2002:779, Table 2).

**Annual Pellet Density and June MNA Hare Estimates**

Pooled counts from summer and winter hare densities were strongly associated with pellet densities \( (r^2 = 0.88, F = 44.38, P = 0.0006) \) for the eight stands live-trapped in northern Maine by Homyack et al. (2006) during 2001-2002 (Figure B.1C). The PRESS statistic (PRESS statistic, see: Mitsa 12 May 2013) for this annual data in northern Maine was 0.83, indicating that the annual regression equation has strong predictive value to estimate hare density from annual pellet counts.
Figure B.1. Linear regressions of hare pellet rates as a predictor of hare density (hares/ha) in Maine for A. summer, B. winter, and C. pooled summer-winter, or annual, pellet densities based on June mark-recapture estimates of hare densities, 2001-2002 (n=8 for each). Points are raw hare densities by pellet counts from the 8 stands, and shaded areas are 95% confidence intervals.
DISCUSSION

Summer pellet counts associated with snowshoe hare trapping MNA estimates as a predictor of hares/ha had low precision $r^2 = 0.428, n=8$. Although these eight data points suggest a positive relationship ($P = 0.078$) between May-June hare densities and summer pellet counts, the predicted residual sum of squares (PRESS statistic, see: Mitsa 12 May 2013) of the linear regression is low (-0.03), so the model has little predictive ability. Only 42% of the variability in hare density is explained by pellets. Thus, I don’t recommend using summer pellet counts to estimate hare densities and suggest that pellet counts be treated as a general, yet relatively imprecise index of relative summer hare densities.

Regression equations to predict hare densities from annual pellet counts and winter pellet counts in Maine (Homyack et.al 2006), and from annual counts from Idaho (Murray et al. 2002) were comparable in performance (Table B.1). The Idaho equation is exponential and used a $ln (x) + 1/6$ transformation of both variables before analysis. Annual pellet counts coupled with a single trapping season have relatively high correlations and have been commonly used to estimate hare densities. In the Yukon, a $log_e-log_e (ln-ln)$ predictive relationship was developed ($r = 0.76, n=85$) (Krebs et al. 2001), and in western Wyoming an $ln-ln$ relationship was also used ($r = 0.94, n=18$) (Berg and Gese 2010). In Idaho, though hares were trapped in four seasons, mean annual MNA estimates were related to annual pellet counts ($r = 0.93, n=24$) (Murray et al. 2002:774). Here, combined summer and winter pellet count data (annual) data collected in 2001-2002 (Homyack et al. 2006) was strongly associated with MNA hare density estimates ($adj \, r^2 = 0.88, F=44.38(1,6), P \leq 0.001, n=8$), a result similar to a predictive
equation developed in Minnesota (McCann et al. 2008) for annual pellet counts calibrated with MNA hare densities trapped in spring ($r^2 = 0.79$, $P \leq 0.001$, n=10). Though using annual counts masks the seasonal variability that is more pronounced in summer (Figure B.1A), the PRESS statistic for this annual dataset in northern Maine was 0.83, and 88% of the variance in hare densities is explained by pellet densities, indicating that the annual regression function has high predictive value.

**MANAGEMENT IMPLICATIONS**

Investigation of seasonal snowshoe hare use of habitat requires semi-annual pellet counts, calibrated to snowshoe hare density estimates in different seasons, when the focus of interest is inter-seasonal differences. These analyses confirm that when comparing leaf-on and leaf-off trends, or investigating differences between seasons, fecal pellet densities rather than hare densities should be used as an indirect index for seasonal snowshoe hare densities in northern Maine. However, annual snowshoe hare fecal pellet counts in northern Maine can reliably serve as a predictor of relative hare densities among forest stand-types if seasonal variation of hare densities and seasonal changes in habitat resource use are not the objectives of the research.

**LITERATURE CITED**


APPENDIX C

Supplemental material
Figure C.1. Schematic of a typical study stand surveyed for snowshoe hare pellets, not drawn to scale. Transect 1, Plot 1 is labeled T1P1 and Transect 4, Plot 7 as T4P7. Seven 1.5 m² plots/transect were randomly oriented on compass bearings along four parallel transects. Every pellet in each plot was counted and removed. Stand area was 7.02 ha (shaded), and 16.75 ha including the 70 m buffers. Total area sampled for pellets in a stand (sample unit) was 42 m².
Figure C.2. Snowshoe hare silhouettes used to quantify lateral cover. A. Summer silhouette in Stand AF1, Transect 2 Plot 4, categorized as trace covered. B. Winter silhouette in same plot, categorized as trace covered on its feet and tail. Silhouettes are life size, and ~20 cm tall at the highest point of their backs.
Figure C.3. A. Overhead schematic of 1.5 m² pellet plot and 10 m² vegetation survey plot. B. Four layers of vegetation were point sampled with a GRS densitometer™: Ground to 7 cm high, 7–50 cm, 50–150 cm high, and overhead to identify vegetation at 18 points/layer, 72 points/plot, 20 plots/stand. Eight of 72 sample points taken/plot are shown. Categories of ground cover and vegetation were identified as: bare ground, water, duff, fern (Psilophyta, Pterophyta), moss (Lycopodium), equisetum (Sphenophyta), fungi, lichen, grass, sedge, herb-monocot, herb-dicot, woody shrub, coarse woody debris, tree (sapling, including bole, branch). Trees were identified as: balsam fir (Abies balsamea), red, black or white spruce (Picea rubens, P. mariana, P. glauca, respectively), yellow, white, or gray birch (Betula alleghaniensis, B. papyrifera, B. populifolia), striped, red, mountain or sugar maple (Acer pensylvanicum, A. rubrum, A. spicatum, A. saccharum), eastern white pine (Pinus strobus), sumac (Rhus typhina), American beech (Fagus grandifolia), speckled alder (Alnus incana), aspen (Populus spp.), eastern hemlock (Tsuga canadensis), larch (Larix laricina), northern white cedar (Thuja occidentalis), pin cherry (Prunus pensylvanica), and broader categories of spruce, fir, maple, birch, ash (Fraxinus spp.) or unknown when species could not be determined.
Table C.1. Hypotheses and accompanying models to assess effects of vegetation structure and composition on the extent of change in snowshoe hare pellet density between two seasons, across 26 stands, that were surveyed for pellets semi-annually during three years in northern Maine (2010-2013). The response variable was snowshoe hare pellet counts in a 1.5 m² plot aggregated to stand level. Table 1.2 describes covariates. Expected seasonal or snow depth interactions with other covariates are indicated with "*".

<table>
<thead>
<tr>
<th>Resource Hypothesis</th>
<th>Models</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>1</strong> Structure &gt; Species composition Summer and winter (full models)</td>
<td>season * (LC + CC + pctUndCov + Saplings + BAtrees)</td>
</tr>
<tr>
<td>Counts explain seasonal change better than Basal Area</td>
<td>season * (BAtrees + BAsaplings)</td>
</tr>
<tr>
<td><strong>2</strong> Saplings: counts &gt; Basal area both seasons</td>
<td>season * (Saplings + Trees)</td>
</tr>
<tr>
<td><strong>3</strong> Trees: counts &gt; Basal area</td>
<td>season * (BAtrees)</td>
</tr>
<tr>
<td><strong>4</strong> Structure Diversity</td>
<td>season * (LC + pctUndCov + Saplings BAtrees)</td>
</tr>
<tr>
<td>Winter: Largest effects</td>
<td>snow depth * LC</td>
</tr>
<tr>
<td>Winter: Less effect</td>
<td>snow depth * ConSaplings</td>
</tr>
<tr>
<td>Structure Diversity</td>
<td>snow depth * pctUndCov</td>
</tr>
<tr>
<td>summer &gt; winter</td>
<td>season * CC</td>
</tr>
<tr>
<td><strong>5</strong> Species Composition (full)</td>
<td>season * LC</td>
</tr>
<tr>
<td>All components</td>
<td>season * (DecSplgs + ConSplgs + UndDec + UndCon + ConTrees + DecTrees)</td>
</tr>
<tr>
<td>Univariate as follows:</td>
<td>season * all conifer components</td>
</tr>
<tr>
<td><strong>6</strong> Con saplings &gt; wtr</td>
<td>season * all deciduous components</td>
</tr>
<tr>
<td><strong>7</strong> Dec sapling &gt; smr</td>
<td>season * ConSplgs</td>
</tr>
<tr>
<td><strong>8</strong> Und Conifer &gt; smr</td>
<td>season * DecSplgs</td>
</tr>
<tr>
<td><strong>9</strong> Und Deciduous &gt; wtr</td>
<td>season * UndCon</td>
</tr>
<tr>
<td><strong>10</strong> Con trees &gt; wtr</td>
<td>season * UndDec</td>
</tr>
<tr>
<td><strong>11</strong> Deciduous trees &lt; wtr</td>
<td>season * ConTrees</td>
</tr>
<tr>
<td><strong>12</strong> CC shades Decid &lt; smr</td>
<td>season * cc * UndDec</td>
</tr>
</tbody>
</table>
APPENDIX D

Statistical approaches, data distributions, and data exploration used for Chapter 1.
Statistical Approach

I used untransformed pellet counts as the response variable, with season as an interacting covariate to assess difference in pellet counts between seasons, and across stands. Count data has often been transformed to normalize the distribution of the residuals, yet count data can contain a disproportionate number of zeros, and transforming the log of zero (by adding some fraction because \( \log 0 = \infty \)) leads to absurd predicted estimates such as negative counts (O'Hara and Kotze 2010), while square-root transformations do not achieve normality (Figure D.2A). Overdispersion (the variance increases as the mean increases), is a common attribute of count data resulting from a highly skewed distribution, and has been ignored when performing linear regression (Warton 2005, Burnham et al. 2011). If overdispersion is ignored, and random effects are mis-specified, then Type I error rates can be inflated (Litiere et al. 2007, Milanzi et al. 2012). Generalized linear mixed models (GLMM) accommodate count data without transformation by using a link function such as a log and specifying a family such as a negative binomial distribution. There are many formulations of the negative binomial model (Hilbe 2011), but it can be described as a mixture model of a Poisson and a binomial distribution, in which Poisson means are defined by a probability distribution function with a gamma distribution (Boyce et al. 2001:500). One common form is distributed with mean \( \mu_i \) and variance \( S^2 \) Equation D.1A, with a model form depicted in Equation D.1B.

A. \( y_i \sim \text{Negbin}(\mu_i, \sigma^2 = \mu + \mu^2/\phi) \)

B. \( \mu_{\text{pellets}} = e^{a_{\text{stand}} + a_{\text{year}} + (b_{\text{stand-type}} \times b_{\text{season}}) + \omega + \varepsilon} \) (D.1)
Where $\varphi$ is a dispersion parameter and as $\varphi$ becomes large, approaching infinity, the distribution approaches a Poisson (Al-Khasawneh 2010). The dispersion parameter in the model, $(\omega)$ does not affect the expected counts, but affects the estimated variance of the expected (or estimated) counts. A negative binomial GLMM with a log-link function accommodates count data that is bounded at zero and overdispersed by appropriately modeling the variance of the error.

The data set for both Objectives one and two in Chapter 1 were zero inflated (>41% zeros) with two probable sources; zeros were real if hares did not visit a plot (detection of absence), or zeros were false when a hare visited a plot but left no scat (no detection of presence). Because several statistical model structures can provide better fits for response variables with zero inflation, I used $\text{AIC}_c$ inference to compare the same global species composition model with five different model structures: zero-inflated negative binomial, zero-inflated Poisson, Poisson, Quasi-Poisson, and negative binomial models. The best performing model was the negative binomial GLMM, which I subsequently used for all subsequent modeling reported as results in Chapter 1.
Table D.1. R statistical packages used to analyze seasonal snowshoe hare use of forest stands to assess seasonal change in snowshoe hare pellet densities in northern Maine across 3 stand-types (2005-2012) with R versions 2.15 and 3.0.2.

<table>
<thead>
<tr>
<th>Package</th>
<th>Use</th>
</tr>
</thead>
<tbody>
<tr>
<td>bbmle</td>
<td>ben bolker max likelihood inference criteria tables</td>
</tr>
<tr>
<td>coda</td>
<td>xy and density plots</td>
</tr>
<tr>
<td>coefplot2</td>
<td>plots location-scale $\beta$ coefficients</td>
</tr>
<tr>
<td>ggplot2</td>
<td>graphs</td>
</tr>
<tr>
<td>corrplot</td>
<td>Correlation coefficient plots</td>
</tr>
<tr>
<td>gimmADMB</td>
<td>negative binomial, Poisson, zero-inflated models</td>
</tr>
<tr>
<td>gridExtra</td>
<td>plot random effect estimates, arrange plots</td>
</tr>
<tr>
<td>lattice</td>
<td>graphical display</td>
</tr>
<tr>
<td>lme4</td>
<td>generalized linear models (glmer) for diagnostics:</td>
</tr>
<tr>
<td></td>
<td>assessing residuals and fits of preliminary models</td>
</tr>
<tr>
<td>MCMCglmm</td>
<td>calculate credible intervals around $\beta$ coefficients</td>
</tr>
<tr>
<td>nlme</td>
<td>nonlinear mixed-effects models to diagnose residual patterns</td>
</tr>
<tr>
<td>PerformanceAnalytics</td>
<td>creates relative performance charts, graphs</td>
</tr>
<tr>
<td>plyr</td>
<td>data manipulation: splits, applies, recombines data frames</td>
</tr>
<tr>
<td>RColorBrewer</td>
<td>heat map colors for correlation plots</td>
</tr>
<tr>
<td>reshape2</td>
<td>to &quot;melt&quot; dataset</td>
</tr>
<tr>
<td>scales</td>
<td>has a &quot;rescale&quot; function needed in correlation heatmaps</td>
</tr>
<tr>
<td>zoo</td>
<td>methods for ordered indexed observations that are irregular</td>
</tr>
<tr>
<td></td>
<td>time series of numeric vectors/matrices and factors.</td>
</tr>
</tbody>
</table>

a reshape2 restructures data frames so that each variable is in its own row, matched with a new unique identifier.
Figure D.1. Objective one dataset: % frequencies of pellet counts/stand in 41 stands repeatedly measured for eight years 2005–2012, across three stand types, and two season periods in northern Maine (n = 455 stand-year-season counts) to assess seasonal change in snowshoe hare pellet densities. The distribution reveals skew > 2, which is greater in summer (skew=8.01) than in winter (skew=4.76).
Figure D.2. Objective one dataset: Diagnostic plots of the distribution of the response variable, pellet counts, used to assess seasonal change in snowshoe hare pellet densities in northern Maine across 3 stand-types (2005-2012). A. The quantile-quantile plot of square-root transformed pellets/ha/month illustrates that transforming does not normalize the residual error structure. B. The response variable “pellet count means/stand” group variances are plotted against group means. Groups are stand means for each season:year:stand-type combination, n=41 stands repeatedly measured from 2005 leaf-on-2012 leaf-off. The loess fit line with slope > one indicates over-dispersion (group variances increase as group means increase). If the data had no overdispersion and fit a Poisson distribution the loess line would have had slope ≈ one, approximating the dotted Poisson line. Diagnostic method adapted from (Bolker et al. 2011).
Table D.2. Number of plots sampled for snowshoe hare pellets corresponding to the plots sampled for vegetation in northern Maine, 2010-2013 for Chapter 1, Objective Two. Forest vegetation-harvest types, stand ID, and periods sampled for hare pellets that were used as the basis for data reported to assess the effects of vegetation on seasonal change in snowshoe hare pellet densities, (smr = summer, and wtr = winter).

<table>
<thead>
<tr>
<th>Type</th>
<th>Stand ID</th>
<th>Period</th>
</tr>
</thead>
<tbody>
<tr>
<td>Regenerating</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conifer</td>
<td>JH01C</td>
<td>20</td>
</tr>
<tr>
<td>Dominated</td>
<td>JH02C</td>
<td>20</td>
</tr>
<tr>
<td>Regenerating</td>
<td>JH03C</td>
<td>20</td>
</tr>
<tr>
<td>Conifer</td>
<td>JH04C</td>
<td>20</td>
</tr>
<tr>
<td>Regenerating</td>
<td>JH05C</td>
<td>20</td>
</tr>
<tr>
<td>Conifer</td>
<td>JH54C</td>
<td>20</td>
</tr>
<tr>
<td>Dominated</td>
<td>JH56C</td>
<td>20</td>
</tr>
<tr>
<td>Regenerating</td>
<td>SM4B</td>
<td>20</td>
</tr>
<tr>
<td>Conifer</td>
<td>SM4C</td>
<td>20</td>
</tr>
<tr>
<td>Regenerating</td>
<td>SM4D</td>
<td>20</td>
</tr>
<tr>
<td>Conifer</td>
<td>SM4E</td>
<td>20</td>
</tr>
<tr>
<td>Mature Mixed and</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mature Conifer</td>
<td>MMX3</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>MSW3</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>MSW9</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>MSW10</td>
<td>0</td>
</tr>
</tbody>
</table>

120
Figure D.3. Objective two dataset: % of pellet counts/plot in 26 stands repeatedly measured semi-annually over three years 2010–2013 used to assess the effects of vegetation on seasonal change in snowshoe hare pellet densities in northern Maine, \( n = 81 \) stand-year-season counts. The data distribution is skewed (skew=6.3), which is greater in summer (skew=7.55) than in winter (skew=4.57).
Figure D.4. Objective two dataset: diagnostic plot of the response variable, pellet count means/stand used to assess the effects of vegetation on seasonal change in snowshoe hare pellet densities in northern Maine (2010-2013). Group variances are plotted against group means of the response variable, pellet counts in a stand. Groups are stand means for each season:year:stand-type combination, \( n=26 \) stands repeatedly measured for six seasons, 2010-2013. The loess fit line with slope \( >1 \) indicates over-dispersion (group variances increase as group means increase). If the data had no overdispersion and fit a Poisson distribution the loess line would have had slope \( \approx 1 \), approximating the dotted Poisson line. Diagnostic method adapted from (Bolker et al. 2011).
Table D.3. Summary statistics for vegetation variables used to assess their influence on seasonal change in snowshoe hare fecal pellet densities across 26 stands in northern Maine (2011). Variable, plot level mean (standard deviation), skew and range of plot counts are displayed. Six of the variables had skew values > 2; therefore, resulting summary statistics are displayed after transforming count variables with a square root transform. Data presented represents 766 plots in 26 stands that were measured in 2011 and 2012. Variables and their units are described in Table 1.2.

<table>
<thead>
<tr>
<th>variable</th>
<th>mean</th>
<th>sd</th>
<th>skew</th>
<th>range</th>
<th>transformed variable</th>
<th>mean</th>
<th>sd</th>
<th>skew</th>
<th>range</th>
</tr>
</thead>
<tbody>
<tr>
<td>BAsplgs</td>
<td>10.9</td>
<td>(8.8)</td>
<td>0.94</td>
<td>0 - 48</td>
<td>t.BAsplgs</td>
<td>2.9</td>
<td>(1.5)</td>
<td>-0.25</td>
<td>0 - 6.9</td>
</tr>
<tr>
<td>BAtrees</td>
<td>19.2</td>
<td>(13.0)</td>
<td>1.22</td>
<td>0 - 70</td>
<td>t.BAtrees</td>
<td>4.1</td>
<td>(1.5)</td>
<td>0.12</td>
<td>0 - 8.4</td>
</tr>
<tr>
<td>con.splgs</td>
<td>513.3</td>
<td>(757.9)</td>
<td>2.46</td>
<td>0 - 5000</td>
<td>t.con.splgs</td>
<td>16.5</td>
<td>(15.5)</td>
<td>0.78</td>
<td>0 - 70.7</td>
</tr>
<tr>
<td>con.trees</td>
<td>178.8</td>
<td>(194.5)</td>
<td>1.09</td>
<td>0 - 900</td>
<td>t.con.trees</td>
<td>10.3</td>
<td>(8.6)</td>
<td>0.11</td>
<td>0 - 30.0</td>
</tr>
<tr>
<td>dead.splgs</td>
<td>252.3</td>
<td>(440.1)</td>
<td>3.49</td>
<td>0 - 3700</td>
<td>t.dead.splgs</td>
<td>11.0</td>
<td>(11.5)</td>
<td>1.12</td>
<td>0 - 60.8</td>
</tr>
<tr>
<td>dead.trees</td>
<td>16.2</td>
<td>(40.0)</td>
<td>3.85</td>
<td>0 - 350</td>
<td>t.dead.trees</td>
<td>1.7</td>
<td>(3.6)</td>
<td>1.90</td>
<td>0 - 18.7</td>
</tr>
<tr>
<td>dec.splgs</td>
<td>242.5</td>
<td>(369.0)</td>
<td>2.21</td>
<td>0 - 2200</td>
<td>t.dec.splgs</td>
<td>10.7</td>
<td>(11.4)</td>
<td>0.78</td>
<td>0 - 46.9</td>
</tr>
<tr>
<td>dec.trees</td>
<td>42.9</td>
<td>(81.8)</td>
<td>2.71</td>
<td>0 - 600</td>
<td>t.dec.trees</td>
<td>3.5</td>
<td>(5.5)</td>
<td>1.25</td>
<td>0 - 24.5</td>
</tr>
<tr>
<td>live.splgs</td>
<td>755.8</td>
<td>(780.4)</td>
<td>1.94</td>
<td>0 - 5000</td>
<td>t.live.splgs</td>
<td>23.6</td>
<td>(14.0)</td>
<td>0.33</td>
<td>0 - 70.7</td>
</tr>
<tr>
<td>SCU&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1782.3</td>
<td>(2236.3)</td>
<td>2.42</td>
<td>0 - 15000</td>
<td>t.SCU</td>
<td>34.9</td>
<td>(23.8)</td>
<td>0.76</td>
<td>0 - 122.5</td>
</tr>
<tr>
<td>totl.splgs</td>
<td>1008.1</td>
<td>(967.4)</td>
<td>1.55</td>
<td>0 - 5600</td>
<td>t.totl.splgs</td>
<td>27.7</td>
<td>(15.5)</td>
<td>0.23</td>
<td>0 - 74.8</td>
</tr>
<tr>
<td>totl.trees</td>
<td>237.9</td>
<td>(189.3)</td>
<td>0.88</td>
<td>0 - 900</td>
<td>t.totl.trees</td>
<td>13.7</td>
<td>(7.2)</td>
<td>-0.34</td>
<td>0 - 30.0</td>
</tr>
</tbody>
</table>

<sup>a</sup> stem cover units = deciduous saplings + (3 x conifer saplings).
Figure D.5. Pearson $r$ correlation-coefficient matrix of leaf-on predictor variables used to assess seasonal change in snowshoe hare pellet densities in northern Maine (2011-2012). Darker, flatter ellipses indicate higher correlation. The shaded ruler bar indicates the degree of correlation and white squares are not significant ($\alpha=0.05$). Only variable pairs with Pearson $r \leq 0.55$ were used in the same models. Leaf-on variables were a subset of the entire annual dataset, and excluded snow. The leaf-off season correlation matrix is shown in Figure D.6. and leaf-off variables were the subset of the dataset that included snow depth. Overhead canopy cover (CC) and lateral cover (LC) were measured in both seasons. Data presented represents 766 plots in 26 stands that were measured in 2011 and 2012. Variables and their units are described in Table 1.2.
Figure D.6. Pearson $r$ correlation-coefficient matrix of leaf-off predictor variables used to assess seasonal change in snowshoe hare pellet densities in northern Maine (2011-2012). Darker, flatter ellipses indicate higher correlation. The shaded ruler bar indicates the degree of correlation and white squares are not significant ($\alpha=0.05$). Only variable pairs with Pearson $r \leq 0.55$ were used in the same models. Leaf-off variables were a subset of the entire annual dataset, and included snow depth. The leaf-on season correlation matrix is shown in Figure D.5. Overhead canopy cover (CC) and lateral cover (LC) were measured in both seasons. Data presented represents 766 plots in 26 stands that were measured in 2011 and 2012. Variables and their units are described in Table I.2.
Table D.4. Variance inflation factors (VIFs) for vegetation covariates used to assess seasonal change in snowshoe hare pellet densities in northern Maine (2010-2013). Sixteen linear regression models calculated VIFs by regressing successive sets of vegetation variables upon lateral cover as a response variable because that variable was the least correlated with all other variables. Count and basal area variables were square root transformed. Subsequent model sets used structural or species composition covariates in a given model with VIFs < 4.0. Data presented represents 766 plots in 26 stands that were measured in 2011 and 2012. Variables and their units are described in Table 1.2.

<table>
<thead>
<tr>
<th>Covariate name</th>
<th>Variance Inflation Factors</th>
<th></th>
<th></th>
<th></th>
<th>Species composition</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>All covariates</td>
<td>Structure</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>snow depth</td>
<td>1.4</td>
<td>1.4</td>
<td>1.4</td>
<td>1.4</td>
<td>1.0</td>
</tr>
<tr>
<td>canopy cover</td>
<td>1.7</td>
<td>1.7</td>
<td>1.7</td>
<td>1.7</td>
<td>1.7</td>
</tr>
<tr>
<td>basal area saplings</td>
<td>2.6</td>
<td>2.6</td>
<td>2.6</td>
<td>2.4</td>
<td>2.4</td>
</tr>
<tr>
<td>BA trees</td>
<td>2.2</td>
<td>2.2</td>
<td>2.2</td>
<td>2.0</td>
<td>2.1</td>
</tr>
<tr>
<td>dead saplings</td>
<td>9.5</td>
<td>9.5</td>
<td>10.0</td>
<td>dropped</td>
<td>2.3</td>
</tr>
<tr>
<td>dead trees</td>
<td>1.7</td>
<td>1.7</td>
<td>1.7</td>
<td>dropped</td>
<td>1.1</td>
</tr>
<tr>
<td>live saplings</td>
<td>705.9</td>
<td>dropped</td>
<td>64.0</td>
<td>dropped</td>
<td>dropped</td>
</tr>
<tr>
<td>% understory</td>
<td>8.6</td>
<td>8.5</td>
<td>8.5</td>
<td>1.7</td>
<td>1.6</td>
</tr>
<tr>
<td>total saplings</td>
<td>64.4</td>
<td>60.1</td>
<td>64.4</td>
<td>7.7</td>
<td>4.0</td>
</tr>
<tr>
<td>total trees</td>
<td>17.2</td>
<td>17.1</td>
<td>17.1</td>
<td>1.5</td>
<td>1.6</td>
</tr>
<tr>
<td>conifer saplings</td>
<td>160.6</td>
<td>43.9</td>
<td>17.2</td>
<td></td>
<td>33.3</td>
</tr>
<tr>
<td>conifer trees</td>
<td>20.3</td>
<td>20.1</td>
<td>20.2</td>
<td></td>
<td>1.7</td>
</tr>
<tr>
<td>% understory conifer</td>
<td>9.3</td>
<td>9.2</td>
<td>9.2</td>
<td></td>
<td>1.9</td>
</tr>
<tr>
<td>deciduous saplings</td>
<td>21.2</td>
<td>4.8</td>
<td>6.5</td>
<td></td>
<td>1.9</td>
</tr>
<tr>
<td>% understory decid</td>
<td>4.0</td>
<td>3.9</td>
<td>3.9</td>
<td></td>
<td>1.4</td>
</tr>
<tr>
<td>deciduous trees</td>
<td>6.7</td>
<td>6.7</td>
<td>6.7</td>
<td></td>
<td>1.4</td>
</tr>
<tr>
<td>SCU</td>
<td>1233.0</td>
<td>112.3</td>
<td>dropped</td>
<td>7.2</td>
<td>29.2</td>
</tr>
</tbody>
</table>

*stem cover units = \text{deciduous saplings} + (3 \times \text{conifer saplings}).
Table D.5. Results of generalized linear mixed model selection to assess effects of tree and sapling basal area or counts on seasonal differences in snowshoe hare pellet densities in northern Maine (2010-2013). Sapling counts had the greatest strength of evidence, with moderate support for basal area of trees. Models, number of parameters (K), model likelihood (logLik), Akaike’s Information Criterion value adjusted for small sample size (AICc), model differences (ΔAICc), and Akaike weight (wi) for stand level models developed from *a priori* hypotheses. Count variables were square root transformed to predict pellet counts/stand (42 m² sampled) for three summer and three winter seasons, 2010–2013. All models except Null had season as an interaction term with all other covariates. Table 1.2 describes variables and their units.

<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>logLik</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>wi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sapling counts</td>
<td>8</td>
<td>-4189.6</td>
<td>8403.7</td>
<td>0</td>
<td>0.921</td>
</tr>
<tr>
<td>BA trees</td>
<td>8</td>
<td>-4192.4</td>
<td>8409.4</td>
<td>5.7</td>
<td>0.054</td>
</tr>
<tr>
<td>Null with season</td>
<td>6</td>
<td>-4197.7</td>
<td>8411.9</td>
<td>8.2</td>
<td>0.015</td>
</tr>
<tr>
<td>BA saplings</td>
<td>8</td>
<td>-4194.5</td>
<td>8413.5</td>
<td>9.8</td>
<td>0.007</td>
</tr>
<tr>
<td>Tree counts</td>
<td>8</td>
<td>-4195.5</td>
<td>8415.4</td>
<td>11.7</td>
<td>0.003</td>
</tr>
<tr>
<td>Null</td>
<td>5</td>
<td>-4234.9</td>
<td>8482.7</td>
<td>79</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

a generalized linear mixed models, except null, used season as an interacting covariate.
b saplings were <7.6 cm DBH, >1.5 m tall, counts were standardized to No./0.1 ha.
c trees were >7.6 cm DBH, basal area (BA) is m²/ha.
d season by (area.std + offset(ln.days) + hareyr).
e area.std + offset(ln.days) + hareyr.
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APPENDIX E

Supplemental results
Table E.1. Percent coverage of the understory layer from 0.5-1.5 m that could serve as food for snowshoe hares, sampled in northern Maine, summer 2011, in 3 forest stand-types. Species shown are considered food resources for snowshoe hares that are available in winter in northern Maine.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mature</th>
<th>Selection harvest</th>
<th>Regenerating conifer</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maple (<em>Acer spp.</em>&lt;sup&gt;b&lt;/sup&gt;)</td>
<td>3.26</td>
<td>9.69</td>
<td>0.50</td>
</tr>
<tr>
<td>Spruce (<em>Picea spp.</em>&lt;sup&gt;c&lt;/sup&gt;)</td>
<td>3.61</td>
<td>3.21</td>
<td>7.30</td>
</tr>
<tr>
<td>Birch (<em>Betula spp.</em>&lt;sup&gt;d&lt;/sup&gt;)</td>
<td>0.97</td>
<td>3.70</td>
<td>0.31</td>
</tr>
<tr>
<td>Alder (<em>Alnus incana</em>)</td>
<td>1.04</td>
<td>1.23</td>
<td>1.23</td>
</tr>
<tr>
<td>Eastern white pine (<em>Pinus strobus</em>)</td>
<td>0.07</td>
<td>0.06</td>
<td>0.35</td>
</tr>
</tbody>
</table>

<sup>a</sup> Sampled points/stand-type: Mature, $n = 1440$, Selection harvest, $n = 3240$, Regenerating conifer, $n = 5436$.

<sup>b</sup> Red maple (*A. rubrum*) and sugar maple (*A. saccharum*) predominated. Striped (*A. pensylvanicum*) and mountain (*A. spicatum*) maples were minor components. so *Acer* species were combined.

<sup>c</sup> Red spruce (*P. rubens*) and black spruce (*P. mariana*) predominated: hybrids or unknowns were common. An occasional white spruce (*P. glauca*) occurred.

<sup>d</sup> White birch (*B. papyrifira*) was dominant with occasional yellow and grey (*B. alleghaniensis, B. populifolia*), respectively.
Figure E.1. A. Estimated seasonal difference in pellets/ha/month by conifer sapling counts/0.1 ha, generated from a generalized linear mixed model. Leaf-on (May-October) line is dotted, leaf-off (November-April) is solid; the two curves depict the seasonal change from summer to winter. B. Leaf-on estimate is displayed with a reduced range of pellet densities. Pellet density was estimated using three winter and three summer seasons, \( n = 26 \) stands, repeatedly sampled from 2010-2013 for \( N = 81 \) stand-seasons in northern Maine. Count of pellets-in-stand was scaled to pellets/ha/month.
Figure E.2. Estimated seasonal difference in pellets/ha/month by deciduous tree density generated from a negative binomial generalized linear mixed model with a log-link. Leaf-off (November-April) is solid, leaf-on (May-October) line is dotted. Pellet density was estimated using three winter and three summer seasons, \( n = 26 \) stands, repeatedly sampled from 2010-2013 for \( N = 81 \) stand-seasons in northern Maine. Count of pellets-in-stand was scaled to pellets/ha/month.
Figure E.3. Winter hare densities of 29 stands in four stand-types in northern Maine that were repeatedly measured 2010–2014. Average winter hare densities were: regenerating conifer stands, (X̄ = 0.97 ± 0.10 hares/ha); overstory removal and shelterwood retention harvest stand-types combined (X̄ = 0.56 ± 0.13 hares/ha), mature mixed-wood, mature softwood, and selection harvest stand-types combined (X̄ = 0.29 ± 0.06 hares/ha). The dashed line at 0.67 hares/ha represents average stand-level hares/ha (se ± 0.26, n = 29). Whiskers are standard errors.
Figure E.4. Average litter size of lynx/all females monitored per year (n=36 lynx) and winter hare densities in 4-15 regenerating-conifer stands in northern Maine. The relationship depicted is derived from annual over-winter hare density estimates for regenerating conifer clearcut stands presented in Harrison et al. (2014) and lynx reproductive data presented in (Vashon et al. 2012: Table 1.5).
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BIOGRAPHY OF THE AUTHOR

Sheryn J. Olson returned to school as a Master of Science candidate at The University of Maine, after a career in Information Technology that culminated in the sale of her Colorado computer consulting business. She grew up a child of the suburbs in Tampa, Florida, in a time when children ran through the woodlots barefoot, fell out of great oak trees often, swam in snake infested rivers and lakes, and rode bicycles in traffic. There was always strong encouragement to stay and play outside until dark, so hungry children ate tangerines and oranges, Surinam cherries and the neighbors’ tomatoes. Favorite past times were mapping ant trails and anole lizard territories, exploring on horseback, reading voraciously, and music and dance. Intending to become a veterinarian, Sheryn obtained a degree in Zoology at The University of South Florida. Her minor in experimental psychology provided opportunities to research models of learning with Herb Kimmel – habituation in planarians, rats, and of the autonomic skin response in humans, resulting in two publications. After graduation, Sheryn attended the University of Montana’s field station on Flathead Lake, and became enamored of both behavioral ecology and the magnificent Rocky Mountains.

After first sampling San Francisco, California, and Eugene, Oregon, Sheryn obtained a biomedical research job at Johns Hopkins School of Medicine. Baltimore and the world of psychopharmacology had its fascinations, but ecological systems became Sheryn’s passion and she returned to graduate school at the University of Maryland, College Park to work with Wolfgang Schleidt in ecology and ethology. She began a thesis researching trophic specializations in four genera of rodents, including the “predatory” grasshopper mouse, the seed obligate Kangaroo Rat, the harvest mouse, and the generalist deer mouse.
on the plains of eastern Colorado. After completing two field seasons and the coursework for her M.S., Sheryn had enough funding left to drive to Fort Collins, Colorado, though not to return to Maryland to complete her thesis. Stranded in Colorado, Sheryn obtained a Forest Service position developing, then managing a database at Colorado State University and the USDA Forest Service Rocky Mountain Research Station, Fort Collins.

Database and computer systems support appealed to Sheryn and she spent some years in that field in beautiful Steamboat Springs, Colorado, eventually owning a computer consulting business for 12 years. In Steamboat Springs, Sheryn learned to telemark ski, led mountain bike trips through the desert, participated in theatre and dance, and went on many a private river and ski hut-to-hut trips. There, she met some of the most talented, supportive, witty, and intelligent folks, but best of all met Bob Shaffer, her partner. Sheryn always planned to return to graduate school to become an ecologist, and to that end, worked for 6 weeks at Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) in Turrialba, Costa Rica as a small mammal field technician investigating conventional vs. organic coffee plantations. She spent two years working intermittently in California for the U.S. Forest service on the Humboldt marten, and taking graduate ecology classes at the University of Colorado, Boulder to prepare for a return to ecological research. Sheryn is a candidate for the Master of Science degree in Wildlife Ecology at the University of Maine, in May, 2015.