ECOLOGICAL RELATIONSHIPS AMONG PARTIAL HARVESTING, VEGETATION, SNOWSHOE HARES, AND CANADA LYNX IN MAINE

By

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An Abstract of the Thesis Presented
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Understanding the ecological factors affecting habitat use by the Canada lynx (*Lynx canadensis*) and its primary prey, the snowshoe hare (*Lepus americanus*), could help formulate conservation strategies for this carnivore, which is federally listed as threatened and occurs in only four regions of the U.S.A. I measured vegetation characteristics and snowshoe hare densities in 15 regenerating conifer clearcuts and 21 partially harvested stands in northern Maine during the leaf-off seasons, 2005 and 2006; and the leaf-on season, 2005. Regenerating clearcut stands had been harvested between 1974 and 1985 and were subsequently treated with an aerial application of herbicide

between 1982 and 1997. Partially harvested stands were last harvested between 1985 and 2004 and included selection harvests, shelterwood harvests, and overstory removal harvests.

Vegetation characteristics varied widely across partially harvested stands. This variance can be described by two principal components associated with the conifer composition and understory density within these stands. Snowshoe hare densities also varied widely in partially harvested stands: 0.26-1.65 hares/ha for the combined 2005-2006 leaf-off seasons. All 21 partially harvested stands had lower hare densities than the mean hare density for regenerating conifer clearcuts (2.10 hares/ha, SE = 0.22) during these two years.

I modeled the relationship of individual vegetation variables to hare densities across the 36 stands surveyed using an information theoretic approach. Hare density during the leaf-off season was positively associated with conifer stem density and basal area removed and was negatively related to the density of logs in the stand. These three variables explained 67% of the variance in observed hare densities; however, conifer stem density was the single variable that was most strongly related to hare densities.

I used GIS modeling to evaluate the relationships between lynx occurrence/non-detection and hare density, bobcat occurrence, fisher harvest density, maximum snow depth, and elevation at the geographic range- and the home range-scales in Maine. At the geographic-scale, lynx occurrence was associated with: 1) areas of higher hare density, and 2) absence of bobcats. Within the geographic range of lynx, simulated home ranges centered on lynx occurrences were associated with: 1) higher hare densities, 2) absence of bobcats, and 3) an interaction between hare density and bobcat occurrence, compared to surveyed areas without lynx detections. Only two surveys detected both bobcats and lynx, but these data suggest geographic- and home range-scale allopatry between these two species.

At the geographic-scale, the area of land in regenerating clearcuts was positively associated with lynx occurrence, likely as a result of the high hare densities supported by regenerating clearcuts. Annual clearcutting in Maine has been decreasing since the early 1990’s and this trend may result in less regenerating forest on the landscape in the future, which might have long-term negative consequences if the objective is to maintain or increase current population levels of Canada lynx in Maine.

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beauty of northern Maine and contributed numerous hours helping me learn how to think like a scientist.

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I thank my first mentor, Merrill Peterson, for introducing me to the wonders of ecology, always fostering my curiosity, and getting me started on this journey.

This work is dedicated to my family: Brett, my sister, best friend, and inspiration; my Dad, Dennis who is a constant source of support in my life; my mother, Diane, who told me I could do whatever I wanted with my life; and my father, Will, who is a part of everything I do.

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PREFACE

Forest harvesting has been a dominant form of land use in the Acadian spruce-fir forest of Maine since the early 1800's (Seymour and Hunter 1992). To salvage timber from the eastern spruce budworm (*Choristoneura fumiferana*) outbreak of the late 1970's to mid 1980's, hundreds of thousands of acres of forest were clearcut, creating contiguous stands of regenerating forest as large as 5,000 acres across northern Maine. In response to the negative public perception of clearcutting, the Maine Forest Practices Act (MFPA) was passed in 1989, which created disincentives for new clearcuts larger than 20 acres (Maine Forest Service 2004). The MFPA, coupled with three public referenda to ban clearcutting during the 1990's, contributed to a dramatic shift in forest management away from clearcutting to partial harvesting and a 56% increase in the total acres harvested annually from 1989 to 2004 (Maine Forest Service 1990, 2005).

"Partial harvesting" is a broad term used to describe many methods of removing overstory trees from a forest stand including selective cuts, shelterwood cuts, and uneven-aged forest management. Today, over 500,000 acres of state and privately owned forest are annually harvested in Maine and 96% of this land is partially harvested (Maine Forest Service 2005). The popularity of partial harvesting extends beyond Maine to much of the U.S.A. From the mid 1980's-mid 1990's, partial harvests constituted 61.7% of the harvests in the U.S., with clearcuts making up the other 38.3% (U.S. Forest Service 2006).

Forest harvesting significantly alters the species composition and structure of vegetation in residual stands. These changes in vegetation affect habitat for numerous species of wildlife including the snowshoe hare (*Lepus americanus*), which plays an important ecosystem-level role as both a consumer and prey. In the northern boreal forest, hares are considered a keystone species and are known to exert top-down effects on producers and bottom-up effects on predators (Krebs et al. 2001). Large changes in hare densities can cause density-dependent effects on the composition and structure of vegetation and may also influence other herbivores (Krebs et al. 2001). Additionally, hares are important prey for many Carnivora in the North America including marten (*Martes americanus*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), fisher (*Martes pennanti*), red fox (*Vulpes vulpes*) (Dibello et al. 1990, Cumberland et al. 2001, Weir et al. 2005), and the U.S.A. federally threatened Canada lynx (*Lynx canadensis*) (O'Donoghue et al. 2001).

Snowshoe hare abundance is closely tied to habitat characteristics. Previous studies have consistently associated snowshoe hare density and habitat use with dense understory characteristics (Converse 1981, Orr and Dodds 1982; Pietz and Tester 1983, O'Donoghue 1983, Litvaitis et al. 1985, Monthey 1986, Parker 1986, Scott and Yahner 1989, Long 1995, Wirsing et al. 2002, Fuller 2006, Homyack 2006b). The primary cause of mortality for snowshoe hares is predation, which comprises > 90% of proximate causes of death in some studies (Boutin et al. 1986, Hodges et al. 2001) and hares select areas of dense structure to avoid predators (Wolff 1980). Dense understories with high stem densities, which are often associated with regenerating forest following disturbances, provide hares with both escape and thermal cover during the winter (Litvaitis et al. 1985).

My first objective was to describe vegetation characteristics and snowshoe hare densities in partially harvested stands. I then compared hare densities and vegetation characteristics known to be important to hares between partially harvested stands and regenerating conifer clearcuts, which represent optimal conditions for snowshoe hares in Maine (Chapter 1). Secondly, I modeled the relationship between individual vegetation variables and snowshoe hare density across partially harvested and regenerating clearcuts to understand which specific vegetation characteristics were associated with the differences in hare density between these two harvest methods (Chapter 2).

The Canada lynx is a wide-ranging felid occupying the boreal and sub-boreal forests of Canada and some northern parts of the U.S.A. (Agee 2000, Aubry et al. 2000) where it was federally listed as threatened in 2000 under the Endangered Species Act (U.S. Fish and Wildlife Service 2000). In addition to being the only verified U.S.A. population of lynx east of Minnesota, the population of lynx occupying Maine and the Gaspé Peninsula of Quebec, Canada is both physically (Hoving et al. 2003) and genetically separated from the remaining lynx populations in central and western Canada (Rueness et al. 2003). Additionally, the historic range of lynx in the eastern U.S.A extended from Pennsylvania to northern Maine (Seton 1929, Hoving et al. 2003), but range contraction over the last century has left the Gaspé population on the southeastern edge of the current geographic distribution of lynx. Populations on the edge of a species' range are important from a conservation standpoint because they allow for dispersal from source populations and for genetic diversity, which could lead to range expansion and even speciation over time (Hunter and Hutchinson 1994).

Lynx are specialist predators of hares, and hare density acts as a regulating factor for lynx populations (Saunders 1963, Van Zyll de Jong 1966, Staples 1995, O'Donoghue et al. 2001), but the importance of this relationship to habitat use by lynx at broad scales has not been tested using empirical field data for snowshoe hare density. In addition to prey abundance, competition, predation, and environmental factors could also influence habitat use by lynx. Understanding and predicting habitat relationships of species at the broad scale requires the use of spatially explicit habitat models using extensive datasets representing these ecological factors.

Animals make habitat choices on several scales (Johnson 1980) and ecological factors affecting these choices may be hierarchical and may differ across scales (Orians and Wittenberger 1991, Bissonette et al. 1997). Thus, my third objective was to describe the relationships between lynx occurrence across northern Maine and five ecological factors: snowshoe hare density, bobcat occurrence, fisher harvest density, maximum snow depth, and elevation at the scale of 1) the geographic range, and 2) the home range (Chapter 3). Understanding the habitat relationships of the Canada lynx at multiple spatial scales could help formulate regional conservation strategies for this carnivore in the southeastern portion of its range and may aid in management to promote lynx habitat.

CHAPTER 1

SNOWSHOE HARE DENSITIES AND VEGETATION CHARACTERISTICS ACROSS PARTIALLY HARVESTED STANDS IN MAINE

ABSTRACT

For more than 200 years, forest harvesting has been a dominant form of land use in the Acadian forest of Maine. Legislation and public referenda to limit clearcutting have contributed to a dramatic shift in forest management away from clearcutting to partial harvesting since the late 1980's. Forest harvesting significantly alters the species composition and structure of vegetation in residual stands and the shift toward partial harvesting potentially affects habitat for numerous species of wildlife including the snowshoe hare, which plays an important ecosystem-level role as both a consumer and prey. I measured vegetation characteristics and estimated hare densities in 36 forest stands in northern Maine (15 regenerating conifer clearcuts and 21 partial harvests). I used principal components analysis to describe the vegetation characteristics associated with partial harvesting and compared four vegetation variables between partially harvested stands and regenerating conifer clearcuts. Hare densities in partially harvested stands were compared to regenerating (19-33 year post-harvest) clearcuts, which represent the optimal stand condition for hares in Maine. Results suggest that partial harvesting is associated with residual stands that vary greatly in their vegetation characteristics and snowshoe hare densities. Variance in vegetation characteristics within partially harvested stands was associated with two principal components related to the conifer component and understory density in these stands. Partially harvested stands had

lower conifer stem densities, higher densities of deciduous trees, and higher log densities than regenerating clearcuts, which may be related to the large discrepancy in hare densities between the two harvest methods studied. Hare densities within 21 partially harvested stands ranged from 0.26-1.65 hares/ha, but were all lower than the mean hare density (2.10 hares/ha, SE = 0.22) found in regenerating conifer clearcuts during the critical leaf-off season. Partially harvested stands did not support the hare density suggested in other studies to be required to maintain a viable lynx population across the landscape. As the dominant harvesting practice, broad-scale partial harvesting in the absence of large regenerating clearcuts might have long-term negative consequences if the objective is to maintain or increase current population levels of Canada lynx in Maine.

INTRODUCTION

Forest harvesting has been a dominant form of land use in the Acadian spruce-fir forest of Maine and the maritime provinces of eastern Canada since the early 1800's (Seymour and Hunter 1992). Today, over 500,000 acres of state and privately owned forest are harvested in Maine annually (Maine Forest Service 2005). Selective harvesting was the dominant form silvicultural management from 1850-1970 in northern Maine, when the eastern spruce budworm (*Choristoneura fumiferana*) reached outbreak levels in the late 1970's (Seymour 1992). Hundreds of thousands of acres of forest were salvaged via clearcutting during the early 1980's, creating contiguous stands of regenerating forest as large as 5,000 acres across northern Maine.

In response to the negative public perception of clearcutting, the Maine Forest Practices Act (MFPA) was passed in 1989, which created disincentives for clearcuts larger than 20 acres (Maine Forest Service 2004). The MFPA, coupled with three public referenda to limit clearcutting during the 1990's, contributed to a dramatic shift in forest management away from clearcutting to partial harvesting. "Partial harvesting" is a broad term used to describe many methods of removing overstory trees from a forest stand including selective cuts, shelterwood cuts, and uneven-aged forest management. In 2004, partial harvests comprised 96% of the land area harvested in Maine (Maine Forest Service 2005); the remaining 4% of harvests were clearcuts, with an average size of 20 acres (only three clearcuts were larger than 75 acres) (Maine Forest Service 2005). Additionally, 507,899 total acres were harvested in 2004 (Maine Forest Service 2005), which is a 56% increase from the 326,057 total acres harvested in 1989 (Maine Forest Service 1990). The popularity of partial harvesting extends beyond Maine to much of the U.S.A. From the mid 1980's-mid 1990's, partial harvests constituted 61.7% of the harvests in the United States, with clearcuts making up the other 38.3% (USDA Forest Service 2006). In Canada, however, this trend is reversed with 91.6% of harvests in the form of clearcuts in 2003 (Canadian Council of Forest Ministers, 2006).

Forest harvesting significantly alters the species composition and structure of vegetation in residual stands. These changes in vegetation affect habitat for numerous species of wildlife including the snowshoe hare (*Lepus americanus*), which plays an important ecosystem-level role as both a consumer and prey. In the northern boreal forest, hares are considered a keystone species and are known to exert top-down effects on producers and bottom-up effects on predators (Krebs et al. 2001). Additionally, hares are important prey for many Carnivora in the North America including marten (*Martes americanus*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), fisher (*Martes pennanti*), red fox (*Vulpes vulpes*) (Dibello et al. 1990, Cumberland et al. 2001, Weir et al. 2005), and the federally threatened (U.S.A.) Canada lynx (*Lynx canadensis*), a specialist predator of snowshoe hares (Saunders 1963, Van Zyll de Jong 1966, Staples 1995, O'Donoghue et al., 2001).

Snowshoe hare abundance is closely tied to habitat characteristics. Previous studies have consistently associated snowshoe hare density and habitat use with dense understory characteristics (Converse 1981, Orr and Dodds 1982; Pietz and Tester 1983, O'Donoghue 1983, Litvaitis et al. 1985, Monthey 1986, Parker 1986, Scott and Yahner 1989, Long 1995, Wirsing et al. 2002, Fuller and Harrison 2005, Homyack et al. 2006b). The primary cause of mortality for snowshoe hares is predation, which comprises > 90% of proximate causes of death in some studies (Boutin et al. 1986, Hodges 2000, Hodges et al. 2001) and hares select areas of complex structure to avoid predators (Wolff 1980). Dense understories with high stem densities, which are often associated with regenerating forest following disturbances, provide hares with both escape and thermal cover during the winter (Litvaitis et al. 1985).

Previous studies have described the effects of many forms of forest management on hare abundance in eastern North America (Lachowski 1997, De Bellefeuille et al. 2001, Newbury and Simon 2005, Fuller and Harrison 2005, Homyack et al. 2006b). In Maine, regenerating conifer-dominated clearcuts support the highest hare densities, achieving mean hare densities of 1.63-2.43 hares/ha approximately 15 to 30 years after cutting and herbicide application (Table 1.1). These regenerating stands provide "optimal" conditions for snowshoe hares and are generally characterized by dense

Table 1.1 Mean estimated snowshoe hare density (SE) for the leaf-off season (October-May) in 8 forest types in northern Maine, U.S.A.

Forest type (number of stands)	hares/ha	Years of sampling	Location[a]	Source
Regenerating forest (7)	2.43 (2.04)	1995-1996	TL	Lachowski 1997
Regenerating forest (13)	1.83 (0.16)	2000-2002	TL	Homyack 2006b
Regenerating forest (2)	1.64 (0.87)	1997-1998	TL	Fuller and Harrison 2005
Regenerating forest (18)	1.62	2001-2003	CL	Mullen 2003, unpub.
Regenerating forest (15)	2.10 (0.22)	2004-2005	TL/CL	This study
Precommercially thinned (17)	0.99 (0.09)	2000-2002	TL	Homyack 2006b
Established partial harvest (21)[b]	0.80 (0.09)	2004-2005	TL/CL	This study
Budworm-killed (2)	0.59 (0.41)	1995-1996	TL	Lachowski 1997
Mixed deciduous/coniferous (7)	0.29 (0.27)	1995-1996	TL	Lachowski 1997
Mixed deciduous/coniferous (7)	0.23 (0.03)	1997-1998	TL	Fuller and Harrison 2005
Mature coniferous (2)	0.23 (0.05)	1995-1996	TL	Lachowski 1997
Mature coniferous (2)	0.24 (0.03)	1997-1998	TL	Fuller and Harrison 2005
Mature deciduous (2)	0.16 (0.00)	1995-1996	TL	Lachowski 1997
Mature deciduous (2)	0.17 (0.00)	1997-1998	TL	Fuller and Harrison 2005
Recent selection harvest (7)[b]	0.17 (0.01)	1997-1998	TL	Fuller and Harrison 2005

[a] TL = Telos Lake in northcentral Maine, CL = Clayton Lake in northern Maine.

[b] Approximately 1-20 years post-harvest.

[c] Approximately 3 years post-harvest.

understories containing high conifer stem densities and little overstory canopy closure. In Maine, hare densities within a range of 0.15-1.50 hares/ha have been strongly associated with stem densities as represented by stem cover units (calculated as 3*conifer stems + deciduous stems) (Litvaitis et al. 1985, Long 1995, Fuller 2006), and with conifer stem densities (Homyack et al. 2006b, Chapter 2) at the scale of the forest stand. Snowshoe hare track abundance was also significantly related to the percent area of the landscape comprised of late regenerating forest (Hoving 2001). Despite previous work, information is still lacking on relationships of snowshoe hares and vegetation across large (> 7 ha) forest stands supporting a wide range of hare densities.

Stands that support low hare densities (< 0.3 hares/ha) include recent clearcuts (De Bellefeuille et al. 2001, Newbury and Simon 2005), mature forest (Lachowski 1997, Fuller and Harrison 2005), and recent partial harvests (Fuller and Harrison 2005) (Table 1.1). Understories within these stands are generally sparse or have not regenerated to a sufficient height to provide protection for hares (Lachowski 1997, Fuller and Harrison 2005) during the leaf-off season, the critical limiting season for hares (Litvaitis et al. 1985). Few studies have described the effects of partial harvesting on hares (Monthey 1986) and no study has yet described hare densities across the range of vegetation conditions exhibited in the array of partially harvested stands ranging from high-graded stands near the legal definition of clearcutting to single-tree selection harvests.

The objectives of this study were to: 1) to document hare densities across a broad range of partially harvested stands, 2) describe the vegetation characteristics associated with partial harvesting, and 3) compare hare densities and vegetation characteristics known to be important to hares in Maine across a broad range of partially harvested stands with regenerating clearcuts, which represent optimal habitat conditions for snowshoe hares in the Acadian forest (Table 1.1). Describing the vegetation characteristics associated with partial harvesting and the hare densities found in these stands is important to evaluating the potential consequences of widespread use of this form of forest harvesting for early successional species, their predators, and the structure of the forest across the landscape.

STUDY AREA

Stands were located in 11 townships in northern Maine and were distributed around two primary study sites near Clayton Lake and Telos Lake in northern Maine (Figure 1.1). Clayton Lake, Maine (69°31′, 46°36′) is located approximately 90 kilometers west of Ashland, ME. Mean temperature for this site was 36.3˚F with total precipitation of 39.40 inches in 2004 (National Oceanic & Atmospheric Administration 2005). Telos Lake (69°8′, 46°3′) is located west of Baxter State Park in north-central Maine. Forests across these 11 townships were managed primarily for sawlogs and pulpwood production by Clayton Lake Woodlands LLC, Irving Woodlands LLC, Seven Islands Land Co., the Maine Chapter of The Nature Conservancy, and Nexfor Paper.

The study area is part of the Acadian forest ecoregion, an ecological transition zone in the northeastern U.S.A. located between the temperate deciduous and eastern boreal forests (Seymour and Hunter 1992). Prior to European settlement, the predominant disturbance agents in this region were insect outbreaks, fire, and windstorms at relatively frequent return intervals, but at a much smaller scale compared to the disturbance regime of the boreal forest (Seymour and Hunter 1992). Currently, forest harvesting is the dominant disturbance agent in this region (Seymour and Hunter 1992). Large areas were

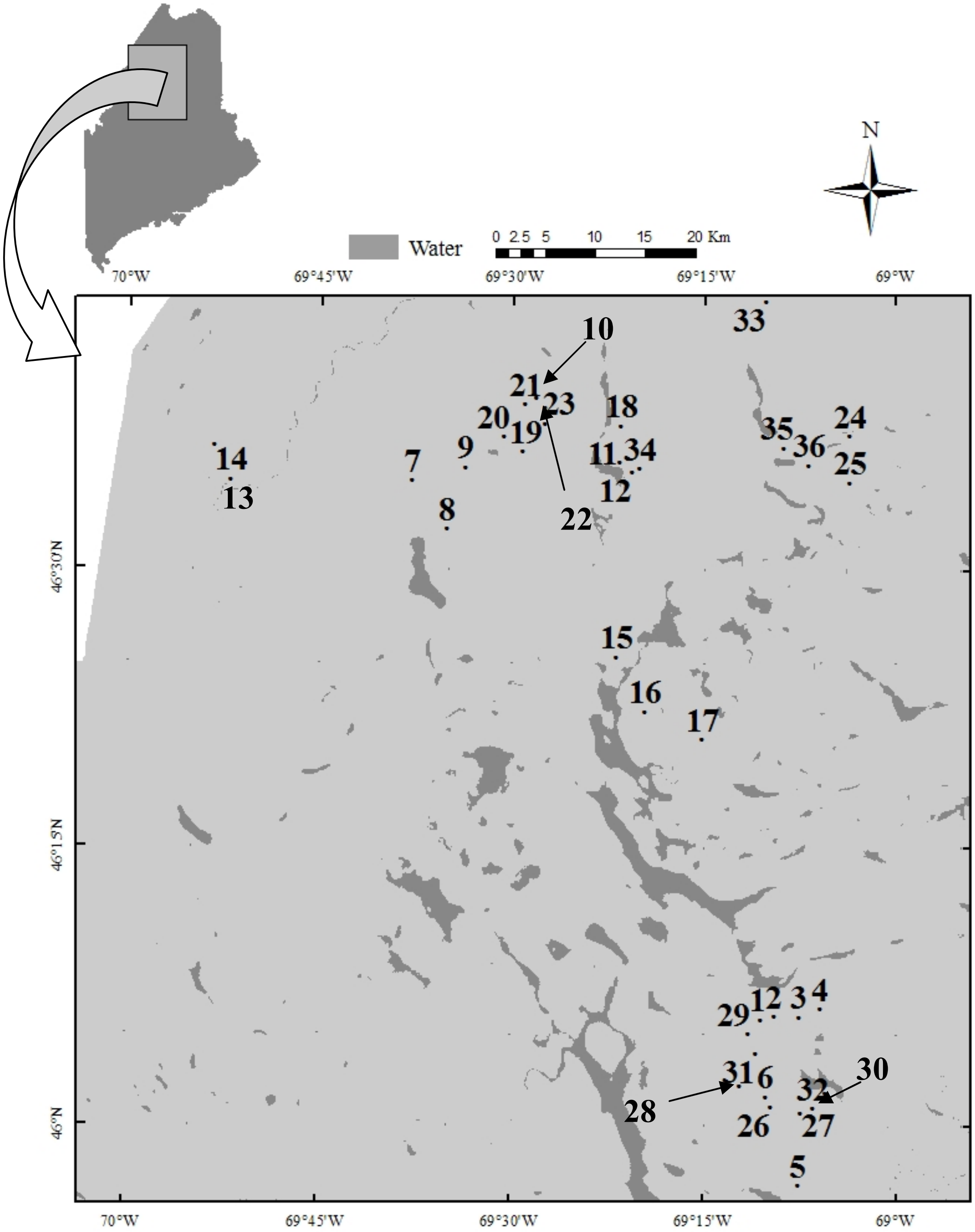


Figure 1.1. Locations of study stands where hare density was estimated and vegetation was measured in northern Maine, U.S.A. during 2005 and 2006. Stands in the northern part of the map are located in the Clayton Lake area and the Telos Lake area encompasses the southern stands. See Table 1.2 for a description of individual stands.

clearcut in the 1970's and 1980's and were subsequently sprayed with herbicides (primarily Glyphosate) to reduce deciduous competition. The resulting dense regenerating stands are dominated by balsam fir (*Abies balsamea*), and white (*Picea glauca*), red (*P. rubens*), and black (*P. mariana)* spruce (Seymour 1994). Species that comprise a minor component of these stands include eastern white pine (*Pinus strobus*), northern white cedar (*Thuja occidentalis*), and eastern hemlock (*Tsuga canadensis*). In areas with significant overstory disturbance, shade-intolerant species such as white birch (*Betula papyrifera*), aspen (*Populus spp.*), red maple (*Acer rubrum*), pin cherry (*Prunus pensylvanica*), and raspberries (*Rubus idaeus*) proliferate. Stands with a predominantly hardwood composition are dominated by sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*) and occur on better drained soils with higher site quality (Seymour 1992, 1995).

STAND HISTORIES

I studied 15 regenerating conifer clearcuts and 21 partially harvested stands in northern Maine. "Partial harvest" describes many methods of removing trees from a forest stand; therefore, I chose to study partially harvested stands that varied widely in species composition and density of residual trees resulting from various harvesting techniques employed by several land owners. Thus, stands were not selected randomly, but were chosen to represent a wide range of vegetation conditions existing in the landscape to sample hares across the full range of potential densities. These stands, therefore, did not constitute replicated observations from a population and were not treated as a population in the statistical sense.

Of the 21 partially harvested stands selected within the study area, 11 were selectively harvested 8-12 years prior to pellet clearing in the fall of 2004 (Table 1.2). These were diameter-limit cuts dominated by deciduous cover with basal areas comprised of residual and post-harvest growth ranging from 19.2-37.7 m^2/ha (Appendix A). Six of these 11 stands were located near Telos Lake and five were located near Clayton Lake (Figure 1.1). The remaining ten partially harvested stands were distributed throughout the study area and ranged in year of harvest from 1985 to 2003 (Figure 1.1, Table 1.2). Of these ten stands, three were conifer-dominated shelterwoods with basal areas ranging from 26.1-33.5 m^2/ha in 2005. Four were recent overstory removals and were characterized by a mixed developed understory 10-30 ft. tall with few overstory trees remaining. The stand history of the remaining two partial harvests is unknown as a result of missing landowner information. In 2005, the 21 partially harvested stands had a median basal area of 28.9 m^2/ha (range: 15.0-37.7 m^2/ha) and a median percent canopy closure of 79.5% (range: 35.4-96.0%) (Appendix A). See Appendix B for photographs of partially harvested stands studied.

The 15 regenerating conifer stands were selected to represent optimal conditions for hares (i.e., regenerating clearcuts 15-30 years old) and had been harvested between 1974 and 1985 and were subsequently treated with an aerial application of herbicide (primarily Glyphosate) between 1982 and 1997 (Table 1.2). Of these 15 stands, seven were located near the Telos Lake site and eight were located near the Clayton Lake site (Figure 1.1, Table 1.2). In 2005, the 15 regenerating conifer stands had a median basal area of 43.2 m^2/ha (range: 24.6-55.4 m^2/ha) and a median percent canopy closure of 79.0% (range: 55.7-90.3%) (Appendix A).

Table 1.2 Township, owner, most recent harvest history, and coordinates for 21 partial harvests and 15 regenerating conifer stands surveyed for snowshoe hare pellets and vegetation characteristics in northern Maine, U.S.A. during 2005-2006. Universal transverse mercators are projected in Zone 19, NAD 83.

Stand Number	Stand ID[a]	Stand type[b]	Township	Easting	Northing	Land owner[c]	Management history[d]
1	AF1	PH	T5R11	486425	5104766	NF	Selection harvest, 1994-1995
2	AF2	PH	T5R11	487798	5105055	NF	Selection harvest, 1994-1995
3	AF3	PH	T5R11	490284	5105017	NF	Selection harvest, 1995
4	AF4	PH	T5R11	492453	5105806	NF	Selection harvest, 1995
5	AF5	PH	T4R11	490175	5088187	NF	Selection harvest, 1992 and 1995
6	AF7	PH	T4R11	486927	5097072	NF	Selection harvest, 1994
7	CLSH1	PH	T11R14	451640	5158738	CLW	Selection harvest, 1995
8	CLSH2	PH	T10R14	455163	5153894	CLW	Selection harvest, 1996
9	CLSH3	PH	T11R14	457032	5160025	CLW	Selection harvest, 1995
10	CLSH4	PH	T11R14	464043	5166913	CLW	Selection harvest, 1996
11	CLSH5	PH	T11R13	472446	5160527	CLW	Selection harvest, 1997
12	S11	PH	T11R12	473649	5159509	CLW	Shelterwood, 1997

Table 1.2 Continued.

Stand Number	Stand ID[a]	Stand type[b]	Township	Easting	Northing	Land owner[c]	Management history[d]
13	S12	PH	T11R17	431958	5162306	TNC	Overstory removal, 2002
14	S13	PH	T11R17	433515	5158914	TNC	Partially harvested prior to 1998
15	S14	PH	T9R13	472069	5141058	SILC	Selection harvest, 1991
16	S15	PH	T8R12	474925	5135538	SILC	Partially harvested prior to 1985
17	S16	PH	T8R12	480638	5132755	SILC	Shelterwood, prior to 1985
18	S17	PH	T11R13	472508	5164119	CLW	Shelterwood, 1997
19	S21	PH	T11R14	462773	5161609	CLW	Overstory removal, 2003
20	S22	PH	T11R14	460831	5163098	CLW	Overstory removal, 2003
21	S23	PH	T11R14	463044	5166332	CLW	Overstory removal, 2004
22	CLREG1	REG	T11R13	464910	5166018	CLW	Clearcut in 1976, herbicided in 1997
23	CLREG2	REG	T11R13	464934	5164407	CLW	Clearcut in 1976, herbicided in 1994
24	CLREG3	REG	T11R10	495444	5163105	CLW	Clearcut in 1984, herbicided in 1991
25	CLREG4	REG	T11R10	495428	5158429	CLW	Clearcut in 1984, herbicided in 1989

Table 1.2. Continued.

Stand Number	Stand ID[a]	Stand type[b]	Township	Easting	Northing	Land owner[c]	Management history[d]
26	JH01C	REG	T4R11	487450	5096050	NF	Clearcut in 1982, herbicided in 1988
27	JH02C	REG	T4R11	490399	5095454	NF	Clearcut in 1979, herbicided in 1983
28	JH03C	REG	T4R11	484328	5098147	NF	Clearcut in 1981, herbicided in 1984
29	JH04C	REG	T5R11	485151	5103344	NF	Clearcut in 1983, herbicided in 1988
30	JH05C	REG	T4R11	492861	5097403	NF	Clearcut in 1976, herbicided in 1985
31	JH54C	REG	T5R11	485954	5101360	NF	Clearcut in 1974, herbicided in 1982
32	JH56C	REG	T4R11	491619	5095916	NF	Clearcut in 1976, herbicided in 1983
33	SM4B	REG	T12R11	487063	5176528	I	Clearcut in 1984, herbicided in 1988
34	SM4C	REG	T11R12	474346	5159876	CLW	Clearcut in 1983, herbicided in 1987
35	SM4D	REG	T11R11	488853	5161919	CLW	Clearcut in 1985, herbicided in 1992
36	SM4E	REG	T11R11	491318	5160179	CLW	Clearcut in 1984, herbicided in 1992

[a] AF = stands surveyed by Fuller (Fuller 1999) in 1997-1998; CLSH = stands selectively harvested 8-12 years prior to survey located near Clayton Lake; S = conifer-dominated partial harvested stands located in northern Maine; CLREG = regenerating conifer stands at 20-30 years post-harvest and treated with herbicide and located near Clayton Lake; JH = stands surveyed by Homyack (Homyack et al. 2006) in 2001-2002; SM = stands surveyed by Mullen (2003) in 2001-2003.

[b] PH = partially harvested stands; REG = regenerating conifer stands at 20-30 years post-harvest and treated with herbicide.

[c] NF = Nexfor Fraser; CLW = Clayton Lake Woodlands, Limited Liability Corporation (LLC); TNC = The Nature Conservancy, Maine Chapter; SILC = Seven Islands Land Co.; I = Irving, LLC

[d] Selection harvest = diameter-limit cuts dominated by deciduous cover; Shelterwood = conifer-dominated partial harvest; Overstory removal = mixed developed understory 10-30 ft. tall with few overstory trees remaining.

METHODS

PELLET COUNTS

A previous study in northern Maine demonstrated the reliability and efficiency of using pellet counts as a method for estimating snowshoe hare density in northern Maine across a range of hare densities from 0.16-3.2 hares/ha (Homyack et al. 2006a). I established 4, 360m parallel transects that were separated by 65 meters and counted pellets in 5 m x 30 cm randomly-oriented rectangular plots located every 60 meters along the transects for a total of 28 pellet plots per stand (Figure 1.2). The design of this sampling grid was similar to that used by Homyack et al. (2006a) with the exception that I increased the spacing between plots to reduce sampling effort per stand based on *post hoc* evaluations of Homyack's (2003) data that indicated 28 plots/stand would yield similar precision to 84 plots/stand (J. A. Homyack, unpublished data, University of Maine, Orono). The goal of my study was to understand the relationship between hare density and vegetation characteristics across a wide range of stand types. Therefore, I opted to give up a small amount of precision in stand-scale hare density estimates in order to sample more stands. This strategy resulted in a change in standard error of only 3% relative to the mean estimated hare density for regenerating conifer clearcuts between the two studies (Table 1.1).

I used the standard 7.02 ha grid layout in 26 forest stands. The remaining 10 stands were irregularly shaped and could not accommodate the standard grid layout; therefore, I established irregular grids containing 28 plots in these stands, and attempted to conform to the standard grid layout as closely as possible in the spacing of

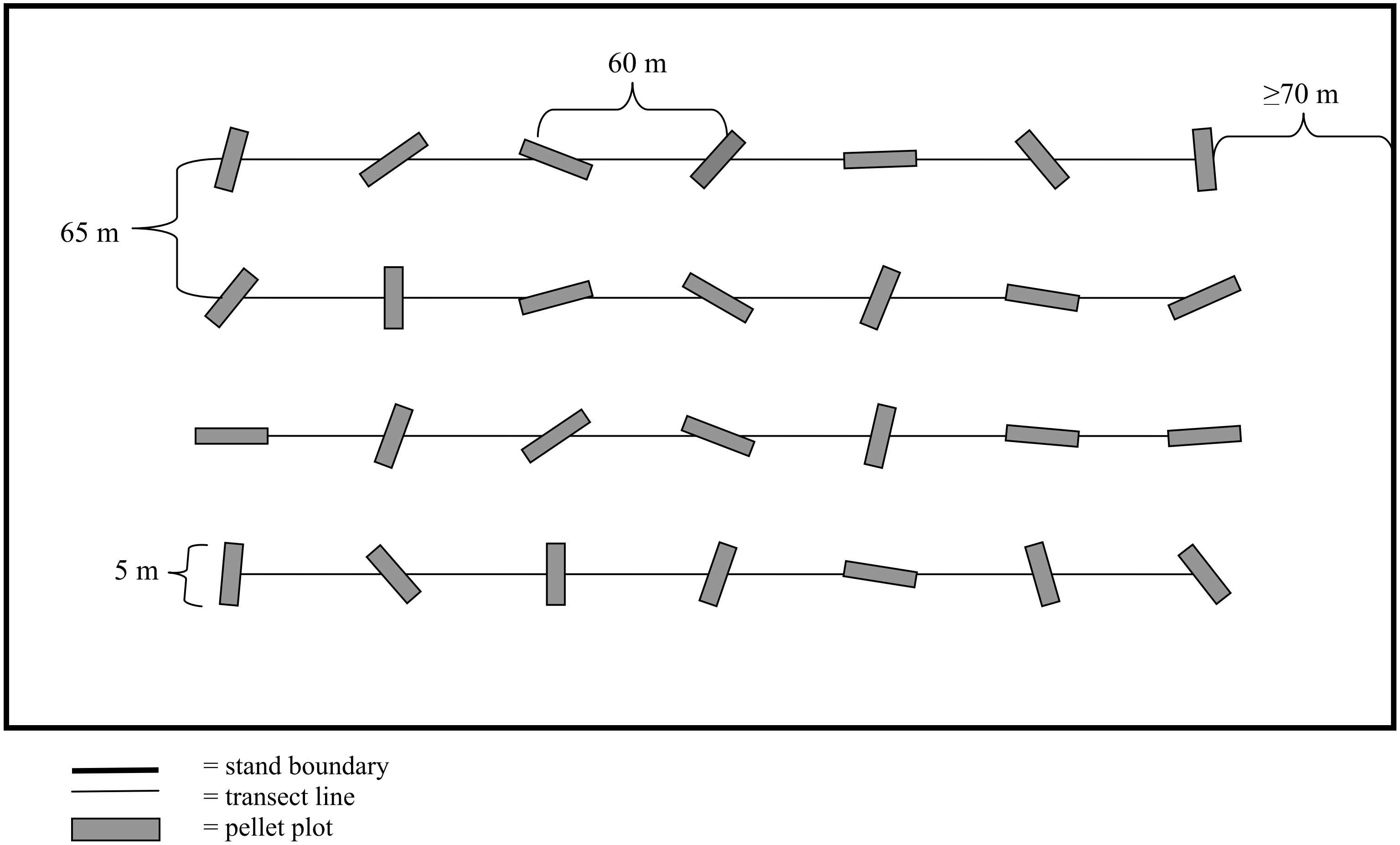


Figure 1.2. Layout of survey grid for snowshoe hare pellets in northern Maine, U.S.A., containing 28 randomly-oriented snowshoe hare pellet plots (of which, 20 were randomly selected for vegetation measurement) along 4, 360 m parallel transects. The total area surveyed was 7.02 ha (not including ≥ 70m buffer to edge of stand) for 26 forest stands. Ten additional stands were surveyed using alternative layouts, each with 28 pellet plots at least 60 meters apart and at least 70 meters from any edge. Figure not drawn to scale.

transects and plots. All pellet plots regardless of grid layout were located at least 60 meters apart and at least 70 meters from any forest edge or road to reduce edge-effects (Fraver 1994). The mean size of home ranges for hares was 6.2 ha in Maine (Litvaitis 1984) and the mean size of 95% convex polygon home ranges for hares in Quebec was 12.8 ha (De Bellefeuille et al. 2001). The size of the study stands (7.02 ha) falls between these two estimates; therefore, the stand was considered to be the unit of observation. Estimated mean hare densities for optimal stand conditions was 1.64 hares/ha (Fuller and Harrison 2005) and 1.83 hares/ha (Homyack et al. 2006b) during two previous studies in northern Maine (Table 1.1). Thus, the size of my study stands was large enough to potentially encompass up to 11.5-12.8 hares and pellet counts within these stands were likely to reflect stand-scale hare densities with little influence by the individual behavior of hares.

The ends of each pellet plot were marked with two wooden stakes placed 5.0 m apart. A string was attached to each stake and a 30 cm dowel was centered along the string to delineate plot boundaries. I cleared pellets between September 18 and October 11, 2004 and then counted pellets between May 13 and June 16, 2005 to estimate hare density for the 2004-2005 leaf-off season. I counted pellets again between September 17 and October 6, 2005 to estimate hare density for the 2005 leaf-on season. I counted pellets again between May 16 and June 4 to obtain estimates for the 2005-2006 leaf-off season.

I divided the pellet count at each plot by the number of days that had elapsed since the plot was cleared and by the size of the pellet plot to obtain pellets/ha/day. I then converted this number to pellets/ha/mo by multiplying by the average number of days in each month since clearing. Pellet densities were converted to estimated hare densities using a regression equation developed for the Acadian forest (Homyack et al. 2006a): hares/ha = 0.15979 + 0.00010*(pellets/ha/month).

I tested bias in pellet counts across the three observers who inventoried the majority of pellet plots; counts on the same plots were not significantly different among observers (Appendix C).

VEGETATION MEASUREMENTS

In each stand where pellets were counted, I measured vegetation characteristics thought to be associated with hare density between June 23 and July 27, 2005. I randomly selected 20 of the 28 pellet plots to describe overall vegetation characteristics for the stand. To ensure that similar numbers of total stems were sampled in each stand, $10m^2$ circular plots were used in regenerating conifer stands and $20m^2$ circular plots were used in partially harvested stands. To reduce sampling time, I used $10m^2$ plots at 6-8 of the vegetation plots in two partially harvested stands because they had total stem densities >10,000 stems/ha.

I measured 16 vegetation characteristics at each vegetation plot (Table 1.3). Coniferous, deciduous, and dead trees (≥ 7.6cm dbh) that were at least half in the plot were tallied and their diameter was measured at 1.4m above ground. I counted logs of decay classes 1 and 2 (Fraver et al. 2004) at least 1 meter from the plot edge (≥ 7.6cm in diameter). I also counted stumps of decay classes 1 and 2 (Fraver et al. 2004), measured their diameter, and used the mean number of stumps per stand and the mean diameter of stumps to calculate the mean basal area removed from the stand as:

$$\text{BAR/ha} = \pi*(1/2*\text{mean stump diameter})^2 * \text{mean number of stumps/stand.}$$

Table 1.3. Descriptions and transformation methods for 16 vegetation variables measured in 36 stands in northern Maine, U.S.A. during the leaf-on season, 2005.

Vegetation variable	Description	Units	Transformation
BA	Basal area measured with a 2m^2/ha wedge prism and includes live and dead trees	m^2/ha	None
BAR	Basal area removed/ha = B*(½*mean stump diameter)*mean number of stumps/stand	m^2/ha	None
C	Conifer stems >1.5m high/ha	stems/ha	Square root
CC	Percent canopy closure measured with a spherical densiometer at 1m above ground	percent	Arcsine
CT	Number of conifer trees/ha more than ½ inside the plot	trees/ha	Square root
D	Dead stems >1.5m high/ha	stems/ha	Logarithm
DBH	Average diameter of all trees measured at 1.4m above ground	cm	None
DEC	Deciduous stems>1.5m high/ha	stems/ha	Logarithm
DECT	Number of deciduous trees/ha more than ½ inside the plot	trees/ha	Square root
DT	Number of dead trees/ha more than ½ inside the plot	trees/ha	Square root
LOGS	Number of logs/ha more than 1m inside the plot of decay class ≤ 2	logs/ha	None
S	Number of stumps/ha more than ½ inside the plot of decay class ≤ 2	stumps/ha	Square root
SCU	(3* the number of conifer stems >1.5m high/ha)+the number of deciduous stems >1.5m high/ha	stems/ha	Logarithm
SD	Mean diameter of stumps more than ½ inside the plot of decay class ≤ 2	cm	Logarithm
T	Conifer+deciduous+dead stems >1.5m high/ha	stems/ha	None
VO	Visual obstruction measured as the distance at which ≥25% of at least 25% of the bands over 1.0m on a cover pole were obscured by vegetation	m	Logarithm

Conifer, deciduous, and dead stems (< 7.6 cm dbh) were counted at > 1.5 m height. I used these values to calculate stem cover units as described by Litvaitis et al. (1985):

$$SCU = 3*\text{conifer stems} + \text{deciduous stems}.$$

In Maine, hare densities within a range of 0.15-1.50 hares/ha have been strongly associated with SCU at the scale of the forest stand (Litvaitis et al. 1985, Long 1995) and on 70 m x 70 m sampling grids (Fuller 2006).

I measured total basal area using a 2 m^2/ha wedge (Avery and Burkhart 1994) prism and percent overhead canopy closure using a spherical densiometer at 1 m height (Lemmon 1956). I measured visual obstruction using a cover pole with alternating red and white 10 cm bands as a continuous variable equal to the distance at which ≥ 25% of at least 25% of the bands over 1.0 m were obscured by vegetation (Griffith and Youtie 1988, Homyack et al. 2004).

ANALYSES

HARE DENSITIES

I wished to compare hare densities in 21 partially harvested stands with those in 15 regenerating conifer clearcuts for both the leaf-off and leaf-on seasons. Because the partially harvested stands were chosen to capture a broad range of vegetation characteristics found in partially harvested stands, these stands were not statistically treated as a replicated sample from a population. Thus, I assumed that the data from these stands would be overdispersed and that measures of central tendency such as mean and standard error would not apply. The regenerating conifer stands, however, were selected to represent replicated observations and were considered a sample from a statistical population. I transformed all vegetation variables that did not appear to be normally distributed in dot density plots (Table 1.3). There were no apparent differences in hare densities between the 2004-2005 and the 2005-2006 leaf-off seasons (non-parametric sign test, $P = 0.13$); therefore, I averaged the two seasons to produce one estimate of hare density for the leaf-off season for each stand.

I tested for a difference in the log of hare densities for regenerating conifer clearcuts between the two study sites (n = 8 for Clayton Lake, n = 7 for Telos Lake). Hare densities were not normally distributed in regenerating clearcuts (Shapiro-Wilk P-value = 0.004 for leaf-off densities and 0.003 for leaf-on densities), so I used a log transformation on this response variable, which resulted in distributions that did not deviate significantly from normal (Shapiro-Wilk P-value > 0.05 for each season). I found no difference between study sites for the 2004-2005 leaf-off season ($t = 1.85$, df = 13, $P = 0.09$), nor for the leaf-on season ($t = -0.99$, df = 13, $P = 0.34$), nor for the 2005-2006 leaf-off season ($t = 0.82$, df = 13, $P = 0.43$); therefore, I pooled the pellet densities between the two sites for regenerating clearcuts to calculate a mean hare density and standard error across all 15 regenerating conifer stands.

To visually compare hare densities in partially harvested stands with those in regenerating conifer clearcuts, I plotted the estimated hare density for each partially harvested stand with its 95% confidence interval and determined if it overlapped with the standard error of the mean for hare density within regenerating conifer clearcuts. I evaluated the statistical significance of this comparison with a non-parametric sign test (Zar 1999).

VEGETATION AND PRINCIPAL COMPONENTS ANALYSIS

I selected partially harvested stands that varied in their species composition, site quality, and residual tree density to capture a range of vegetation characteristics reflecting this diversity (Appendix A). The 16 variables used to describe these vegetation characteristics are likely to be highly correlated due to natural processes occurring within the stands. To understand the patterns of variation in vegetation characteristics within the context of this multicollinearity of variables, I performed Principal Components Analysis (PCA) on the 16 transformed vegetation variables (Kutner et al. 2005, Table 1.3). A component loading score was given to each variable in each component to represent the magnitude and direction of that variable's contribution to the component. I considered all component loadings > 0.5 to indicate an important contribution by a single variable to the composite index (McGarigal et al. 2000).

I performed a PCA on the 16 vegetation variables within only the 21 partially harvested stands to understand the trends in vegetation across this broad range of stand conditions. I then plotted values for four vegetation variables known to be important to hares in Maine (DECT, C, BAR, and LOGS) based on results of the PCA and modeling results from Chapter 2 for partially harvested and regenerating clearcuts. This allowed me to graphically compare vegetation characteristics known to be important to hares between the broad range of partially harvested stands studied and regenerating conifer stands.

RESULTS

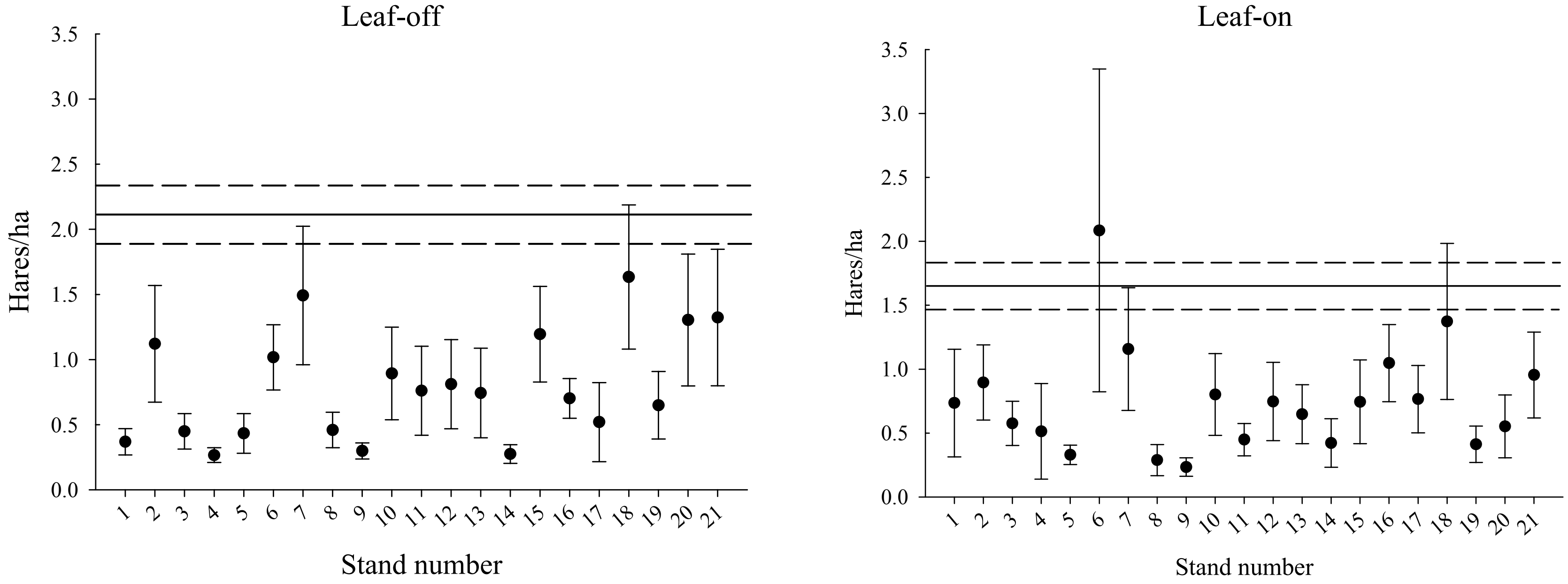
HARE DENSITIES

Thirty-six stands (15 regenerating conifer clearcuts and 21 partial harvests) were surveyed for hare density and vegetation characteristics, resulting in 1,064 pellet plots surveyed during the leaf-off season, 2004-2005 and 2005-2006; and during the leaf-on season, 2005 (Appendix D). A total of 720 vegetation plots were surveyed for 16 vegetation characteristics during the leaf-on season, 2005 (Appendix A). Mean estimated hare densities in the 15 regenerating conifer stands were 2.10 (SE = 0.22) hares/ha during the combined 2004-2005 and 2005-2006 leaf-off season and 1.65 (SE = 0.18) hares/ha during the 2005 leaf-on season. No obvious outliers in log transformed hare density were present within regenerating stands for the three seasons studied.

During the combined 2004-2005 and 2005-2006 leaf-off seasons, mean estimated hare densities in the 21 partially harvested stands ranged from 0.26-1.65 hares/ha (Appendix D). All of the 21 estimates were below the mean-1 standard error for regenerating stands ($P < 0.001$; Figure 1.3). During the leaf-on season, partially harvested stands ranged from 0.23-2.09 hares/ha, and 20 of 21 estimates were below the mean-1 standard error for regenerating stands ($P < 0.001$; Figure 1.3).

PRINCIPAL COMPONENTS ANALYSIS

The results of PCA for the 21 partially harvested stands identified 3 principal components that described 64.9% of the variance in vegetation characteristics within these stands (Table 1.4). PC1 explained 28.7% of the variance in the data and described the overall conifer component in the stand with high positive factor loadings for conifer stem density, SCU, conifer tree density, and dead tree density (Table 1.4). High negative factor loadings were observed for deciduous tree density, stump diameter, canopy closure, and deciduous stem density (Table 1.4). The inverse relationship between conifer and deciduous species is expected given that these groups compete for space and light in the understory. Stump diameter is associated with partially harvested stands because



Leaf-off

Leaf-on

Figure 1.3 Estimated hare densities and 95% confidence intervals for 21 partially harvested stands in northern Maine, U.S.A. for the combined 2005 and 2006 leaf-off seasons (left) and the 2005 leaf-on season (right). Horizontal lines represent the mean (solid line) and standard error (dashed lines) for estimated hare densities in 15 regenerating conifer clearcuts (i.e., “optimal stand conditions”) concurrently estimated in northern Maine.

Table 1.4 Principal component loading values (those > 0.5 are bolded) and the percent of variance explained for 16 vegetation variables measured in 21 partially harvested stands in Maine during the leaf-on season, 2005. Refer to Table 1.3 for a description of vegetation variables and variable transformations.

	Principal Components		
Vegetation variable	PC1 (conifer composition)	PC2 (horizontal obstruction)	PC3 (past harvesting)
CC	**-0.589**	**0.676**	-0.215
BA	0.001	**0.708**	**-0.516**
VO	-0.299	**-0.691**	-0.124
CT	**0.568**	-0.112	-0.327
DECT	**-0.743**	0.389	-0.139
DT	**0.584**	0.167	0.243
DBH	-0.318	-0.388	0.472
LOGS	0.255	-0.044	0.479
S	0.202	0.133	**0.673**
SD	**-0.663**	0.231	0.253
BAR	-0.497	0.260	**0.712**
C	**0.924**	0.140	-0.010
DEC	**-0.548**	**0.545**	0.132
D	-0.026	**0.711**	-0.176
T	0.459	**0.803**	0.318
SCU	**0.826**	0.495	0.147
% Variance explained	28.7	22.7	13.5

larger trees were selectively removed during the harvesting of these stands relative to the mean diameter of harvested trees in regenerating clearcuts (Appendix A).

PC2 explained 22.7% of the variance in the vegetation data and described horizontal obstruction in the stand; this component had high positive factor loadings for total stem density, dead stem density, basal area, canopy closure, and deciduous stem density and a high negative factor loading for visual obstruction (Table 1.4). Visual obstruction is measured as the distance to obstruction so lower values for this variable indicated a denser understory in the stand.

The third principal component explained 13.5% of the variance and likely represented the amount of previous harvesting in the stand with high positive component loadings for basal area removed and stump density and a high negative component loading for basal area (Table 1.4).

Both conifer stem density (C) and the density of deciduous trees (DECT) were important variables in the component that described the majority of the variance in vegetation in partially harvested stands (PC1). Additionally, C, BAR, and LOGS were important variables in describing the relationship between vegetation and hare density in modeling efforts described in Chapter 2. Scatterplots of C, DECT, BAR, and LOGS for all 36 stands (regenerating clearcuts and partially harvested stands) were able to graphically distinguish partially harvested from regenerating conifer stands for all of these vegetation variables except BAR (Figure 1.4). Overall, partial harvests had higher densities of deciduous trees and logs and lower conifer stem densities than regenerating clearcuts (Figure 1.4). Only six of 21 partially harvested stands had values for conifer stem density and deciduous tree density that were encompassed by the range of

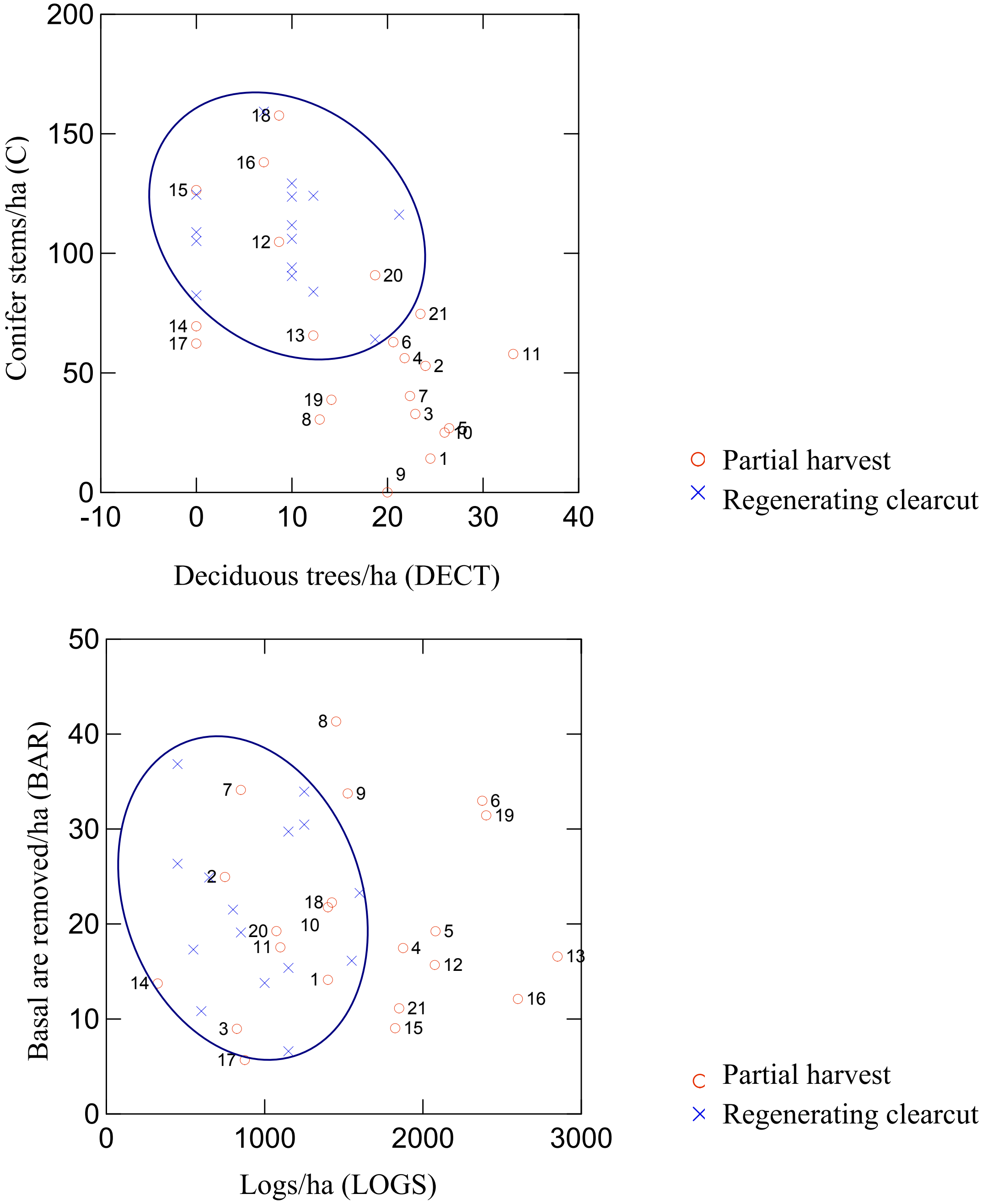


Figure 1.4 Scatterplots for C versus DECT (top), and BAR versus LOGS (bottom) measured in 36 forest stands in northern Maine, U.S.A. during the leaf-on season, 2005 showing the difference between partial harvests (n = 21) and regenerating conifer clearcuts (n = 15). Circles encompass all regenerating conifer clearcuts and partially harvested stands are labeled with stand numbers (Table 1.2). Refer to Table 1.3 for a description of vegetation variables and variable transformations.

regenerating clearcuts studied (Figure 1.4). Although BAR did not unequivocally distinguish these two harvest types, 12 of 21 partial harvests had a higher log density than the 15 regenerating clearcuts (Figure 1.4).

DISCUSSION

This study was designed to describe the range of vegetation conditions present in many forms of partially harvested stands. Therefore, results from this study cannot describe the effect of any particular method of partial harvesting on vegetation or hare density. Rather, this study describes vegetation characteristics in a broad group of partially harvested stands and compares the snowshoe hare densities across this range of conditions to the optimal densities in regenerating clearcut stands with a past history of deciduous suppression via herbicides (typically Glyphosate application 5-9 years post-clearcut).

Partially harvested stands varied widely in their vegetation characteristics (Appendix A) and this variation was primarily described by the amount of conifer species and horizontal obstruction found within these stands (Table 1.4). This variation is likely a reflection of the different methods of partial harvesting and the degree of stand development occurring with increasing time since harvesting. Horizontal obstruction is related to the degree of understory development, which occurs naturally over time. Therefore, the results from PCA analysis across the 21 partially harvested stands studied suggest that this broad range of silvicultural techniques and stand histories (selection harvest, overstory removal, and softwood shelterwood) is associated primarily with variance in the representation of conifer species in residual stands. The wide variation within partially harvested stands in densities of conifer stems and deciduous trees that were important in PC1 is evident in scatterplots of these variables (Figure 1.4).

Three vegetation variables were able to distinguish partially harvested stands from regenerating conifer clearcuts and this separation may be related to the difference in hare densities observed between these two stand types. Two of these variables (C and DECT) successfully distinguished the majority of partially harvested stands from regenerating conifer clearcuts, with regenerating conifer clearcuts having a higher conifer stem density and a lower density of deciduous trees than partially harvested stands (Figure 1.4). Modeling results of vegetation variables with hare densities indicated that conifer stem density was the most important variable in explaining this relationship (Chapter 2). Conifer stem density is likely a surrogate variable describing dense understory conditions that provide thermal and escape cover for hares during the leaf-off season.

BAR and LOGS were important in modeling snowshoe hare densities across these 36 stands (Chapter 2), but only LOGS separated partially harvested stands from regenerating clearcuts; partially harvested stands generally had higher log densities than regenerating conifer clearcuts (Figure 1.4). The higher log density in partially harvested stands may be the result of more recent removal of overstory trees and subsequent blowdown of residual trees after harvest. This suggests that the importance of the LOGS variable in modeling results may be related to its ability to separate the two harvest methods, but that the importance of the BAR variable to hares may be related to variance within either partial harvests or regenerating clearcuts.

The wide range of vegetation conditions in partially harvested stands was reflected in the hare densities supported by these stands (0.26-1.65 hares/ha during the leaf-off seasons, Figure 1.3). The amount of conifer species and horizontal obstruction in the residual stand could be related to dense understory conditions important to hares; therefore, the variance in these components may be related to the wide range of hare densities observed in partially harvested stands.

Horizontal obstruction is a characteristic that increases with time after harvesting and partially harvested stands may therefore provide high quality escape cover for snowshoe hares after understory stems have grown to be taller than 1.5 m (i.e., above snow level) or during the summer when deciduous stems have leaves. As the stand matures and the remaining canopy develops, understories will be increasingly shaded and will likely self-thin, thus providing less cover for snowshoe hares. Partially harvested stands may provide ephemeral snowshoe hare habitat during the critical leaf-off season when stem densities are tall enough to provide winter cover to hares and before the stand reaches a stage of self-thinning. Stands 1-6 were surveyed three years after harvest and at that time, the mean hare density for those stands was only 0.15 hares/ha (Fuller and Harrison 2005, Table 1.1), but these densities increased to a mean of 0.61 hares/ha by 10-11 after harvesting (Figure 1.3, Appendix D). This suggests that understories may regenerate to a sufficient height and density to provide cover for hares by 10-11 years post-harvesting, although additional studies are needed to evaluate the effects of further understory development on hare densities in partially harvested stands.

Although hare densities varied greatly in partially harvested stands, these densities were uniformly lower than those found in more optimal hare habitat (Figure 1.3). Partially harvested stands reflected a wide range of harvesting techniques and objectives and were represented by highly variable vegetation conditions. However, all

21 stands had estimated hare densities lower than the mean-1 standard error (SE) for the optimal conditions observed in regenerating clearcuts during the leaf-off season, and 20 of the 21 partially harvested stands had estimates lower than this value during the leaf-on season. The 95% confidence interval on estimated hare densities overlapped the mean-1SE for regenerating clearcuts for only two partially harvested stands during the leaf-off season, and for only three of the 21 stands during the leaf-on season. The decrease in the mean hare density in regenerating clearcuts between the leaf-off season and the leaf-on season may reflect a weakening habitat association of hares with regenerating clearcuts during the leaf-on season, perhaps because deciduous-dominated partial harvests have leaves and can therefore provide cover for hares during the leaf-on season. Overall, partial harvesting as the dominant silvicultural practice in the Maine landscape is currently supporting fewer hares than the regenerating clearcuts associated with the widespread clearcutting of the 1970’s-1980’s.

An important question is whether the density of hares supported by partially harvested stands is sufficient to maintain a population of Canada lynx in Maine. Modeling results of reintroduction efforts for lynx in the southern portion of the range estimated the minimum range of hare densities required for the persistence of a lynx population at 1.1-1.8 hares/ha (Steury and Murray 2004). Additionally, Ruggiero et al. (2000) concluded that the hare density needed for lynx persistence is greater than 0.5 hares/ha, and Krebs et al. (2001) observed changes in lynx survival and emigration when hare densities decreased to 0.3-0.8 hares/ha. The majority of partially harvested stands in this study supported a lower hare density than the recommended value of 1.1 hares/ha (15 of 21 stands for the combined leaf-off seasons and 18 of 21 for the leaf-on season; Figure

1.3). However, this recommendation of 1.1 hares/ha may be higher than hare densities occurring within occupied lynx habitat in Maine; estimated home range-scale hare densities in areas of lynx occurrences averaged 0.86 hares/ha (SE = 0.04 hares/ha) (Chapter 3). This value of 0.86 hares/ha is still higher than the estimated hare density for 13 of 21 partially harvested stands during the combined leaf-off seasons, suggesting that, without regenerating conifer clearcuts on the landscape, partially harvested stands by themselves may not be able to support the hare densities required to maintain a lynx population.

Regenerating clearcuts approximately 15-30 years post-harvest support the highest hare densities of any forest type studied in Maine to date (Table 1.1) and additionally, landscape-scale densities of hares were associated with the extent of late regenerating clearcuts (Hoving 2001). Lynx select for regenerating clearcuts at both the landscape (Hoving et al. 2004, Chapter 3) and sub-stand scales in Maine (Fuller 2006), likely as a result of the (> 1.5 hares/ha) hare densities found in these stands. Since 1989, clearcutting has decreased from 145,357 to 18,779 acres annually (an 87% decrease), while partial harvesting has more than doubled from 180,700 to 481,153 annual acres (Maine Forest Service 1990, 2005). Given the large difference in snowshoe hare densities observed in these two stand types, the recent shift from clearcutting to partial harvesting might have long-term negative consequences if the objective is to maintain or increase current population levels of Canada lynx in Maine.

CONCLUSIONS

Results of this study demonstrate that partial harvesting is associated with residual stands that vary greatly in their vegetation characteristics and snowshoe hare densities.

Partial harvesting affects the residual conifer component and understory density in these stands and both of these components are likely related to the wide range of hare densities that I observed in partially harvested stands. Partially harvested stands had lower conifer stem densities, higher densities of deciduous trees, and higher log densities than regenerating clearcuts. Conifer stem density and log density are known to be related to hare density and the differences in these variables between partially harvested stands and regenerating clearcuts may be related to the large discrepancy in hare densities observed between the two harvest methods studied.

Hare densities within partially harvested stands ranged from 0.26-1.65 hares/ha, but densities in all 21 stands were lower than those found in regenerating conifer clearcuts during the critical leaf-off season (2.10 hares/ha, SE = 0.22). Partially harvested stands did not support the hare density estimated in other studies as required to maintain a viable lynx population across the landscape. Habitat use by lynx is associated with regenerating clearcuts, likely because of the high hare densities supported by these stands and the recent decrease in clearcutting and concurrent increase in partial harvesting could have negative long-term consequences for lynx conservation in Maine if objectives are to increase populations or to maintain lynx at current densities.

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CHAPTER 2

MODELING STAND-SCALE DENSITIES OF SNOWSHOE HARES IN MAINE USING VEGETATION CHARACTERISTICS

ABSTRACT

The snowshoe hare plays an important ecosystem-level role as both a consumer and prey. Habitat characteristics affect hare abundance at the scale of the forest stand and previous studies have associated snowshoe hare density and habitat use with dense understories. Forest harvesting can profoundly affect vegetation and forest structure and can produce stands with dense understory characteristics. I surveyed hare densities and vegetation characteristics across 36 stands (15 clearcut, 21 partial harvests) and used an information-theoretic approach to evaluate alternative *a priori* hypotheses describing hare density-vegetation relationships. Additionally, I developed a set of 14 *post hoc* models to further evaluate the relationships with other frequently measured vegetation characteristics. At the stand-scale in northern Maine, hare densities are most strongly associated with conifer stem density (+), basal area removed (+), and log density (-) during the leaf-off season. Conifer stem density was the most important variable of those studied in describing the variation in pellet counts in this dataset. A model for estimating hare densities from these 3 vegetation variables explained 67% of the variance in the data during the leaf-off season; however, the vegetation variables that I measured were unable to adequately describe the relationship between vegetation and pellet density during the leaf-on season. Vegetation variables most directly influencing hare densities during the

limiting leaf-off season are directly affected by forest management practices; therefore, landowners in the Acadian forest seeking high hare densities should manage to produce conditions with high conifer stem densities, comparable to those found in regenerating conifer clearcuts approximately 15-30 years after harvest.

INTRODUCTION

The snowshoe hare (*Lepus americanus*) is important both as a consumer and prey species. In the northern boreal forest, hares are considered a keystone species and are known to exert top-down effects on producers and bottom-up effects on predators (Krebs et al. 2001). Large changes in hare densities can cause density-dependent effects on the composition and structure of vegetation and may also influence other herbivores (Krebs et al. 2001). Additionally, hares are important prey for many Carnivora in the North America including marten (*Martes americanus*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), fisher (*Martes pennanti*), red fox (*Vulpes vulpes*) (Dibello et al. 1990, Cumberland et al. 2001, Weir et al. 2005), and the Canada lynx (*Lynx canadensis*), a specialist predator of snowshoe hares (Saunders 1963, Van Zyll de Jong 1966, Staples 1995, O'Donoghue et al. 2001).

In the northern boreal forest, hare populations undergo 8-11 year cycles and exhibit 5-25 fold changes in density throughout the course of the cycle (Brand et al. 1976; Krebs et al. 2001). Evidence is inconclusive, however, for a population cycle on the southern edge of the hare range (Hodges 2000b). The weight of evidence in Maine currently suggests that hare populations fluctuate, but neither undergo the 5-25 fold changes in density nor exhibit the 10-year periodicity that characterize cycling populations in the northern boreal forest (D. J. Harrison, unpublished data, University of Maine, Orono).

Habitat characteristics also affect hare abundance at the scale of the forest stand. Previous studies have consistently associated snowshoe hare density and habitat use with dense understory characteristics (Converse 1981, Orr and Dodds 1982; Pietz and Tester 1983, O'Donoghue 1983, Litvaitis et al. 1985, Monthey 1986, Parker 1986, Scott and Yahner 1989, Long 1995, Homyack et al. 2006b, Fuller 2006). Dense understories with high stem densities, which are often associated with regenerating forest following disturbances, provide hares with both escape and thermal cover during the winter (Litvaitis et al. 1985). Because the primary cause of mortality for snowshoe hares is predation, which comprises > 90% of proximate causes of death in some studies (Boutin et al. 1986, Hodges 2000[a], Hodges et al. 2001), hares select areas of dense structure to avoid predators (Wolff 1980) and escape cover can be considered a habitat requirement.

In Maine, hare densities within a range of 0.15-1.50 hares/ha have been highly correlated with stem densities, as represented by stem cover units (calculated as 3*conifer stems + deciduous stems), at the scale of the forest stand (Litvaitis et al. 1985, Long 1995). Hare pellet densities at the sub-stand scale have also been associated with stem cover units (positive association) and canopy closure (negative association) (Fuller 2006), but no studies have simultaneously examined relationships of snowshoe hares and vegetation at the stand-scale across a wide range of hare densities and among many forest stands that are large enough (> 7 ha) to potentially encompass home ranges of many individual hares.

Natural and human-caused disturbances produce the early successional vegetation characteristics associated with high quality habitat for hares. In the northern boreal forest, fires produce large areas of early successional habitat (Staples 1995, Paragi et al. 1997, Mowat and Slough 2003). In the Acadian Forest, these conditions occur after windstorms and insect infestations from species like the eastern spruce budworm (*Choristoneura fumiferana*) (Blais 1983). Forest harvesting practices can also profoundly affect vegetation and forest structure and can produce regenerating and residual stands with dense understory characteristics (Homyack et al. 2004). Regenerating conifer-dominated clearcuts with previous herbicide treatment to suppress competing deciduous species support mean hare densities of 1.63-2.43 hares/ha approximately 15 to 30 years after cutting (Litvaitis et al. 1985, Fuller and Harrison 2005, Newbury and Simon 2005, Homyack et al. 2006b; Table 1.1).

Clearcutting and partial harvesting are the most common methods of timber management in North America (U.S. Forest Service 2006, Canadian Council of Forest Ministers 2006). Clearcutting constituted 91.6% of harvests in Canada in 2003 (Canadian Council of Forest Ministers, 2006) and 38.3% of all timber harvests in the U.S.A. from the mid 1980’s to the mid 1990’s, with partial harvesting making up the other 61.7% (U.S. Forest Service 2006). Partial harvesting is a broad term used to describe many methods of removing overstory trees from a forest stand including selective cuts, shelterwood cuts, and uneven-aged forest management (Maine Forest Service 2005). Partial harvesting is associated with a wide range of vegetation conditions and hare densities in residual stands, however, all partially harvested stands studied supported lower hare densities than those found in regenerating clearcuts 20-30 years post harvest

(Fuller and Harrison 2005, Chapter 1). Understanding the mechanism of the relationship between vegetation characteristics and hare densities in partially harvested stands and regenerating conifer clearcuts will identify those vegetation variables important in describing the discrepancy in hare densities associated with these two harvest methods.

Regenerating stands as large as 5,000 ha are widespread throughout Maine as a result of past clearcutting in response to an outbreak of eastern spruce budworm throughout the Acadian forest during the late 1970's and early 1980's. Subsequently, the Maine Forest Practices Act of 1989 created disincentives on clearcuts larger than 20 acres (Maine Forest Service 2004); that law and three subsequent public referenda to limit clearcutting during the 1990's contributed to a shift in forest management in Maine away from clearcutting with increased prevalence of partial harvesting in its various forms (Seymour and Hunter 1992). In 2004, the average size of a clearcut in Maine was 20 acres and only three clearcuts were larger than 75 acres (Maine Forest Service 2005). In contrast, partial harvests comprised 95% of the 507,899 acres harvested in Maine in 2004 (Maine Forest Service 2005). This decreasing trend in clearcutting and concurrent increase in partial harvesting may affect many early successional species in Maine, including the snowshoe hare. Describing the relationship between specific vegetation characteristics and hare density across the two most prevalent types of harvesting practices could help to formulate management recommendations to increase habitat characteristics important to early successional species on harvested land in Maine.

Forest harvesting is the dominant land use practice in the mixed coniferous-deciduous Acadian forests of eastern North America (Seymour and Hunter 1992); therefore understanding relationships among forest management and potential keystone species (e.g., snowshoe hare) is instrumental to sustainable management of forests and biodiversity in the region. The objective of this study was to model the relationship between hare density and vegetation characteristics in regenerating conifer clearcuts 20-30 years after harvesting (i.e., “optimal conditions”) and across many partially harvested forest stands representing a wide range of vegetation conditions.

STUDY AREA

Stands were located in 11 townships in northern Maine and were distributed around two primary study sites near Clayton Lake and Telos Lake in northern Maine (Figure 2.1). Clayton Lake, Maine (69°31′, 46°36′) is located approximately 90 kilometers west of Ashland, ME. Mean temperature for this site was 36.3˚F with total precipitation of 39.40 inches in 2004 (National Oceanic & Atmospheric Administration 2005). Telos Lake (69°8′, 46°3′) is located northwest of Baxter State Park in north-central Maine. Forests across these 11 townships were managed for sawlog and pulpwood production by Clayton Lake Woodlands, Irving Woodlands, Seven Islands Land Co., the Maine Chapter of The Nature Conservancy, and Nexfor Paper.

The study area is part of the Acadian forest ecoregion, an ecological transition zone in the northeastern U.S.A. located between the temperate deciduous and eastern boreal forests (Seymour and Hunter 1992). Prior to European settlement, the predominant disturbance agents in this region were insect outbreaks, fire, and windstorms at relatively frequent return intervals, but at a much smaller scale compared to the disturbance regime of the boreal forest (Seymour and Hunter 1992). Currently, forest harvesting is the dominant disturbance agent in this region (Seymour and Hunter 1992). Large areas of

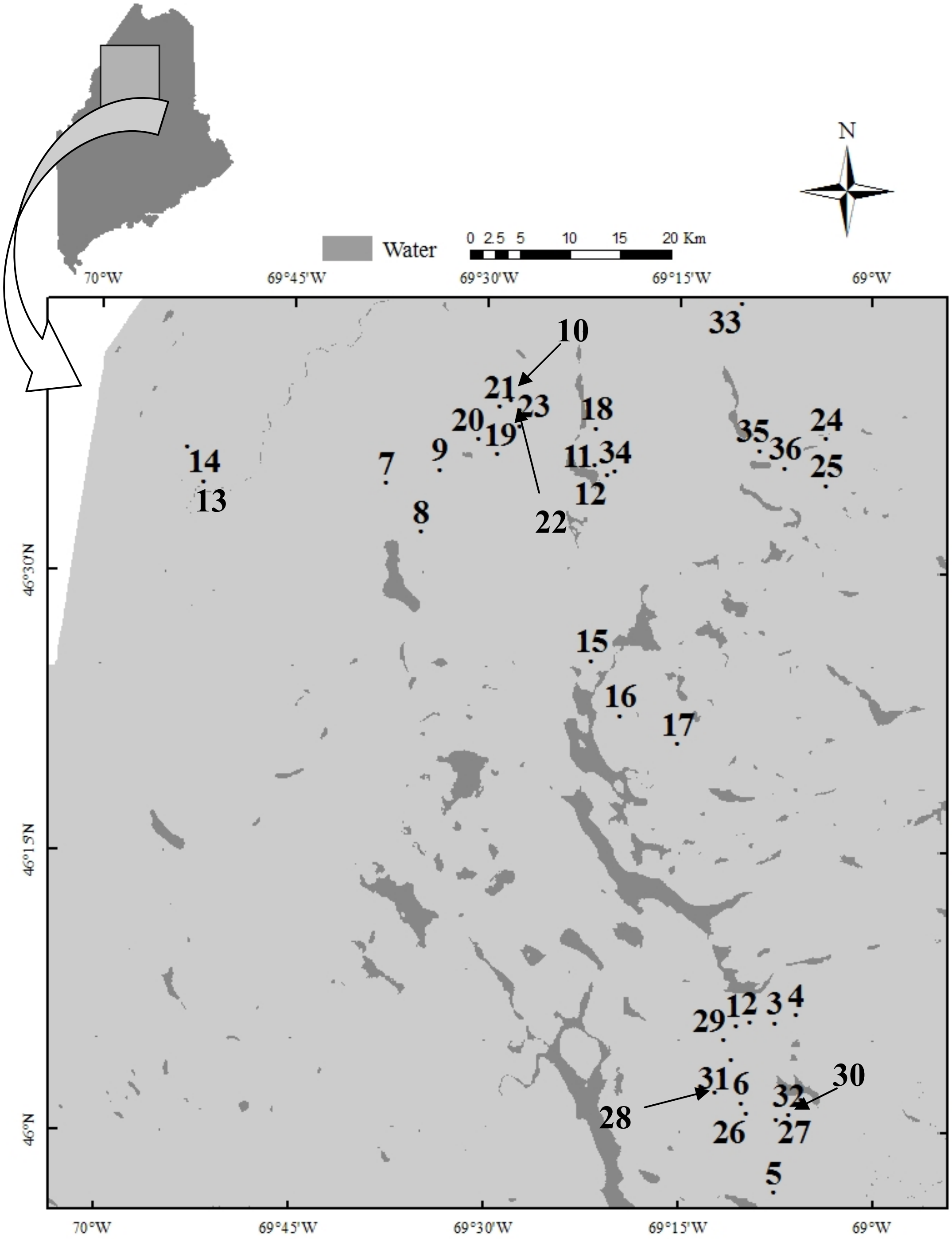


Figure 2.1. Locations of study stands where hare density was estimated and vegetation was measured in northern Maine, U.S.A. during 2005 and 2006. Stands in the northern part of the map are located in the Clayton Lake area and the Telos Lake area encompasses the southern stands. See Table 1.2 for a description of individual stands.

land were clearcut in the 1970's and 1980's and were subsequently sprayed with herbicides (primarily Glyphosate) to reduce deciduous competition. The resulting dense regenerating stands are dominated by balsam fir (*Abies balsamea*) and white (*Picea glauca*), red (*Picea rubens*), and black (*Picea mariana)* spruce (Seymour 1994). Species that comprise a minor component of these stands include eastern white pine (*Pinus strobus*), northern white cedar (*Thuja occidentalis*), and eastern hemlock (*Tsuga canadensis*). In areas with significant overstory disturbance, shade-intolerant species such as white birch (*Betula papyrifera*), aspen (*Populus spp.*), red maple (*Acer rubrum*), pin cherry (*Prunus pensylvanica*), and raspberries (*Rubus idaeus*) proliferate. Stands with a predominantly hardwood composition are dominated by sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*) and occur on better drained soils with higher site quality (Seymour 1992, 1994).

STAND HISTORIES

I studied 15 regenerating conifer clearcuts and 21 partially harvested stands in northern Maine. Partial harvest describes many methods of selectively removing trees from a forest stand; therefore, I chose to study partial harvest stands that varied widely in species composition and density of residual trees resulting from varying partial harvesting techniques employed by several land owners. This was necessary to understand the effects of vegetation on hares across the full range of ecological conditions occurring on the landscape. Thus, stands were not selected randomly, but were chosen to represent the wide range of structural variation and associated hare densities existing in the landscape.

Of the 21 partially harvested stands selected within the study areas, 11 were selectively harvested 8-12 years prior to pellet clearing in the fall of 2004 (Table 1.2). Six of these 11 stands were located near Telos Lake and five were located near Clayton Lake. The remaining ten partially harvested stands were distributed throughout the study area and ranged in year of harvest from 1985 to 2003 (Figure 2.1, Table 1.2). The 21 partially harvested stands had a median basal area of 28.9 m^2/ha (range 15.0-37.7 m^2/ha) and a median percent canopy closure of 79.5% (range 35.4-96.0%) when surveyed in 2005 (Appendix A).

The 15 regenerating conifer stands were selected to represent the current perception of optimal conditions for hares and had been harvested between 1974 and 1985 and were subsequently treated with an aerial application of herbicide (primarily Glyphosate) between 1982 and 1997 (Table 1.2). Of these 15 stands, seven were located near the Telos Lake site and eight were located near the Clayton Lake site (Figure 2.1). The 15 regenerating conifer stands had a median basal area of 43.2 m^2/ha (range 24.6-55.4 m^2/ha) and a median percent canopy closure of 79.0% (range 55.7-90.3%) in 2005 (Appendix A).

METHODS

PELLET COUNTS

A previous study in northern Maine demonstrated the reliability and efficiency of using pellet counts as a method for estimating snowshoe hare density in northern Maine across a range of hare densities from 0.16-3.2 hares/ha (Homyack et al. 2006a). I established 4, 360 m parallel transects that were separated by 65 meters and counted pellets in 5 m x 30 cm randomly-oriented rectangular plots located every 60 meters along

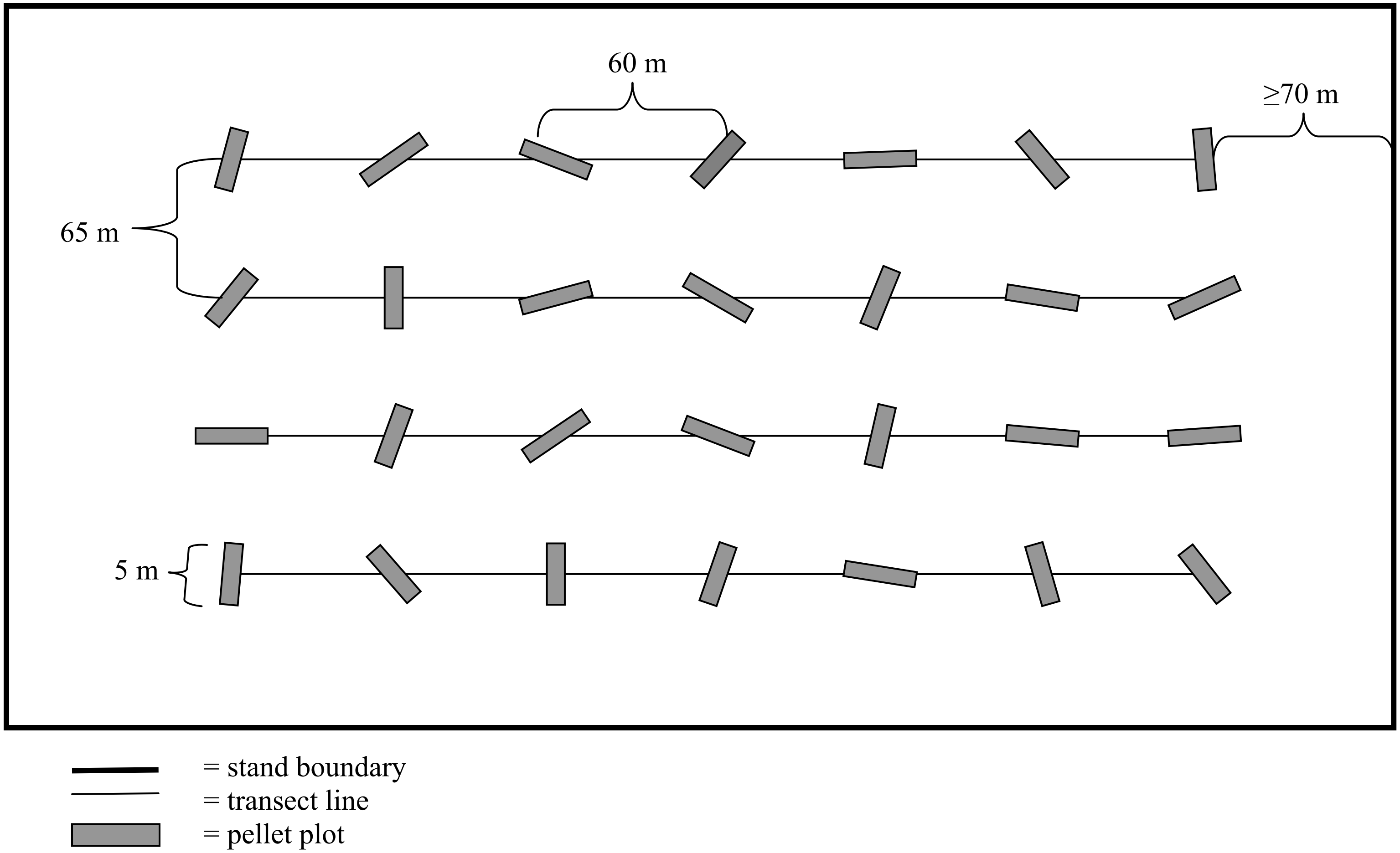


Figure 2.2. Layout of survey grid for snowshoe hare pellets in northern Maine, U.S.A., containing 28 randomly-oriented snowshoe hare pellet plots (of which, 20 were randomly selected for vegetation measurement) along 4, 360 m parallel transects. The total area surveyed was 7.02 ha (not including ≥ 70m buffer to edge of stand) for 26 forest stands. Ten additional stands were surveyed using alternative layouts, each with 28 pellet plots at least 60 meters apart and at least 70 meters from any edge. Figure not drawn to scale.

the transects for a total of 28 pellet plots per stand (Figure 2.2). The design of this sampling grid is similar to that used in Homyack et al. (2006a) with the exception that I increased the spacing between plots to reduce sampling effort per stand based on *post hoc* evaluation of Homyack's (2003) data, which indicated that 28 plots/stand would yield similar precision to 84 plots/stand (J. A. Homyack, unpublished data, University of Maine, Orono). The goal of this study was to understand the relationship between hare density and vegetation characteristics across a wide range of stand types; therefore, I gave up a small amount of precision in stand-scale hare density estimates in order to sample more stands. This strategy resulted in a change in standard error of only 3% relative to the mean estimated hare density for regenerating conifer clearcuts between the two studies (Table 1.1).

I used the standard 7.02 ha grid layout in 26 forest stands. The remaining 10 stands were irregularly shaped and could not accommodate the standard grid layout; therefore, I established irregular grids containing 28 plots in these stands, and attempted to conform to the standard grid layout as closely as possible in the spacing of transects and plots. All pellet plots regardless of grid layout were located at least 60 meters apart and at least 70 meters from any forest edge or road to reduce edge-effects (Fraver 1994). The mean size of home ranges for hares was 6.2 ha in Maine (Litvaitis 1984) and the mean size of 95% convex polygon home ranges for hares in Quebec was 12.8 ha (De Bellefeuille et al. 2001). The size of the study stands (7.02 ha) occurred between these two estimates; therefore, the stand was considered to be the unit of observation. Estimated mean hare densities for "optimal" stand conditions (i.e., regenerating clearcuts 20-30 years old) was 1.64 hares/ha (Fuller and Harrison 2005) and 1.83 hares/ha

(Homyack et al. 2006b) for two studies in northern Maine (Table 1.1). Thus, the size of study stands was large enough to potentially encompass up to 12-13 hares and pellet counts within these stands were considered to reflect stand-scale hare densities with little influence by individual behavior of hares.

The ends of each pellet plot were marked with two wooden stakes placed 5.0 m apart. A string was attached to each stake and a 30 cm dowel was centered along the string to delineate plot boundaries. I cleared pellets between September 18 and October 11, 2004 and then counted pellets between May 13 and June 16, 2005 to estimate hare density for the 2004-2005 leaf-off season. Pellets were counted a second time between September 17 and October 6, 2005 to estimate hare density for the 2005 leaf-on season. I counted pellets again between May 16 and June 4 to obtain estimates for the 2005-2006 leaf-off season.

I divided the pellet count at each plot by the number of days that had elapsed since the plot was cleared and by the size of the pellet plot to obtain pellets/ha/day. I then converted this number to pellets/ha/mo by multiplying by the average number of days in each month since clearing. I used a regression equation developed for the Acadian forest (Homyack et al. 2006a) to estimate hare density from pellet counts:

$\text{hares/ha} = 0.15979 + 0.00010(\text{pellets/ha/month})$.

I tested bias in pellet counts across the 3 observers who inventoried the majority of pellet plots; counts on the same plots were not significantly different among observers (Appendix C).

VEGETATION MEASUREMENTS

In each stand where pellets were counted, I measured vegetation characteristics thought to be associated with hare density between June 23 and July 27, 2005. I randomly selected 20 of the 28 pellet plots in each stand to describe overall vegetation characteristics. To ensure that similar numbers of total stems were sampled in each stand, $10m^2$ circular plots were used in regenerating conifer stands and $20m^2$ circular plots were used in partially harvested stands. To reduce sampling time, I used $10m^2$ plots at 6-8 of the vegetation plots in 2 partial harvest stands because they had total stem densities >10,000 stems/ha.

I measured 16 vegetation characteristics at each vegetation plot (Table 2.1). Coniferous, deciduous, and dead trees (≥7.6 cm dbh) that were at least half in the plot were tallied and diameter was measured at 1.4 m above ground. Additionally, I counted logs of decay classes 1 and 2 (Fraver et al. 2004) at least 1 meter from the plot edge (≥7.6cm in diameter). I also counted stumps of decay classes 1 and 2 (Fraver et al. 2004), measured their diameter, and used the mean number of stumps per stand and the mean diameter of stumps to calculate the mean basal area removed from the stand as:

$$\text{BAR/ha} = \pi * (1/2 * \text{mean stump diameter})^2 * \text{mean number of stumps/stand}.$$

Conifer, deciduous, and dead stems (< 7.6cm dbh) were counted at > 1.5m height. I used these values to calculate stem cover units as described by Litvaitis et al. (1985):

$$\text{SCU} = 3 * \text{conifer stems} + \text{deciduous stems}.$$

In Maine, hare densities within a range of 0.15-1.50 hares/ha have been highly correlated with SCU at the scale of the forest stand (Litvaitis et al. 1985, Long 1995) and on 70 m x 70 m sampling grids (Fuller 2006).

Table 2.1. Descriptions and transformation methods for 16 vegetation variables measured in 36 stands in northern Maine, U.S.A. during the leaf-on season, 2005.

Vegetation variable	Description	Units	Transformation
BA	Basal area measured with a $2m^2$/ha wedge prism and includes live and dead trees	m^2/ha	None
BAR	Basal area removed/ha = B*(½*mean stump diameter)*mean number of stumps/stand	m^2/ha	None
C	Conifer stems >1.5m high/ha	stems/ha	Square root
CC	Percent canopy closure measured with a spherical densiometer at 1m above ground	percent	Arcsine
CT	Number of conifer trees/ha more than ½ inside the plot	trees/ha	Square root
D	Dead stems >1.5m high/ha	stems/ha	Logarithm
DBH	Average diameter of all trees measured at 1.4m above ground	cm	None
DEC	Deciduous stems>1.5m high/ha	stems/ha	Logarithm
DECT	Number of deciduous trees/ha more than ½ inside the plot	trees/ha	Square root
DT	Number of dead trees/ha more than ½ inside the plot	trees/ha	Square root
LOGS	Number of logs/ha more than 1m inside the plot of decay class ≥2	logs/ha	None
S	Number of stumps/ha more than ½ inside the plot of decay class ≥2	stumps/ha	Square root
SCU	(3* the number of conifer stems >1.5m high/ha)+the number of deciduous stems >1.5m high/ha	stems/ha	Logarithm
SD	Mean diameter of stumps more than ½ inside the plot of decay class ≥2	cm	Logarithm
T	Conifer+deciduous+dead stems >1.5m high/ha	stems/ha	None
VO	Visual obstruction measured as the distance at which ≥25% of at least 25% of the bands over 1.0m on a cover pole were obscured by vegetation	m	Logarithm

I measured total basal area using a 2m^2/ha wedge (Avery and Burkhart 1994) prism and percent overhead canopy closure using a spherical densiometer at 1 m height (Lemmon 1956). I measured visual obstruction using a cover pole with alternating red and white 10 cm bands as a continuous variable equal to the distance at which ≥ 25% of at least 25% of the bands over 1.0 m were obscured by vegetation (Griffith and Youtie 1988, Homyack et al. 2004).

A PRIORI MODELING

I developed a set of 21 *a priori* candidate models to statistically evaluate the relationship between vegetation variables and pellet counts. I transformed all independent variables that did not appear to be normally distributed in dot density plots (Table 2.1). Of the original 16 vegetation variables, I selected 9 for consideration in *a priori* models. I used a correlation matrix between vegetation variables (Table 2.2) and Principal Components Analysis (PCA; see Chapter 1) of the 16 vegetation variables to identify those that were highly correlated or explained the same variation within the dataset (see Chapter 1 for PCA results). Correlation coefficients among descriptor variables were ≤ |0.74| (Table 2.2); therefore, all variables were retained for subsequent modeling (Burnham and Anderson 2002). I wished to evaluate the relationship between vegetation and pellet counts for both the leaf-off and leaf-on seasons; therefore, I compared these 21 *a priori* candidate models using both leaf-off pellet count and leaf-on pellet count as response variables. There were no apparent differences in log transformed pellet densities (non-parametric sign test) between the 2004-2005 and the 2005-2006 leaf-off seasons ($P = 0.13$); therefore, I averaged the two years to produce one response variable for the leaf-off season for each stand.

Table 2.2. Correlation matrix among 9 vegetation variables measured in northern Maine, U.S.A. during the leaf-on season, 2005 and selected for use in a candidate set of 21 *a priori* Poisson regression models evaluated using Akaike's Information Criterion (AIC). See Table 2.1 for a description of variables.

	Variable								
Variable	C	DEC	D	T	SCU	BA	LOGS	BAR	CC
C	1								
DEC	-0.57	1							
D	0.25	-0.14	1						
T	0.31	0.11	0.56	1					
SCU	0.66	-0.35	0.33	0.74	1				
BA	0.32	-0.21	0.76	0.40	0.33	1			
LOGS	-0.12	0.29	-0.16	0.09	-0.06	-0.35	1		
BAR	-0.24	0.23	0.19	0.24	-0.05	-0.04	-0.02	1	
CC	-0.33	0.38	0.43	0.23	-0.16	0.56	-0.18	0.12	1

When developing my candidate models, I based several candidate models on findings from previous research in Maine (Litvaitis et al. 1985, Long 1995, Fuller 2006) to evaluate whether these variables best explained data from my study. Based on previous research, I made the assumption that conifer stem density is an important factor in the relationship between vegetation and pellet counts. Thus, I included conifer stem density in many candidate models. I also developed several candidate models with variables that had not been previously studied and which could potentially better describe pellet densities. I hypothesized that above a certain threshold of stem densities (i.e. ideal cover for hares), hare densities in these stands may begin to level off in a non-linear fashion. Thus, I also developed a model to test for a density-dependent response of hares in relation to conifer stem densities by including a C*C term. My response variable was pellet count, which is count data. Count data are assumed to be non-normally distributed; therefore, I assumed a Poisson distribution and used Poisson regression to model the relationship between pellet counts and vegetation variables (Kutner et al. 2005). The Poisson regression model assumes the error terms are independent and normally distributed with constant variance and that no outliers exist in the dataset. To test these assumptions for the top models for each response variable, I plotted the residuals against the estimated values. I also created normal probability plots and correlated the residuals against their expected values under normality. I tested for constant variance using a Brown-Forsythe test.

Akaike's Information Criterion (AIC) is a method of model selection based on a maximum likelihood method that balances model fit and parsimony to select the best model from a set of candidate models (Burnham and Anderson 2002). AIC seeks to minimize the Kullback-Leibler distance (representing the amount of information “lost” or unexplained) while penalizing models for each parameter used to achieve this goal. I used the AIC equation corrected for small sample size because in this study, $n/K < 40$ (Burnham and Anderson 2002):

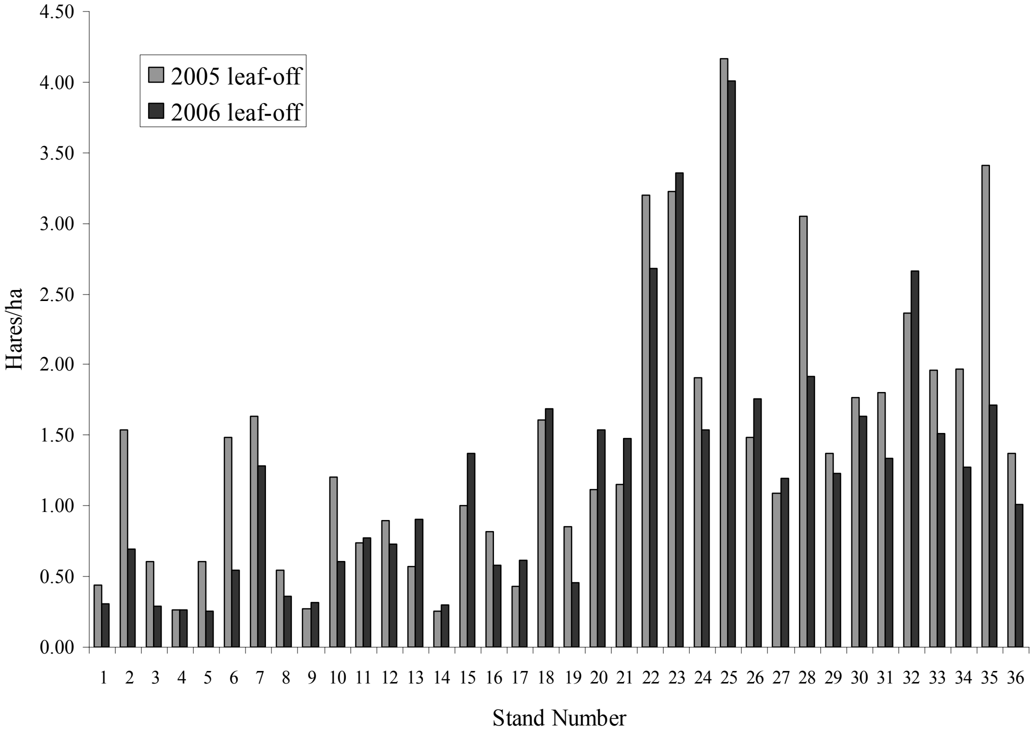
$$\text{AIC}_c = -2\log(L(2)) + 2K + ((2K(K + 1))/(n-K-1)).$$

The AIC model selection process emphasizes the necessity of *a priori* model development instead of comparing all possible models in a “data dredging” exercise (Anderson and Burnham 2002, Burnham and Anderson 2002). In addition, AIC can only select the best model from the set of candidate models; it has no way to associate the best model with “truth.” I therefore used the Akaike weights (w_i) as a measure of the weight of evidence in favor of the best model (Burnham and Anderson 2004):

$$w_i = \exp(-)_i/2)/(\textstyle\sum_{r=1} \exp(-)_i/2))$$

I also used the r^2 value to assess the ability of the best model to explain the variation in the dataset (Stephens et al. 2005).

For each season, I tested the validity of the global model using the log-likelihood ratio of the global model to the constant model. This tests the difference in loss values between the global and the constant models as a ratio subject to a chi-square distribution. A *P*-value greater than 0.05 suggests that the global model is unable to fit the data better than a null model. For both the combined leaf-off seasons and the leaf-on season, dot density plots showed one stand (#25, CLREG4) having much higher pellet densities than the other 35 stands (Figure 2.3). This stand had the highest residual value in the data set (17.6) and it is possible that this data point could have exerted significant leverage on the resulting models. Thus, I analyzed all models both with and without this datum and found



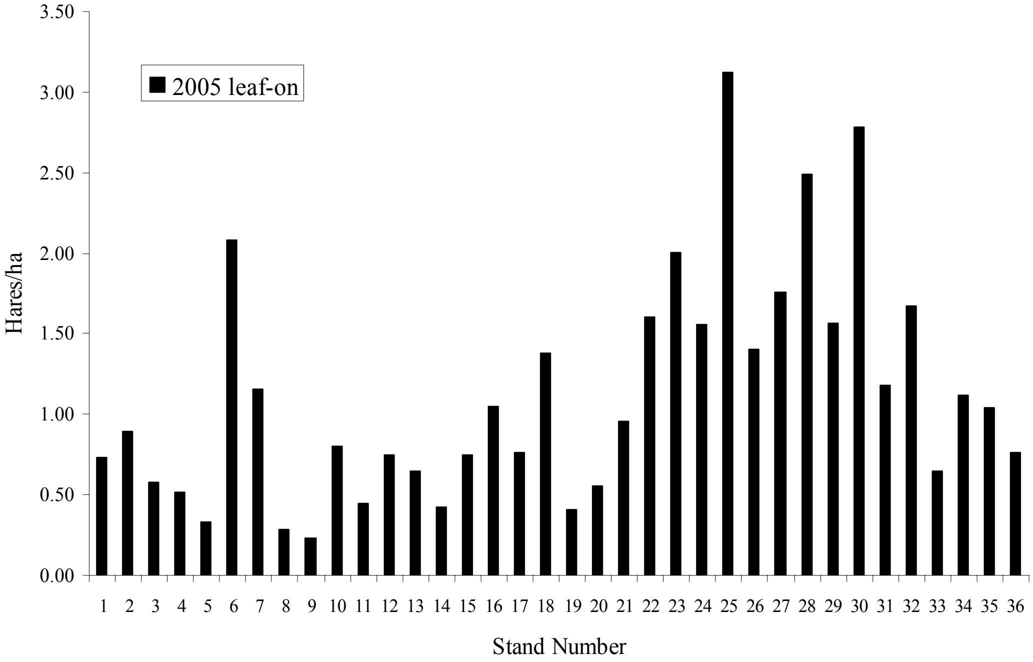


Figure 2.3. Estimated densities of snowshoe hares for 21 partial harvests (stands 1-21) and 15 regenerating conifer clearcuts (stands 22-36) in northern Maine, U.S.A. during the leaf-off (October–April) seasons for 2005 and 2006 and the leaf-on (May-September) season, 2005. See Table 1.2 for a description of numbered stands.

that this one value did have a significant effect on the AIC results for the leaf-on season. To avoid spurious conclusions driven by a single outlier, I excluded stand #25 (Figure 2.3) from further analyses and modeled based on the remaining 35 stands.

POST HOC MODELING

I wished to develop a predictive model for leaf-off pellet density based on the results of the model selection. The global model was equivalent to the C+BAR+LOGS model, suggesting that some combination of variables is present in the global model that was not tested in the original candidate set of *a priori* models that may be better able to explain the variation in the data set. In an attempt to better understand the relationships between the vegetation data and pellet densities, I used a multiple linear regression (MLR) analysis to relate principal components identified in previous Principal Components Analysis (PCA) representing 16 vegetation characteristics (Chapter 1) to log transformed pellet densities. For the PCA conducted among partial harvest stands, only PC2 was related to log transformed pellet densities for the combined leaf-off seasons in the form:

Log(pellets/ha/day) = 5.086 + 0.171*PC2 ($F = 3.685$, df = 19, $P = 0.070$, $r^2 = 0.162$).

This principal component represents understory density and the variables with the highest component loadings of the 16 were basal area (BA), canopy closure (CC), dead stem density (D) and total stem density (T), all of which had positive component loadings (Table 1.4).

I used this information to develop a set of 14 *post hoc* models to test the ability of BA, CC, D, and T to explain pellet counts as secondary variables. The *a priori* model selection identified C, BAR, and LOGS as important in explaining the variation in pellet counts so BA, CC, D, and T were used in combination with the C, BAR, and LOGS variables. A previous study identified two variables as important in describing pellet density at the sub-stand scale: SCU (positive association) and CC (negative association) (Fuller 2006). I wished to test the applicability of this model to this data set and I included a SCU+CC model in the *post hoc* analysis. I also included the top two models from the *a priori* selection for reference, in addition to including a model with only BAR and LOGS to evaluate the importance of C in the top model.

RESULTS

Thirty-six stands (14 regenerating conifer clearcuts and 21 partial harvests) were surveyed for hare density and vegetation characteristics resulting in 1,064 pellet plots surveyed during the leaf-off seasons, 2004-2005 and 2005-2006; and during the leaf-on season, 2005. A total of 720 vegetation plots were surveyed for 16 vegetation characteristics during the leaf-on season, 2005 (Appendix A). After removal of the outlying value, estimated hare densities ranged from 0.25-3.22 hares/ha for the 2004-2005 leaf-off season, 0.23-2.01 hares/ha for the 2005 leaf-on season, and 0.26-3.35 hares/ha for the 2005-2006 leaf-off season (Figure 2.3, Appendix D).

A PRIORI MODELING

For the 2004-2005 and 2005-2006 combined leaf-off seasons, two of the 21 *a priori* candidate models had competitive (i.e.,)AIC$_c$ value < 2) AIC$_c$ values: the global model and the C+BAR+LOGS model (Table 2.3), indicating that the top two models were essentially equivalent (Burnham and Anderson 2002). The C+BAR+LOGS model

Table 2.3. Akaike Information Criterion (AIC) model selection results for 21 *a priori* candidate models compared using Poisson regression to describe the relationship between 9 vegetation variables and pellet counts conducted in 35 stands in northern Maine, U.S.A. for the combined leaf-off seasons, 2004-2005 and 2005-2006. K = number of estimable parameters, Loss = the maximized log-likelihood, AIC$_c$ = AIC value corrected for small sample size, w_i = Akaike weight. See Table 2.1 for a description of vegetation variables.

Model	K	Loss	AIC$_c$	)AIC$_c$	w_i
C+D+C^2+CC+BA+BAR+LOGS+DEC+T+SCU	12	99.18	236.54	0.0	0.65
C+BAR+LOGS	5	112.88	237.83	1.3	0.34
C+CC+LOGS	5	117.31	246.69	10.2	0.00
C+LOGS	4	118.88	247.10	10.6	0.00
C+D	4	128.40	266.12	29.6	0.00
C+BAR	4	128.45	266.24	29.7	0.00
C+CC+D	5	128.35	268.77	32.2	0.00
C+BA	4	130.38	270.09	33.6	0.00
C+CC+BA	5	130.23	272.53	36.0	0.00
C+C^2	4	133.94	277.22	40.7	0.00
C+CC	4	134.76	278.84	42.3	0.00
C+DEC	4	134.99	279.31	42.8	0.00
C	3	138.67	284.11	47.6	0.00
SCU	3	147.36	301.50	65.0	0.00
DEC	3	156.70	320.18	83.6	0.00
D	3	159.17	325.11	88.6	0.00
BA	3	164.07	334.91	98.4	0.00
LOGS	3	164.71	336.20	99.7	0.00
T	3	178.90	364.56	128.0	0.00
BAR	3	183.61	373.99	137.5	0.00
CONSTANT	2	186.02	376.41	139.9	0.00
CC	3	185.97	378.71	142.2	0.00

was therefore accepted as the best model based on its relative simplicity, and can be expressed as:

Pellets/ha/mo = 201,667*[Exp(-3.892+0.0125* $C^{1/2}$+0.0189*BAR-0.00045*LOGS)].

The Akaike weight for the global model was 0.65 with the C+BAR+LOGS model receiving 34% of the weight of evidence as the best model (Table 2.3). Sixty-seven percent of the variation in hare pellet density across 35 stands was accounted for by the density of conifer stems (+), basal area removed in previous harvests (+), and the density of logs (-).

The AIC_c values for the leaf-on season were lowest for the C+D model and this model received 44% of the weight of evidence supporting it as the best model (Table 2.4). The C+D model can be expressed as:

Pellets/ha/mo = 205,000*[Exp(-5.455 + 0.0052* $C^{1/2}$ + 0.2475*D)].

The best models for each season (C+BAR+LOGS for leaf-off and C+D for leaf-on) met the assumptions of the Poisson regression model. Residuals were normally distributed at $\alpha = 0.10$ with correlation coefficients between residuals and their expected values under normality of 0.983 for leaf-off counts and 0.979 for leaf-on counts. The Brown-Forsythe tests did not indicate non-constant variance in the error terms ($t = 0.49$, df = 33, $P = 0.63$ for leaf-off counts and $t = -0.83$, df = 33, $P = 0.41$ for leaf-on counts). The log-likelihood ratio test validated the global model for the leaf-off season ($P < 0.001$), but not the leaf-on season ($P = 0.16$), indicating that the leaf-on global model did not fit the data better than the constant-only model. Further, the r^2 value for the top leaf-on season model was only 0.173, indicating poor fit and predictive capability.

Table 2.4 Akaike Information Criterion (AIC) model selection results for 21 *a priori* candidate models compared using Poisson regression to describe the relationship between 9 vegetation variables and pellet counts conducted in 36 stands in northern Maine, U.S.A. for the leaf-on season, 2005. K = number of estimable parameters, Loss = the maximized log-likelihood, AIC$_c$ = AIC value corrected for small sample size, w_i = Akaike weight. See Table 2.1 for a description of vegetation variables.

Model	K	Loss	AIC$_c$	)AIC$_c$	w_i
C+D	4	84.54	178.41	0.0	0.44
C+CC+D	5	84.47	181.01	2.6	0.12
C+BAR	4	86.06	181.45	3.0	0.10
C+BA	4	86.14	181.61	3.2	0.09
D	3	87.86	182.50	4.1	0.06
C+BAR+LOGS	5	85.30	182.66	4.3	0.05
C+CC	4	86.93	183.19	4.8	0.04
C+C^2	4	87.22	183.77	5.4	0.03
C+CC+BA	5	86.04	184.14	5.7	0.02
C+CC+LOGS	5	86.39	184.84	6.4	0.02
C	3	89.57	185.92	7.5	0.01
C+LOGS	4	88.42	186.17	7.8	0.01
CONSTANT	2	91.28	186.93	8.5	0.01
BA	3	90.22	187.21	8.8	0.01
C+DEC	4	89.22	187.77	9.4	0.00
SCU	3	90.88	188.54	10.1	0.00
C+D+C^2+CC+BA+BAR+LOGS+DEC+T+SCU	12	77.03	192.24	13.8	0.00
DEC	3	92.67	192.12	13.7	0.00
T	3	95.17	197.11	18.7	0.00
LOGS	3	95.71	198.19	19.8	0.00
BAR	3	96.17	199.11	20.7	0.00
CC	3	97.05	200.87	22.5	0.00

Table 2.5. Akaike Information Criterion (AIC) model selection results for 14 *post hoc* candidate models compared using Poisson regression to describe the relationship between 9 vegetation variables and pellet counts conducted in 35 stands in northern Maine, U.S.A. for the combined leaf-off seasons, 2004-2005 and 2005-2006. K = number of estimable parameters, Loss = the maximized log-likelihood, AIC$_c$ = AIC value corrected for small sample size, w_i = Akaike weight. See Table 2.1 for a description of vegetation variables.

Model	K	Loss	AIC$_c$	)AIC$_c$	w$_i$
C+BAR+LOGS+D+T	7	101.12	220.4	0.0	0.97
C+LOGS+D+T	6	106.80	228.6	8.2	0.02
C+BAR+D+T	6	106.96	228.9	8.5	0.01
C+BAR+LOGS+D	6	109.85	234.7	14.3	0.00
C+BAR+LOGS+T	6	110.30	235.6	15.2	0.00
C+D+C^2+CC+BA+BAR+LOGS+DEC+T+SCU	12	99.18	236.5	16.2	0.00
C+BAR+LOGS+BA	6	111.30	237.6	17.2	0.00
C+BAR+LOGS	5	112.88	237.8	17.5	0.00
C+BAR+LOGS+CC	6	112.43	239.9	19.5	0.00
SCU+BAR+LOGS	5	121.24	254.6	34.2	0.00
C+BAR+T	5	121.51	255.1	34.7	0.00
C+BAR+D	5	123.49	259.1	38.7	0.00
SCU+CC	4	146.41	302.2	81.8	0.00
BAR+LOGS	4	162.55	334.4	114.0	0.00

POST HOC MODELING

The results of the *post hoc* modeling identified C+BAR+LOGS+D+T as the best model with 97% of the support for this model (Table 2.5) The C+BAR+LOGS+D+T model can be expressed as:

$\text{Pellets/ha/mo} = 201{,}667*[\text{Exp}(-5.459 + 0.0150*C^{1/2} + 0.0203*BAR - 0.00029*LOGS + 0.2575*D - 0.000049*T)]$.

The r^2 value for this model was 0.764.

The C+BAR+LOGS+D+T model met the assumptions of the Poisson regression model. A plot of the residuals against the predicted values did not indicate that outliers were present in the data. Residuals were normally distributed at $\alpha = 0.10$ with correlation coefficients between residuals and their expected values under normality of 0.983. The Brown-Forsythe test did not indicate non-constant variance in the error terms ($t = -0.40$, df = 33, $P = 0.69$).

DISCUSSION

Results of the model selection process indicated that conifer stem density (C) was the most important variable describing the relationship between pellet counts and vegetation at the stand-scale in the Acadian forest. If the Akaike weights are summed over all models in which a given variable appears to provide a measure of variable importance (Burnham and Anderson 2002), C receives a value of 0.99 for the leaf-off models and 0.93 for the leaf-on models. BAR and LOGS also receive values of 0.99, but other stem density variables such as SCU, T, D, and DEC receive no more than 0.65 for variable importance in either datasets. As a single variable model, C outperformed all other variables in the leaf-off data and all but D in the leaf-on data. Conifer stem density is directly related to understory cover during the critical leaf-off season and the importance of C in these models is not surprising given the large number of previous studies demonstrating the close association of hares and dense understory characteristics (Converse 1981, Orr and Dodds 1982, Pietz and Tester 1983, O'Donoghue 1983, Monthey 1986, Parker 1986, Scott and Yahner 1989, Homyack 2006b). Although the mechanisms of this relationship have not been fully studied, habitat quality for hares is hypothesized to be related to the escape cover and thermal insulation provided by dense understory conditions (Litvaitis et al. 1985). Because conifer stems retain their needles in the winter, they likely provide superior concealment, escape cover and thermal cover for hares over deciduous stems during the leaf-off season.

The importance of conifer stem density to describing the variance in hare densities among these 35 stands may be related to the difference in conifer stem densities between partially harvested stands and regenerating conifer clearcuts (Figure 1.4). Regenerating conifer clearcuts have generally higher conifer stem densities than partially harvested stands (Figures 1.4, 2.4). The median conifer stem density for regenerating clearcuts was 11,850 stems/ha (range: 4,100-25,350 stems/ha), whereas the median for partially harvested stems was 3,350 (range: 0-24,825) (Figure 2.4, Appendix A). Three partially harvested stands (15, 16, and 18) had conifer stem densities higher than the median for regenerating clearcuts, but these stands still supported a hare density lower than the mean minus one standard error for regenerating clearcut stands (2.10 hares/ha, SE = 0.22) during the combined 2005-2006 leaf-off season (Appendices A and D). The relationship between vegetation and hare density is multivariate; conifer stem density functions with BAR and LOGS to explain the variance in hare densities. Although

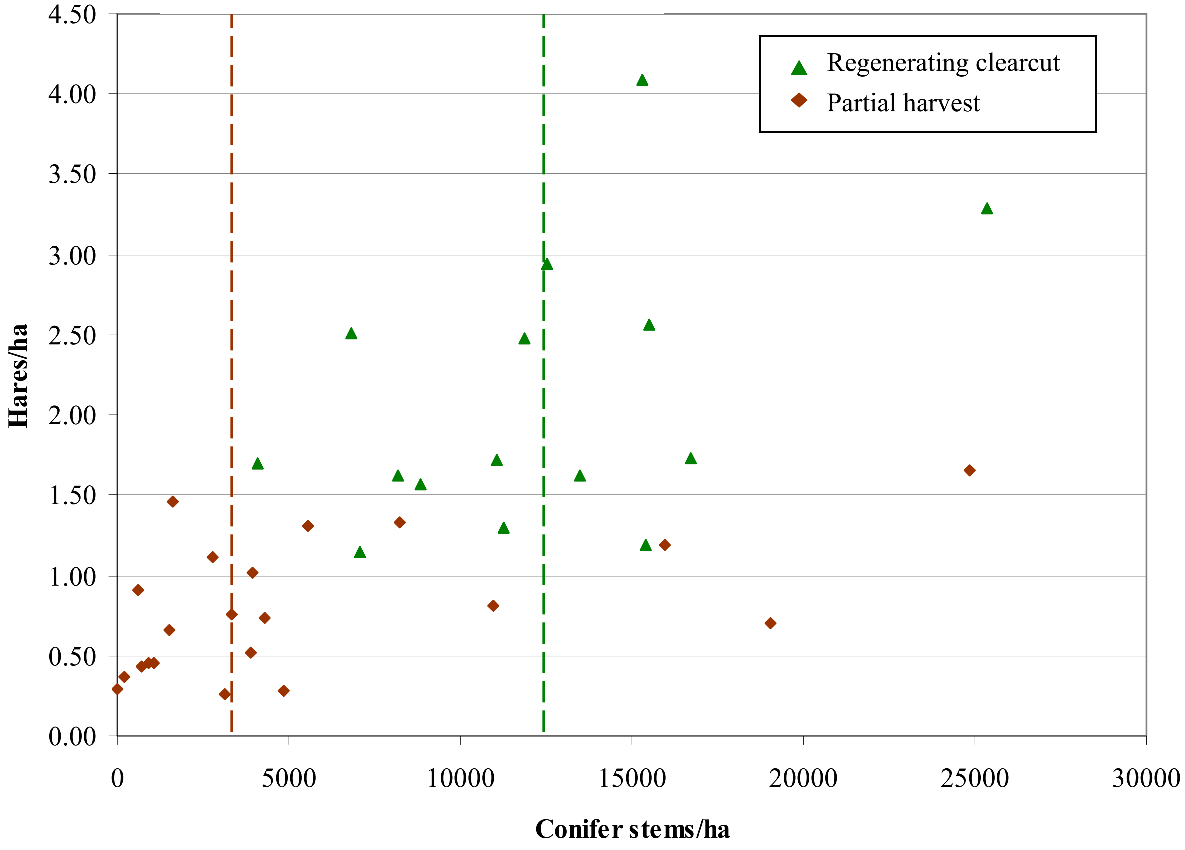


Figure 2.4. Conifer stem densities (measured during the leaf-on season, 2005) and snowshoe hare densities (combined for the 2005 and 2006 leaf-off seasons) in 15 regenerating clearcuts and 21 partially harvested stands surveyed in northern Maine, U.S.A. Dashed vertical lines represent the median conifer stem density for partially harvested stands (left, 3350 stems/ha) and regenerating clearcuts (right, 11,850 stems/ha).

conifer stem density was the most important variable in this model, we cannot assume that higher stem densities will always lead to higher hare densities and this variable should not be used alone to predict stand-scale densities of hares. Further, this relationship was modeled across partially harvested stands and regenerating clearcuts with hare densities ranging from 0.30-3.29 hares/ha for the 2005-2006 combined leaf-off seasons. Hence, within either of these two harvesting types, the density of conifer stems may be insufficient to explain the observed variance in hare densities and should not be used in a predictive sense.

Basal area removed (BAR) during past harvesting activities and log density (LOG) were important secondary variables in describing pellet counts when added to conifer stem density, although the coefficients for these two variables were not significantly different from zero for either the leaf-off or leaf-on seasons (based on Wald 95% confidence intervals). When compared to the C+BAR+LOGS model, the)AIC$_c$ is 9.3 for the C+LOGS model and 28.4 for the C+BAR model for the combined leaf-off season, indicating that the addition of both the BAR and the LOGS variables to the model substantially improved the fit (Table 2.3). The positive relationship of BAR with pellet counts indicates that a larger volume of wood harvested from the stand is associated with higher hare densities. More wood harvested in the past may result in an increased amount of sunlight reaching the understory, thereby allowing a denser understory to develop. This is not a cause and effect relationship, however, and the volume of wood removed from a stand may also be influenced by pre-existing site conditions that allowed for the growth of more crop trees in the stand. Further, biases may be associated with the measurement of the BAR variable because of different decay rates of different tree species and because clearcut stands were harvested sooner and may have experienced more stump decay. I measured only sound stumps and coniferous stumps may have decayed faster than deciduous stumps, which could potentially underestimate the BAR in conifer-dominated stands such as regenerating clearcuts and clearcuts that had regenerated longer at the time of measurement.

The coefficient for the LOGS variable was negative, indicating that a higher log density is related to a lower pellet count in the stand. The log density in a stand may be related to recent removal of overstory trees and subsequent blowdown of residual trees after harvest. Thus, LOGS may act as a surrogate for recent harvesting. Two examples of stands experiencing recent harvest were recent partial harvests (Fuller and Harrison 2005) and recent clearcuts (De Bellefeuille et al. 2001); both supported low hare densities in the Acadian forest.

Secondary variables such as DEC, BA and CC resulted in lower AIC$_c$ values when added to C, although not to the extent of the BAR and LOGS variables. This can be interpreted to mean that these variables failed to explain significant variance not already explained by BAR and LOGS in the model. The density-dependent function for conifer stems (in the form C+C^2) outperformed the C model ()AIC$_c$ = 6.9 between C and C+C^2), suggesting that conifer stem density may exhibit a density-dependent response in its ability to support hares. Although not statistically significant, the coefficient for the C^2 was negative, suggesting that as conifer stem density increases, hare density may increase in a non-linear fashion (Figure 2.4).

The log-likelihood ratio test failed to validate the fit of the global model for the leaf-on season, suggesting that these ten variables were unable to fit the data better than the null model. The C+D model had a poor fit (low r^2 value) and neither of the two variables in this model was statistically significant (using a 95% Wald confidence interval). The weaker relationship between vegetation and pellet density during the leaf-on season suggests that hares may expand their habitat use to a wider range of understory conditions when deciduous leaves and herbaceous vegetation provide both cover and food during this season. This would support previous studies that have documented a shift in habitat use by hares between the leaf-off and leaf-on seasons (Wolff 1980, O'Donoghue 1983, Parker et al. 1986, Litvaitis et al. 1985).

The results of the *post hoc* analyses identified two additional secondary variables (D and T) as important in describing the relationship between vegetation and pellet density for the leaf-off season. The r^2 for the C+BAR+LOGS+D+T model was 0.76 versus 0.38 for the C model without the secondary variables, thereby doubling the explanatory power. Dead stem density (D) was positively associated with pellet density, likely because dead stems are indicative of self-thinning conditions associated with thick regenerating conifer conditions. Total stem density (T) was negatively associated with pellet counts, possibly because this composite variable includes deciduous stem density, which by itself is negatively related to pellet counts.

The addition of D and T to the C+BAR+LOGS model developed in our *a priori* modeling resulted in a lower AIC_c value based on *post-hoc* models, but within the C+BAR+LOGS+D+T model, only the C variable was statistically significant (using Wald 95% confidence intervals). Although the secondary variables improved the fit of the model, the relationship between pellet density and these variables may be more tenuous than the relationship between conifer stem density and pellet density. The large

)AIC$_c$ value for the BAR+LOGS model compared with the C+BAR+LOGS model in the *post hoc* analysis (96.5) is strong evidence affirming the dominant contribution of conifer stem density (C) to explaining the variance in this dataset.

The SCU+CC model did not perform well in the *post hoc* modeling and had a)AIC$_c$ value of 18.9 when compared with the C model (Tables 2.3, 2.5). The SCU variable had a statistically significant positive association with pellet counts, but the CC variable was not significant in that model and was positively associated with pellet densities. In contrast, CC was negatively associated with pellet densities at the sub-stand scale (Fuller 2006). These findings suggest that hares may respond differently to canopy closure at the stand and sub-stand scales. Given the past importance of SCU in describing hare densities in Maine (Litvaitis et al. 1985, Long 1995, Fuller 2006), it is important to note that conifer stem density outperformed SCU in both the *a priori* and *post hoc* model selection processes (Tables 2.3, 2.5). This is understandable given that SCU is a composite variable developed in a region with different understory composition than northern Maine. In eastern Maine, where much of the data for the 1985 study was collected, hare density was positively associated with deciduous stem densities (Litvaitis et al. 1985). In this study, however, deciduous stem density had a negative relationship with pellet counts. It is therefore not surprising that a composite variable that combined conifer and deciduous stems would perform poorer than a variable with only conifer stems or with conifer stems and deciduous stems as separate variables ()AIC$_c$ = 17.4 between C and SCU models, Table 2.3). Thus, I conclude that conifer stems are more closely related to stand-scale hare densities in northern Maine than are stem cover units.

The model with the highest r^2 value identified in these analyses was the C+BAR+LOGS+D+T model, which explained 76% of the variance in the combined leaf-off pellet counts. The C+BAR+LOGS model described 67% of the variance in the data and although the C+BAR+LOGS+D+T model described slightly more variance (9%), the previous model contained two fewer variables. The cost and energy required to measure these two variables (D and T) in the field may not be worth the 9% improvement in model fit over the 3 variable model. I therefore conclude that the C+BAR+LOGS model is the most efficient model for predicting hare densities in northern Maine.

Models were constructed using data for only 35 stands and data were not reserved to test the predictive ability of the model. Because the vegetation characteristics varied so widely across these 35 stands, the modeling process likely identified the variables that explain the broad-scale relationships between hare density and vegetation; therefore, my best model is unlikely to accurately predict small differences in hare densities within a group of stands with similar vegetation characteristics. Additionally, the 35 stands studied were dispersed throughout the landscape of northern Maine (Figure 2.1), and the modeling did not directly address variation in hare densities due to potential landscape and metapopulation processes that may affect the performance of the predictive model.

The discrepancy in hare densities observed between regenerating clearcuts and partially harvested stands is described primarily by differences in conifer stem density between these two harvest types. Thus, we cannot conclude that this relationship holds within either of these harvest types and land managers should not assume that increasing conifer stem densities within types of partial harvests will always be associated with higher hare densities.

CONCLUSIONS

Modeling results identified a three variable model that explained 67% of the variance in stand-scale densities of snowshoe hares during the leaf-off season; models inadequately described the relationship between vegetation and pellet density for the leaf-on season. At the stand-scale in northern Maine, hare densities are associated with conifer stem density (+), basal area removed (+), and log density (-) during the limiting leaf-off season. Conifer stem density was the most important variable of those studied in describing the variation in pellet counts in this dataset and likely describes the differences in hare densities observed between regenerating clearcuts and partially harvested stands. The addition of the BAR, LOGS, D, and T variables resulted in the lowest AIC_c value, although these variables were not statistically significant by themselves.

Understory structure is directly affected by forest management practices. Landowners in the Acadian forest seeking high hare densities should manage to produce conditions with high conifer stem densities, comparable to those found in regenerating conifer clearcuts approximately 15-30 years after harvest (4100-25350 stems/ha, Appendix A).

To predict hare densities based on vegetation measurements in northern Maine, the following equation can be used:

$\text{Pellets/ha/mo} = 201{,}667*[\text{Exp}(-3.892+0.0125*\ C^{1/2}+0.0189*\text{BAR}-0.00045*\text{LOGS})]$.

This equation accounted for 67% of the variation in hare densities across the stands used to build the model, but warrants further testing with independent data to evaluate its reliability and spatial consistency.

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CHAPTER 3

FACTORS ASSOCIATED WITH CANADA LYNX OCCURRENCE ACROSS TWO SPATIAL SCALES IN MAINE

ABSTRACT

Many ecological factors could influence patterns of occurrence of the Canada lynx, a species listed as threatened in the U.S.A., including prey abundance, the occurrence of potential competitors and predators, and environmental factors. I used an information theoretic approach and logistic regression modeling to describe the relationships between lynx occurrence and ecological variables at the geographic range- and the home range-scales in northern Maine. Variables considered in the modeling process were snowshoe hare density, bobcat occurrence, snow depth, fisher harvest density, and elevation. At the geographic-scale, hare density and bobcat occurrence best defined the distribution of lynx in northern Maine ($n = 31$ townships within the lynx range; $n = 19$ townships outside the lynx range). At the home range-scale, simulated home ranges centered on lynx occurrences ($n = 56$) were associated with higher hare densities, the absence of bobcats, and an interaction between hare density and bobcat occurrence relative to surveyed areas without lynx detections ($n = 126$). Data from two townships with occurrences of both bobcats and lynx suggest geographic- and home range-scale allopatry and a competitive relationship between bobcats and lynx.

In *post hoc* analyses, hare density best described the relationship between the ecological variables studied and home range-scale occurrence of lynx within the species' geographic range in Maine. This model accurately predicted model build data (83.4%

correct classification, n = 169) and validation data (89.6% correct classification, n = 96). At the geographic-scale, results of *post hoc* model selection suggest that the area of regenerating clearcuts can describe the relationship between hare density and lynx occurrence. The annual extent of clearcutting has decreased dramatically since 1989, which may result in less regenerating clearcut forest on the landscape of northern Maine. This could have negative implications for management objectives to maintain or expand current populations of lynx.

INTRODUCTION

The Canada lynx (*Lynx canadensis*) is a wide-ranging felid occupying the boreal and sub-boreal forests of Canada and some northern parts of the U.S.A. (Agee 2000, Aubry et al. 2000). In the U.S.A. portion of its geographic range, the lynx was listed as threatened in 2000 under the Endangered Species Act (U.S. Fish and Wildlife Service 2000). Prey and habitat relationships differ geographically (Buskirk et al. 2000); therefore, understanding these relationships at multiple spatial scales could aid in understanding of the ecology of little studied populations in eastern North America and may enhance recovery efforts for lynx in that region. Additionally, this information could aid in mapping of potential recovery habitat and with planning and management to promote lynx habitat on federal, state, and other lands.

The population of lynx occupying Maine and the Gaspé Peninsula of Quebec, Canada is both physically (Hoving et al. 2003) and genetically (Rueness et al. 2003) separated from the remaining lynx populations in central and western Canada. Additionally, the historic range of lynx in the eastern U.S.A extended from Pennsylvania to northern Maine (Seton 1929, Hoving et al. 2003), but range contraction over the last century left the Gaspé population on the southeastern edge of the current geographic distribution of lynx. Populations on the edge of a species' range are important because they allow for dispersal from source populations and for genetic diversity, which can lead to range expansion over time (Hunter and Hutchinson 1994). The Maine population is the largest of four remaining lynx populations in the continental U.S.A. and is the only known U.S.A. population east of Minnesota. Critical habitat has been proposed by the U.S. Fish and Wildlife Service in the four areas of the U.S.A. where lynx currently occur, and the largest of these covers 10,633 square miles in northern Maine (U.S. Fish and Wildlife Service 2006).

Animals make habitat choices on several scales (Johnson 1980) and ecological factors that influence these choices may be hierarchical and therefore, may differ across scales (Orians and Wittenberger 1991, Bissonette et al. 1997). For example, lynx occurrence at the regional scale of the northeastern U.S.A. was best predicted by snowfall (Hoving et al. 2005), but this variable was not important within northern Maine (Hoving et al. 2004). Thus, selection of different habitat features at different scales has been documented for this species, highlighting the importance of considering scale in understanding habitat relationships of lynx.

This study examines habitat selection by lynx at two scales: the geographical range- (or first-order) and the home range- (or second-order) scales (Johnson 1980). The habitat choices made by animals at the first- and second-orders often reflect larger scale life history processes, whereas those on third- (within home range) and fourth-orders (microsite) may reflect finer scale behavior such as hunting and resting site selection (Bissonette et al. 1997). Although several studies have examined third-order selection of habitat by lynx within the home range (Murray et al. 1994, Poole et al. 1996, Maletzke 2004, Fuller 2006), few have examined these relationships at broader scales. The ecological factors associated with the placement of a home range within the geographic range are likely factors that are directly related to lynx survival, mating, and reproduction. The factors associated with the geographic distribution of lynx are likely related to population persistence and may directly influence recovery efforts for the species. Understanding geographic-scale habitat relationships of lynx in eastern North America is important for regional conservation planning, which is essential for a wide ranging species such as the lynx that may exhibit metapopulation dynamics (Ruggiero et al. 2000). Range contraction at the southern extent of lynx distribution has been documented across the U.S.A. (Ruggiero et al. 2001), but the current range limit is still relatively unknown and the mechanisms for this contraction remain unexplained. This study was designed to better define the southeastern extent of the lynx range in the U.S.A. and to explore the factors influencing the geographic distribution of lynx in this region.

Understanding and predicting habitat relationships of species at broad scales is enhanced via spatially explicit habitat models (Mackenzie 2006). Such a model was developed for lynx occurrence in Maine (Hoving et al. 2004), but since the habitat (1991-1993) and lynx occurrence (1994-1999) data were collected for this model, forest management in northern Maine has changed dramatically. Timber salvaging associated with the eastern spruce budworm (*Choristoneura fumiferana*) outbreak of the late 1970's to early 1980's resulted in hundreds of thousands of acres of clearcuts, which created contiguous stands of regenerating forest as large as 5,000 acres across northern Maine. In response to the negative public perception of clearcutting, the Maine Forest Practices Act (MFPA) was passed in 1989, which created disincentives for clearcuts larger than 20 acres (Maine Forest Service 2004). The MFPA, coupled with 3 public referenda to ban clearcutting during the 1990's, contributed to a dramatic shift in forest management away from clearcutting to partial harvesting. In 1993, many of those large clearcuts had not aged sufficiently to regenerate dense understory conditions able to provide cover for snowshoe hares (Litvaitis et al. 1986a, Newbury and Simon 2005), but these areas are presently in a state of advanced regeneration and able to support high hare densities (Fuller and Harrison 2005, Homyack et al. 2006, Chapter 1). Additionally, the mean size of clearcuts has decreased to 20 acres and the annual number of acres in Maine that are partially harvested has increased 21% from 398,743 acres in 1993 to 481,153 acres in 2004 (Maine Forest Service 2005). Thus, the applicability of the previous lynx occurrence model (Hoving et al. 2004) to the current landscape of northern Maine is uncertain. Additionally, several recent studies have quantified hare densities across a range of forest stand conditions in northern Maine (Fuller and Harrison 2005, Homyack et al. 2006, Chapter 1), which provides an opportunity to use field-derived estimates of hare density as a potential predictor variable when modeling lynx occurrence at the geographic- and home range-scales in northern Maine.

To understand the ecological factors associated with lynx occurrence at broad scales, spatially extensive datasets representing prey abundance, the occurrence of potential predators and competitors, in addition to information on abiotic factors that affect hunting and competitive success, are needed. Of these, understanding the relationship of lynx occurrence and snowshoe hare (*Lepus americanus*) abundance is critical because lynx are specialist predators of hares and hare density acts as a regulating factor for lynx populations (Krebs et al. 2001). The importance of hares to lynx populations is evident in several characteristics of lynx ecology. Hares are the primary food item for lynx in almost all studies of lynx diet, regardless of season or hare density (Saunders 1963, Van Zyll de Jong 1966, Staples 1995, O'Donoghue et al., 2001). During hare declines in the northern boreal forest, lynx survival decreases and recruitment falls to near zero (Brand and Keith 1979, Poole 1994, Krebs et al. 2001). Lynx home ranges are larger and the number of dispersing individuals in a lynx population increases during hare declines (Poole 1994, Poole 1997, Slough and Mowat 1996, Krebs et al., 2001). Further, the geographic ranges of snowshoe hare and lynx overlap extensively today and did so to an even greater degree historically (Seton 1928, Seton 1929, Krebs et al. 2001). Previous studies have estimated the hare densities needed for the persistence of a lynx population in the southern portion of the lynx range (Ruggiero et al. 2000, Steury and Murray 2004), but none have evaluated the influence of hare density on the occurrence of lynx across the landscape using empirically-derived field data.

Lynx occurrence in northern Maine was best predicted by regenerating forest and was negatively associated with recent clearcuts, partial harvests, and forested wetlands during previous modeling efforts (Hoving et al. 2004). These variables appear to be surrogates for hare density, which is relatively low in recent clearcuts (Newbury and Simon 2005) and recent partial harvests (Fuller and Harrison 2005) and relatively high in regenerating forest stands (Homyack et al. 2006). Correspondingly, relative hare abundance was positively related to the extent of regenerating forests across 1 km landscapes in northern Maine (Hoving 2001). Other studies have associated third and fourth order habitat use by lynx with dense understory conditions and the presumably higher hare densities in these habitat types (Murray et al. 1994, Poole 1996, Paragi et al. 1997, Mowat and Slough 2003, Fuller 2006). Although lynx occurrence was negatively associated with partial harvests at the statewide scale in Hoving et al.'s (2004) lynx model for northwestern Maine, the land cover data used in that model were collected during 1991-1993, a time when partial harvesting was less common. Recent partial harvests may support a low hare density initially (Fuller and Harrison 2005), but these stands may increase substantially in their ability to support hares by 10-11 years after harvesting (Chapter 1). Based on studies of third-order habitat selection, lynx use areas of established partial harvests within their established home ranges in northern Maine (Fuller 2006), but the relationships between lynx occurrences and landscape-scale predominance of partial harvesting have not been evaluated at broader scales.

In addition to prey abundance, competition could also influence lynx occurrence in northern Maine. Ecological theory posits that two species with similar body sizes and patterns of resource use should compete and exhibit allopatric distributions in areas of co-occurrence (MacArthur 1972, Caughley and Sinclair 1994, Dayan and Simberloff 1996). The bobcat (*Lynx rufus*) inhabits a broad range of habitat conditions throughout the U.S.A. and is slightly larger than the lynx where their geographic distributions overlap. Although a competitive relationship between bobcats and lynx in some regions of North America has been suggested (McCord and Cardoza 1982, Parker et al. 1983, Buskirk 2000), historical and empirical evidence to support this idea are limited (Hoving et al. 2003), likely because the geographic ranges of these species are known to overlap in few places. Throughout their ranges, the diets of both species are dominated by leporids (e.g., Delibes et al. 1997, O'Donoghue et al. 2001), and in Maine, bobcats, like lynx, are specialist predators of snowshoe hares (Litvaitis et al. 1986, Major and Sherburne 1987, Litvaitis and Harrison 1989, Dibello et al. 1990). Additionally, bobcats in Maine are known to use similar habitat types as lynx (i.e., forests with dense conifer understories) at the home range-scale (Litvaitis et al. 1986, Major and Sherburne 1987, Fuller 2006), which likely reflects high hare densities in these areas (Fuller and Harrison 2005, Homyack et al. 2006, Fuller 2006, Chapter 1). This overlap in diet and habitat use would allow for potential exploitation competition between the two species, and additionally, the larger body size of bobcats may facilitate interference competition between these species in some areas (Parker et al. 1983).

Lynx, however, have a lower foot loading and longer limb length than bobcats (Buskirk 2000, Krohn et al. 2004) and may be more successful at hunting snowshoe hares in deep snow conditions. Bobcats in Maine are known to become physically stressed during harsh winters with deep snow, and these conditions could limit their northern distribution (Litvaitis et al. 1986b). Snow depth, therefore, potentially influences lynx distribution at the geographic scale by mediating competition with bobcats. In the Northeast, lynx occurrence has been associated with snowfall >268 cm/year (Hoving et al. 2005), which could indicate that snow depth is a surrogate variable explaining competition with bobcats (Hoving et al. 2003). Snow may be important to lynx occurrence at the geographical scale; however, this variable was not associated with lynx occurrence within Maine where spatial resolution of snowfall data was restricted by a limited number of monitored snow stations in remote areas of the lynx range (Hoving et al. 2004). Relatively high resolution and spatially extensive snow data are recently available (Barrett 2003) to evaluate this relationship among lynx, bobcat, and snow depth with finer resolution.

Fishers (*Martes pennanti*) are medium sized mustelids and, like bobcats, are potential competitors with lynx as a result of similar prey and habitat use. Snowshoe hares comprise a large portion of the fisher diet in Maine (Rego 1984, Arthur et al. 1989) and additionally, fishers select for dense conifer-understories where hares are relatively common (Arthur et al. 1989). Fishers were also known to kill radiocollared lynx during a study in Maine (J. Vashon, personal communication), which could cause lynx to avoid some areas with high fisher densities. Fishers, however, have higher foot loading than lynx (Krohn et al. 2004), and snow depth apparently limits higher densities of fishers in Maine to an area south of the primary distribution of lynx (Krohn et al. 1995).

The objectives of this study were to describe the relationships between lynx occurrence and ecological variables such as the densities of prey, competitors, and predators at the scale of the geographical range and at the scale of the home range across the landscape of northern Maine. Additionally, because forest harvesting significantly affects hare density in Maine (Fuller and Harrison 2005, Homyack et al. 2006, Chapters 1 and 2), I evaluated the relationship between regenerating clearcuts, partial harvests, and mature forest and the occurrence of lynx in northern Maine.

STUDY AREA

Northern Maine is part of the Acadian forest ecoregion, an ecological transition zone in the northeastern U.S.A. located between the temperate deciduous and eastern boreal forests (Seymour and Hunter 1992). Prior to European settlement, the predominant disturbance agents in this region were insect outbreaks, fire, and windstorms at relatively frequent return intervals, but at a much smaller scale compared with the disturbance regime of the boreal forest (Seymour 1992).

Currently, forest harvesting is the dominant disturbance agent in this region (Seymour and Hunter 1992). To salvage timber from a spruce budworm outbreak, hundreds of thousands of acres were clearcut in the 1970's and 1980's and were subsequently sprayed with herbicides (primarily Glyphosate) to reduce deciduous competition. The resulting dense regenerating stands are dominated by balsam fir (*Abies balsamea*) and white (*Picea glauca*), red (*Picea rubens*), and black (*Picea mariana)* spruce (Seymour 1994). Species that comprise a minor component of these stands include eastern white pine (*Pinus strobus*), northern white cedar (*Thuja occidentalis*), and eastern hemlock (*Tsuga canadensis*). In areas with significant overstory disturbance, shade-intolerant species such as white birch (*Betula papyrifera*), aspen (*Populus spp.*), red maple (*Acer rubrum*), pin cherry (*Prunus pensylvanica*), and raspberries (*Rubus idaeus*) proliferate. Stands with a predominantly hardwood composition are dominated by sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*) and occur on better drained soils with higher site quality (Seymour 1992, 1994).

The area of snowtracking surveys in northern Maine was defined as the region of total snow depth > 268 cm to coincide with areas associated with lynx occurrence throughout the northeastern U.S.A. and the Gaspé Peninsula (Hoving et al. 2005) (Appendix E). Over the winters of 2004-2005, the mean snow depth for the surveyed areas was 113 cm (Appendix F). The surveyed area encompasses the interface between the current distributions of bobcats and lynx in Maine, and the annual bobcat harvest for the region surveyed ranged from 0-20 per year across those wildlife management districts during 2002-2005 (Figure 3.4). The mean fisher harvest density in surveyed townships was 0.05/mi^2 and ranged from 0-0.20 fishers/mi^2 during the trapping seasons of 1995-2004 (Appendix G).

METHODS

LYNX AND BOBCAT SURVEYS

The Maine Department of Inland Fisheries and Wildlife (MDIFW) conducted snowtracking surveys to detect lynx and bobcat tracks in northern Maine during the winters of 2003-2005 (Appendix E). Surveys were conducted from snowmobiles and occasionally trucks from January through March and each track location was georeferenced using a Global Positioning System (GPS). Surveyed townships numbered 17 in 2003, 19 in 2004, and 14 in 2005. In addition to these surveys, I used data from two snowtracking surveys conducted on the Clayton Lake study site during the winters of 2001 and 2004 (Appendix E). For complete survey methods, see Vashon et al. (2003).

Survey protocols, which were designed to detect at least one resident lynx present in the township, required at least 55 km of road to be surveyed in each 100 km^2 township from 24 to 72 hours after snowfall (S.M. Crowley, J.H. Vashon, W.J. Jakubas, and G.J. Matula, A comparison of survey techniques to detect Canada lynx [*Lynx canadensis*] in northern Maine, unpublished report, MDIFW, Bangor, U.S.A.). These standards increase the probability that the failure to detect lynx tracks during a survey represents non-occurrence of lynx in that township. If a sufficient road density was not surveyed or if little time had passed since the last snow event, lynx may not have had time to leave tracks or not enough distance may have been surveyed to detect tracks, thereby lowering the level of confidence that lynx were not present in the township (Mackenzie 2006). For surveys that detected lynx tracks, minimum survey distance and time criteria were not necessary because these detections are very likely to represent lynx occurrence; therefore, I applied these standards to non-detection townships only.

GEOGRAPHIC-SCALE

I described the relationships between predictor variables and lynx occurrence at two scales. The broader scale evaluated the factors related to geographic distribution of lynx occurrence in northern Maine. For this scale of analysis, I considered the surveyed township to be the unit of observation and used logistic regression models to compare surveyed townships within the range of lynx distribution to those outside of this range. I defined the geographic distribution of lynx occurrence in northern Maine by drawing a polygon around the outermost points of the townships with lynx detections (Figure 3.1). This definition of the lynx range in Maine was intended solely for use in these analyses and does not encompass all recent documented occurrences of lynx in Maine; only those observed during these systematic snowtracking surveys. All townships encompassed within or bisected by the lynx range polygon were considered to be within the geographic range of lynx in Maine (n = 32 townships). All surveyed townships not intersected or encompassed by this polygon were considered outside of this range (n = 20 townships).

HOME RANGE-SCALE

To understand the factors associated with the occurrence of lynx within the geographic range, a finer scale analysis was limited to the townships encompassed within the geographic range polygon. Within these 32 townships, I simulated home range cores around areas with and without lynx detections to model the distribution of occurrences

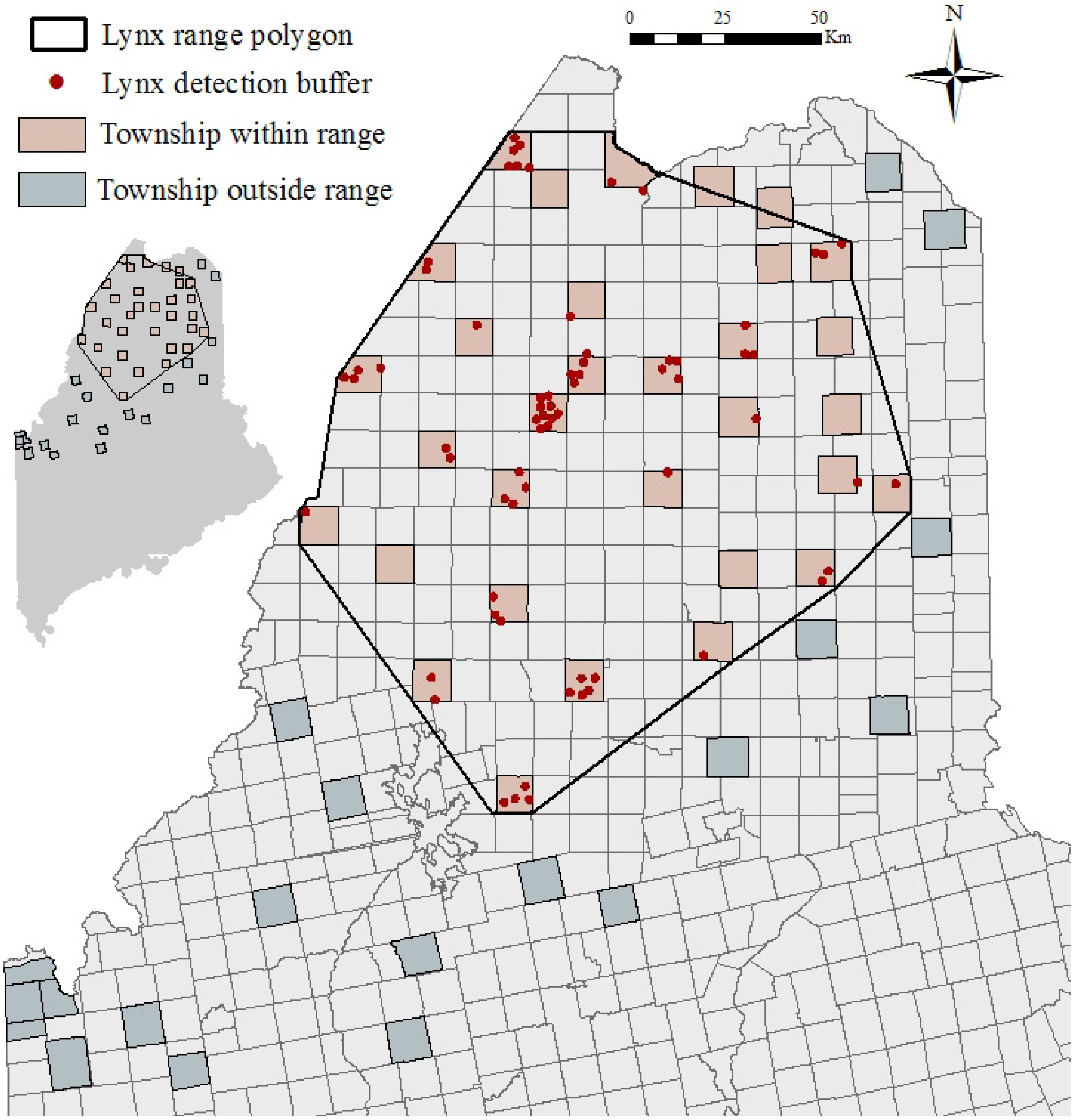

Figure 3.1. Locations of townships surveyed for Canada lynx tracks by snowtracking in northern Maine, U.S.A. during January to March, 2003-2005. For the geographic-scale of analysis, townships inside the lynx range polygon were considered detections (n = 31) and townships outside of this line were considered non-detections (n = 19). Data courtesy of the Maine Department of Inland Fisheries and Wildlife.

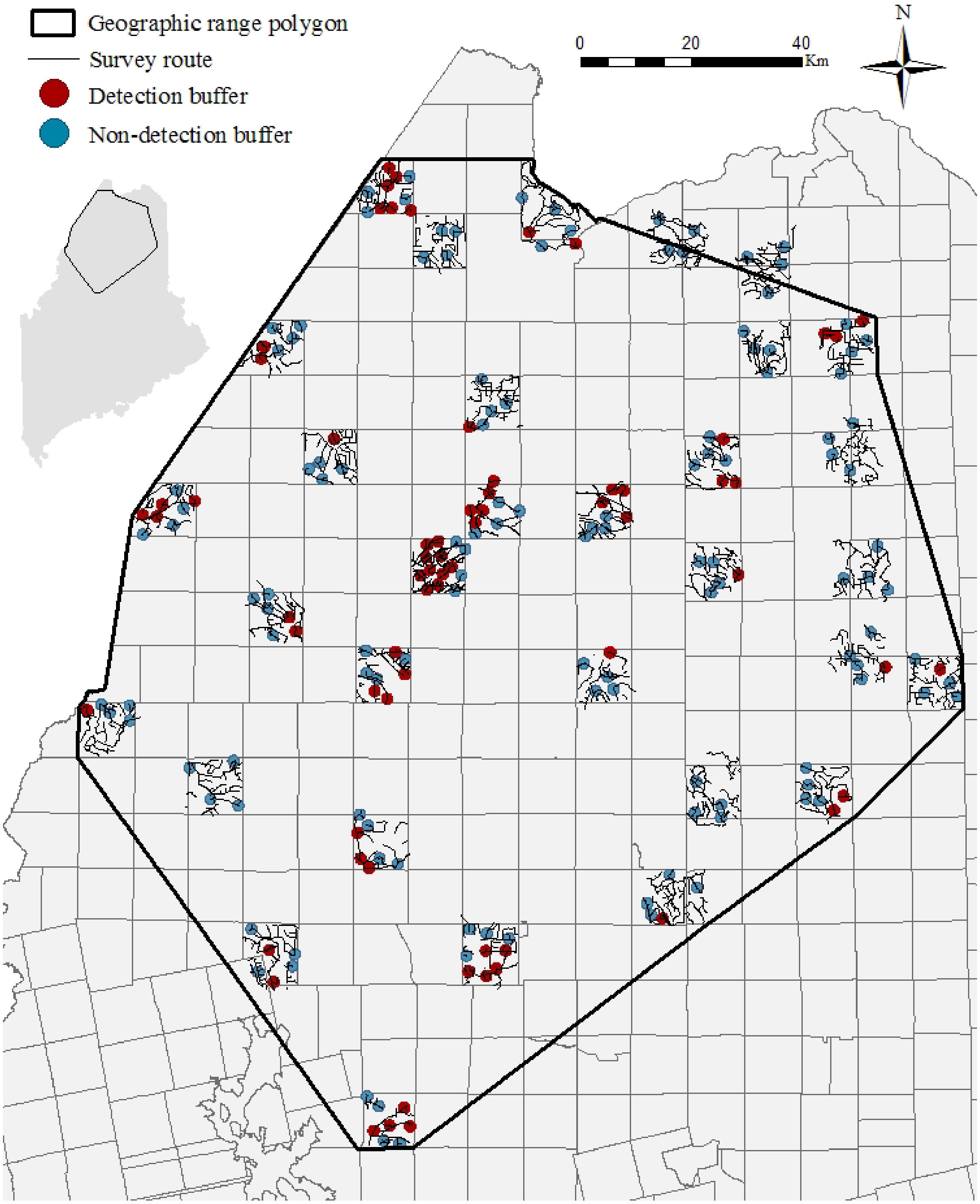

Figure 3.2. Locations of 3.15 km^2 simulated home ranges representing lynx detections (n = 56) and non-detections (n = 126) based on results of snowtracking surveys conducted in northern Maine, U.S.A. during January to March, 2003-2005. Data courtesy of the Maine Department of Inland Fisheries and Wildlife.

(Figure 3.2). Lynx tracks cannot be considered independent observations, thus I employed a distance criterion to reduce pseudoreplication (Thomas and Taylor 2006). I created circular buffers equivalent in size to the mean for 50% kernel areas used by radiocollared female lynx in northern Maine (J.H. Vashon, A. L. Meehan, W. J. Jakubas, and G. J. Matula, Preliminary diurnal home-range and habitat use by Canada lynx [*Lynx Canadensis*] in northern Maine, unpublished report, MDIFW, Bangor, U.S.A.). Fifty percent kernel areas for female lynx are biologically relevant because they represent areas of high use and are therefore likely the smallest areas needed to support a reproducing individual throughout the critical denning season. Additionally, using a large buffer size would decrease the probability of detecting ecological factors associated with lynx occurrence at this scale. As the distance from a track increases, the ecological factors associated with the occurrence of that track in that location may become weaker and therefore more difficult to detect during analyses.

The total buffer area for this scale of analysis was 3.15 km^2, which resulted in a radius of 1.00 km. I simulated home ranges around lynx detections by first calculating the geometric center of each of the original 227 detection points using the 1.00 km radius. This method allows nearby points to spatially influence the location of the resulting centroid and results in each point becoming more centered with respect to near points. I then created a buffer with a 1.00 km radius around each new point. Of the resulting 227 buffered centroids, I selected out only those that did not overlap to create a group of 69 buffers representing “independent” simulated core areas for female lynx.

Potential home ranges in areas without lynx detections were randomly positioned in surveyed areas within the geographic range of lynx by generating random points along survey routes that were at least 2.00 km away from any lynx track. I then buffered each random point by 1.00 km to create non-detection simulated home ranges. To improve the likelihood that non-detection buffers were unused by lynx, these areas were required to have at least 2 km (the diameter of the buffer) of road surveyed within the bounds of the buffer.

To reduce pseudoreplication of observations, the number of buffers included in the analyses was limited to 4 detection and 4 non-detection buffers per township, leaving 56 detection and 128 non-detection simulated home ranges (Figure 3.2). When the number of buffers per township exceeded these maxima, I randomly selected buffers for removal and these removed buffers were reserved as the validation dataset (Appendix H).

PREDICTOR VARIABLES

I chose predictor variables for the logistic regression model based on previous studies of habitat use by lynx (Von Kienast 2003, Hoving et al. 2004, Meletzke 2004, Steury and Murray 2004, Hoving et al. 2005, Fuller 2006) to describe the ecological relationships between lynx occurrence and prey, competitors, and environmental factors. Each predictor variable was analyzed in a Geographic Information System (GIS) in raster format (NAD 83, zone 19). I overlaid detection and non-detection townships and buffers on these rasters and used zonal statistics in ArcMap, Version 9 to calculate the mean for each variable throughout each buffer and township.

SNOWSHOE HARE DENSITY

The densities of snowshoe hares for land cover types were based on estimates from companion field studies conducted in northern Maine (Table 3.1). I applied these

Table 3.1. Land cover classes, associated hare density estimates, and proportion of the landscape represented for an updated version of the 1993 Maine GAP map based on 2004 Landsat thematic-mapper imagery for northern Maine, U.S.A. See text for justification of applied hare densities without sources.

GAP class	Hares/ha	Source	Hectares	Percentage
Regenerating clearcut	2.0	Homyack et al. 2006, Chapter 1	409962	8.3
Thinned	1.0	Homyack et al. 2006	76298	1.6
Established partial cut	0.8	Chapter 1	916121	18.6
Dead forest	0.6	Lachowski 1997	1462	0.0
Recent cut	0.2	Fuller and Harrison 2005	480151	9.8
Mature forest uncut	0.2	Fuller and Harrison 2005	2187648	44.5
Abandoned field	0.2		2603	0.1
Deciduous forested wetland	0.2		24653	0.5
Deciduous scrub-shrub	0.2		81227	1.7
Coniferous scrub-shrub	0.2		10380	0.2
Dead scrub-shrub	0.2		57	0.0
Peatland	0.2		24125	0.5
Sparse residential	0.2		15423	0.3
Alpine tundra	0.2		1837	0.0
Non-regenerating clearcut	0	De Bellefeuille et al. 2001, Newbury and Simon 2005	31022	0.6
Blueberry field	0		15	0.0
Grasslands	0		63805	1.3
Crops/ground	0		22198	0.5
Wet meadow	0		9944	0.2
Gravel shore	0		3422	0.1
Rock shore	0		3437	0.1
Dense residential	0		2368	0.1
Highways/runways	0		43	0.0
Exposed rock/talus	0		1682	0.0
Fresh aquatic bed	non-habitat[a]		3	0.0
Fresh emergent	non-habitat[a]		38643	0.8
Mudflat	non-habitat[a]		177	0.0
Shallow water	non-habitat[a]		11734	0.2
Open water	non-habitat[a]		268916	5.5
Salt water	non-habitat[a]		1059	0.0
Cloud	non-habitat[a]		227723	4.6

[a] Non-habitat refers to areas unavailable for use by lynx.

density estimates to cover types classified in a 2004 updated version of the GAP vegetation map for Maine, which was originally created using remotely sensed satellite imagery from 1991-1993 (Hepinstall et al. 1999). This updated vegetation map was produced using change detection techniques for periods between 1993-2000 and 2000-2004. This method evaluates biomass increase and decrease for each of the original 1993 GAP classes to produce a 2004 classification of cover types in northern Maine. For example, if a pixel was classified as a clearcut in 1993 and both the 2000 and 2004 satellite imagery identified "biomass increase" for that pixel, then it was reclassified as "regenerating clearcut."

The 2004 updated GAP map was based on land cover classes determined by the original 1993 GAP and is therefore subject to the misclassifications of 1993 land cover classes. The 1993 GAP had very low correct classification rates for late regeneration (8.5%) and partial cuts (17.8% for light and heavy cuts combined) (Hepinstall et al. 1999). The change detection procedure could have improved the misclassifications of the 1993 map, however, because multiple years of satellite data were used to reclassify the land cover classes. If the 1993 land cover class was incorrect, then subsequent biomass increase or decrease detections could be used to rectify the misclassification. For example, if a partial harvest was misclassified as mature forest in 1993, then "biomass increase" detected in 2000 and in 2004 would allow the resulting updated class to be considered "established partial harvest" instead of "mature forest." This raster dataset has a 30 meter resolution. See Legaard and Simons (University of Maine, Orono, *in prep*) for details of the updating procedure.

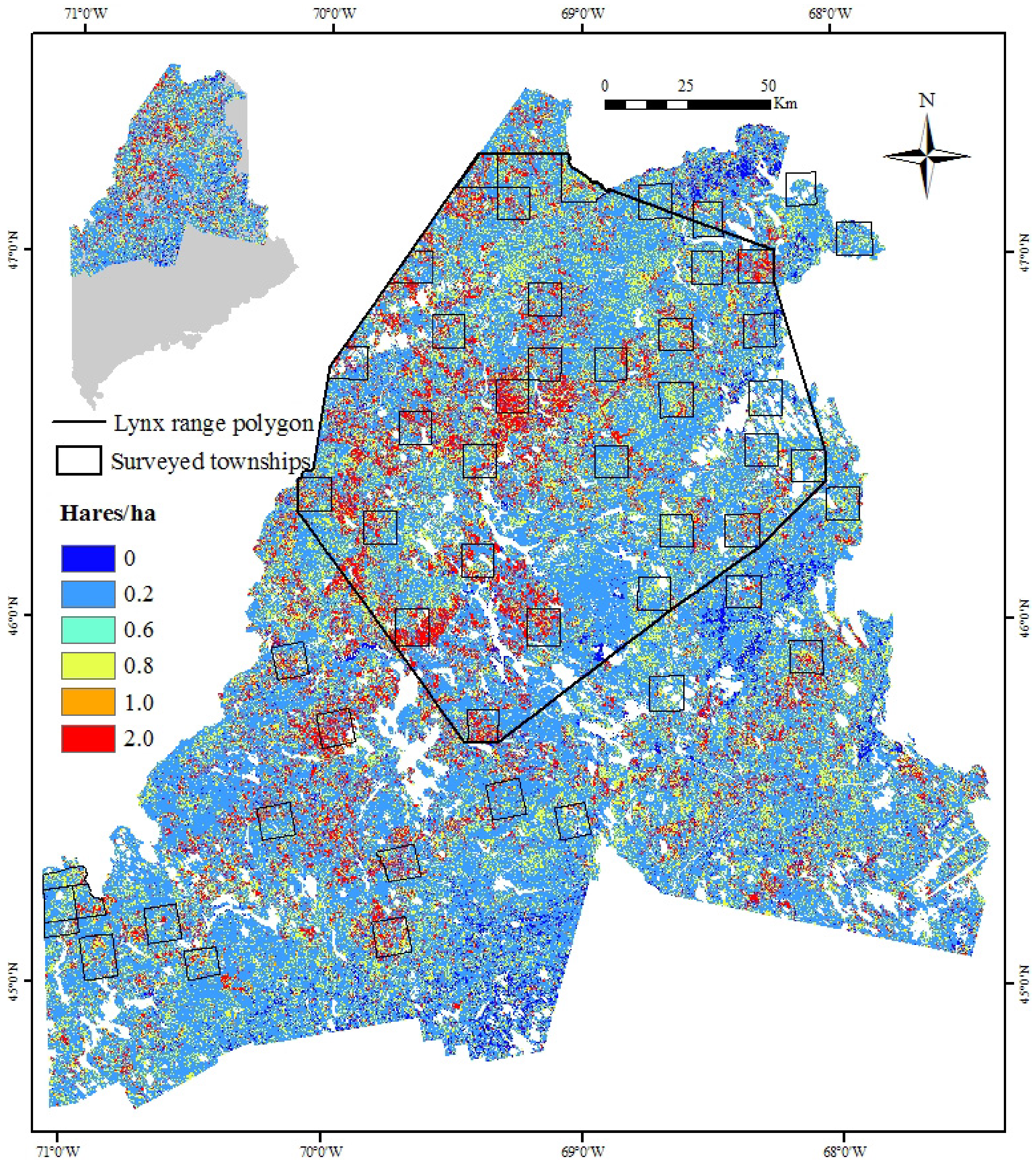

Figure 3.3. Estimated hare densities (hares/ha) based on a 2004 updated vegetation map for northern Maine, U.S.A. (see Table 3.2 for descriptions of classes) and townships surveyed for lynx and bobcat tracks via snowtracking from January to March, 2003-2005.

I applied estimated hare densities to the land cover types in the updated 2004 GAP map according to previous studies (Table 3.1, Figure 3.3). Regenerating conifer clearcuts received a value of 2.0 hares/ha based on the mean of 2003, 2005, and 2006 leaf-off hare density estimates in 15-30 year old regenerating conifer clearcuts in Maine that had been sprayed with herbicide (Homyack et al. 2006, Chapter 1). The "established partial harvest" classification was applied to cover classes that had been classified as "partial harvest" or "mature forest" in the 1993 GAP map and had experienced a biomass increase for either the 2000 or the 2004 satellite imagery. I assigned a value of 0.8 hares/ha to established partial harvests based on the median value for 21 partially harvested stands surveyed during the leaf-off season, 2005 (Chapter 1). I assumed thinned stands had been precommercially thinned and gave this class a value of 1.0 hares/ha (Homyack et al. 2006). I assigned a value of 0.6 hares/ha to the dead forest class based on a previous study of budworm-killed stands in northern Maine (Lachowski 1997). The classification of "recent cut" was assigned to "partial harvest" and "mature forest" that had undergone biomass decrease in either the 2000 or the 2004 satellite imagery. Recent cuts are likely to be recent partial harvests; this form of harvest has constituted > 90% of all annual harvests in Maine since 1995 (Maine Forest Service 1999, 2000, 2001, 2002, 2003, 2004, 2005), and this class received a value of 0.20 hares/ha based on companion studies by Fuller and Harrison (2005). Several classes received a value of 0.20 hares/ha because they are likely to support low levels of hare density. Mature forest classes, regardless of species composition, support uniformly low hare densities of approximately 0.20 hares/ha (Lachowski 1997, Fuller and Harrison 2005). Other classes likely to support a low hare density as a result of their sparse cover (see Chapter 1) are abandoned field, deciduous forested wetland, scrub-shrub forest, peatland, sparse residential, and alpine tundra (Table 3.1). Non-regenerating clearcuts received a zero value based on De Bellefeuille (2001) and Newbury and Simon (2005). Several other classes received zero values including blueberry field, grasslands, crops/ground, wet meadow, gravel shore, rock shore, dense residential, highways/runways, and exposed rock/talus (Table 3.1).

Small portions of the study area were covered by clouds when the satellite imagery was obtained and these areas were clipped out of the updated GAP map. These are missing data, were classified as non-habitat, and were not considered in calculations. This assumes that the habitat hidden by cloud cover is similar to the habitat analyzed. To minimize the risks associated with this assumption, I removed all buffers from the analysis that contained > 25% of pixels in cloud cover. This resulted in the removal of one detection and one non-detection township from the geographic-scale analysis, and two non-detection buffers from the home range-scale analysis.

I identified several classes as “non-habitat” under the premise that they were unusable to lynx. These classes were removed from calculations of hare density for each buffer. I compared detection and non-detection buffers for the total amount of non-habitat (including clouds) using a nonparametric Mann-Whitney U test (Zar 1999) and found no difference between these two groups at the geographic-scale ($P = 0.38$) or at the home range-scale ($P = 0.56$), suggesting that the distribution of non-habitat features such as lakes and clouds did not differ between detection and non-detection areas.

BOBCAT OCCURRENCE

Bobcats are a potential competitor for lynx and it is possible that bobcat occurrence is negatively associated with lynx occurrence in northern Maine (Parker et al. 1983, Hoving et al. 2003). In addition to recording lynx tracks, the locations of all bobcat tracks were georeferenced in snowtracking surveys. A total of 86 bobcat tracks were recorded in 14 townships during the three years of survey (Figure 3.4). I used the occurrence of bobcats as a binary variable to evaluate the relationship between the occurrence of bobcat and lynx. I buffered each bobcat detection by a 4.47 km diameter circle, the size of a 90% MCP home range for bobcats in Maine based on radiotelemetry data for male and female bobcats at two study sites in Maine (Litvaitis et al. 1986a). I assigned a value of one to a township or simulated lynx home range if it overlapped with the bobcat buffer and a zero if not. Bobcat tracks are easily distinguished from lynx tracks in the field because they are roughly half as large as lynx tracks (Halfpenny and Bruchac 2001). Additionally, the distribution of bobcat tracks detected during the snowtracking surveys generally coincides with harvest data for the trapping seasons of 2002-2005, suggesting that observers were able to reliably distinguish the two felids (Figure 3.4).

FISHER HARVEST

Fishers are a potential competitor (Arthur et al. 1989) and predator (J. Vashon, personal communication) of lynx in northern Maine. I used 10-year mean fisher harvest data for the 1995-2004 trapping seasons on the township scale provided by the MDIFW to evaluate the effect of fisher density on lynx occurrence (Appendix G). Fisher harvest

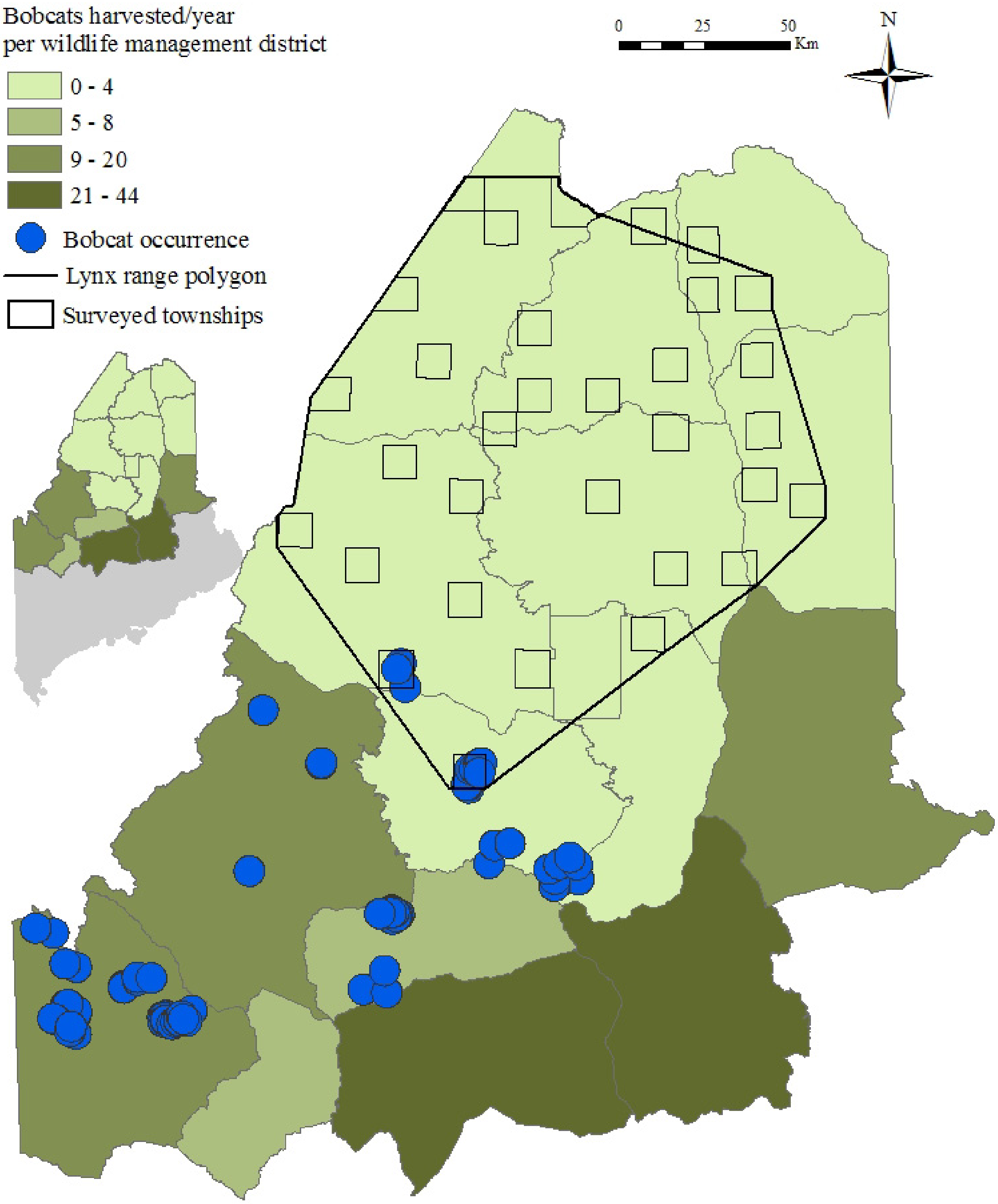

Figure 3.4. Locations of bobcat occurrences (90% minimum convex polygon buffers around bobcat tracks) during snowtracking surveys conducted in northern Maine, U.S.A. from January to March, 2003-2005 and annual bobcats harvested per wildlife management district during the trapping seasons of 2002-2005. Data courtesy of the Maine Department of Inland Fisheries and Wildlife.

may not be a direct measure of fisher density, but these data were used in a relative sense to compare areas where lynx were detected to areas where they were not detected and biases were likely to be consistent across the study area, as long as trapping for fisher and marten occurred throughout the region (Krohn et al. 1995). Two of 50 townships surveyed had no records of fisher harvest over the 10 years considered; I assigned these townships a zero value in the analyses. I converted GIS data provided by the MDIFW into raster format at a 50 meter pixel resolution.

SNOW DEPTH

Previous studies have noted the importance of snow conditions to lynx occurrence and population dynamics at the regional scale (Stenseth et al. 2004, Hoving et al. 2005). Lynx have lower foot loading than competitors (e.g., bobcats, fishers, coyotes *Canis latrans*) and are highly adapted to deep snow conditions (Buskirk 2000, Krohn et al. 2004). In contrast, bobcats have high foot loading and are likely to be less successful than lynx at hunting hares in deep snow conditions. Thus, deep snow may act as a mediator for competition between lynx and bobcats and high snow depths may be positively associated with lynx detection (Hoving et al. 2005). At the stand scale, however, snow depth may be less important than snow crusting conditions that allow for easier travel through the home range (Meletzke 2004).

I used data on snow depth developed by the National Oceanic and Atmospheric Administration (NOAA) National Weather Service's National Operational Hydrologic Remote Sensing Center (NOHRSC) and distributed by the National Snow and Ice Data Center (NSIDC) (Appendix F). Snow depth is an output of the NOHRSC's Snow Data Assimilation System (SNODAS), which uses output from an energy and mass-balance snow model (produced by Numerical Weather Prediction models) in addition to remotely sensed, aerial, and ground based observations of snow cover and snow water equivalent (Barrett 2003). Model outputs from SNODAS including snow depth are updated for each day at a 1 km resolution.

I downloaded data for snow depth for February 1, February 15, March 1, March 15, and April 1 during two years of lynx surveys (2004 and 2005) to correspond with the months of highest snow depth in northern Maine. I took the maximum depth of these 5 dates for each year and averaged between 2004 and 2005 to obtain a mean of the maximum snow depths throughout the winter across the two years (Appendix F). These maximum depths represent the deepest snow depths over these time periods and therefore the most limiting conditions likely to be encountered by bobcats and lynx. I resampled this raster dataset to reduce the pixel size to 50 meters to facilitate the averaging of values in square pixels over circular buffers.

ELEVATION

Elevation may mediate competition between carnivores by allowing the partitioning of ecological niches (Fuller and Harrison 2006) and at high densities of lynx and bobcats, the less successful competitor may use less preferred areas of high elevation (Parker et al. 1983). Additionally, elevation may be correlated with snowfall, with high elevation areas having deeper snow. If either of these scenarios is true, lynx detection is expected to be positively related to elevation. To obtain mean elevation for each simulated home range, I used a digital elevation model (DEM) at a 30 meter resolution for Maine (Appendix I).

ANALYSES

I used these five predictor variables to evaluate the relationships between prey density (hares), the occurrence of competitors (bobcat and fisher harvest), and environmental factors (snow depth and elevation) and lynx occurrence and non-detection in northern Maine. I developed a set of 15 *a priori* candidate models to evaluate these relationships at both the broad and fine scales. I used multiple logistic regression analysis to statistically evaluate these models because the response variable (lynx detection) is binary. In addition to testing for main effects for all predictor variables, I tested for interaction effects between predictor variables. Interaction effects are most likely to occur between predictor variables representing different aspects of the ecological niche. For example, interaction effects are unlikely to be present between bobcats and snow because these variables are likely both related to potential competition between lynx and bobcats. Thus, I tested for interaction effects between hares and bobcats, hares and snow, hares and fisher, and fisher and bobcat.

I compared these logistic regression models using Akaike's Information Criterion (AIC) which is a method of model selection based on a maximum likelihood method that balances model fit and parsimony to select the best model from a set of candidate models (Burnham and Anderson 2002). AIC seeks to minimize the Kullback-Leibler distance (representing the amount of information "lost" or unexplained) while penalizing models for each parameter used to achieve this goal. I used the AIC equation corrected for small sample size because in this study, $n/K < 40$ (Burnham and Anderson 2002):

$$AIC_c = -2\log(L(2)) + 2K + ((2K(K + 1))/(n-K-1)).$$

The AIC model selection process emphasizes the necessity of *a priori* model development instead of comparing all possible models in a "data dredging" exercise (Anderson and Burnham 2002, Burnham and Anderson 2002). Additionally, AIC can only select the best model from the set of candidate models; it has no way to associate the best model with "truth." I therefore used the Akaike weights (w_i) as a measure of the weight of evidence in favor of the best model (Burnham and Anderson 2004):

$$w_i = \exp(-)_i/2)/(\sum_{r=1} \exp(-)_i/2)).$$

I also used McFadden's ρ^2 to assess the relative ability of the best models to explain the variation in the dataset (Stephens et al. 2005).

I transformed all independent variables that did not appear to be normally distributed in dot density plots. I used a Hosmer-Lemeshow test to assess the goodness of fit of the logistic regression model for the best model and the global model in each dataset, using groups of 5 for the broad scale and 18 for the fine range scale to produce groups of approximately 10 cases each (Kutner et al. 2005).

RESULTS

Snowtracking surveys resulted in 227 formal lynx detections over 4,136 km surveyed (Table 3.2). Twenty-three of 31 (74%) townships within the geographic range of lynx had detections for lynx and 14 of 19 (74%) townships outside the lynx range had bobcat detections (Figures 3.1, 3.4; Table 3.2). Bobcat and lynx distributions were largely allopatric at the township- and home range-scales; only two of 50 (4%) townships contained both lynx and bobcat tracks and only 13 of 182 simulated home ranges around lynx detections intersected bobcat detections.

Table 3.2. Townships surveyed by snowtracking for lynx and bobcat tracks in northern Maine, U.S.A. during the winters of 2003-2005. Data courtesy of the Maine Department of Inland Fisheries and Wildlife.

Township	Date	Year	Survey distance (km)	Lynx tracks detected	Bobcat tracks detected
T10R15	15-Jan	2003	96.8	7	0
T14R11	24-Jan	2003	85.9	2	0
T12R9	25-Jan	2003	96.5	17	0
T9R13	28-Jan	2003	71.2	16	0
T15R15	29-Jan	2003	71.2	15	0
Hammond	7-Feb	2003	95.3	0	0
T4R15	8-Feb	2003	102.3	10	3
T9R9	12-Feb	2003	66.8	15	0
T12R17	13-Feb	2003	83.4	13	0
T18R13	21-Feb	2003	84.6	35	0
T18R10	22-Feb	2003	109.8	10	0
T7R16	25-Feb	2003	87.1	0	0
T13R14	26-Feb	2003	97.0	2	0
T17R12	27-Feb	2003	91.3	0	0
T4R11	7-Mar	2003	94.8	21	0
T8R18	11-Mar	2003	84.8	1	0
T6R13	12-Mar	2003	62.5	11	0
T13R7	17-Jan	2004	74.5	8	0
New Canada/T16R6	18-Jan	2004	99.3	0	0
T15R6	21-Jan	2004	83.3	0	0
T15R5/Westmanland	27-Jan	2004	85.7	15	0
Hersey	28-Jan	2004	80.5	0	0
T13R5/Wade	1-Feb	2004	94.0	0	0
T11R7	2-Feb	2004	84.4	5	0
T7R7	6-Feb	2004	96.1	0	0
TCR2	10-Feb	2004	100.0	0	0
Wallgrass/St. John's	12-Feb	2004	105.5	0	0
Cyr/Hamlin	16-Feb	2004	71.2	0	0
Grand Isle/T17R3	17-Feb	2004	101.7	0	0
Soldiertown/T2R8	18-Feb	2004	98.7	0	0
Ashland/T11R4	24-Feb	2004	89.3	0	0
T9R3	25-Feb	2004	99.0	3	0
T7R5	8-Mar	2004	79.8	4	0
T3R3/T3R4	9-Mar	2004	90.9	0	0
T5R7/T5R8	11-Mar	2004	113.8	1	0

Table 3.2 continued.

Township	Date	Year	Survey distance (km)	Lynx tracks detected	Bobcat tracks detected
Masardis/Squapan	14-Mar	2004	75.9	1	0
Shirley/East Moxie	9-Jan	2005	66.1	0	12
T5R9	18-Jan	2005	56.9	0	10
Bowdoin College Grant East	25-Jan	2005	66.3	0	3
Brassua	13-Feb	2005	97.8	0	2
Mayfield	14-Feb	2005	69.4	0	3
Lower/Upper Cupsuptics	18-Feb	2005	84.9	0	10
Coplin/Redington	19-Feb	2005	66.5	0	16
Parmachenee/Oxbow	24-Feb	2005	224.3	0	4
Tim Pond	25-Feb	2005	84.9	0	6
T1R13	17-Mar	2005	52.2	15	13
Upper Enchanted	30-Mar	2005	61.3	0	4
Total			4135.5	227	86

GEOGRAPHIC-SCALE

The AIC model selection process identified the H+B model as the best model of the set of 15 candidates for the 50 townships analyzed to differentiate characteristics of townships within versus townships outside of the geographic range of lynx (Table 3.3). These models take the forms:

ln (B/1-B) = 5.956 + 6.638**ln*(hares) – 5.835 if bobcat are present and *ln* (B/1-B) = 5.956 + 6.638**ln*(hares) if bobcat are absent. McFadden's ρ^2 for this model was 0.495, suggesting that the model performed well. Further, all parameters were significant ($P < 0.01$) in this model. The H+B model received the majority of the weight of evidence ($w_i = 0.60$), indicating that this model is the best of the candidate set (Table 3.3). Hosmer-Lemeshow results indicated that the both the H+B model ($P = 0.43$) and the global models ($P = 0.73$) met the assumptions of the logistic regression model (Kutner et al. 2005).

The surveyed townships within the lynx range had a mean hare density of 0.64 hares/ha (SD = 0.19, n = 31) versus 0.54 hares/ha (SD = 0.17, n = 19) for townships outside the lynx range (Figure 3.5).

HOME RANGE-SCALE

Within the range of lynx distribution, 182 buffers of 3.15 km^2 were analyzed and the H+B+H*B model was identified as the best of the 15 candidates (Table 3.4). These models took the forms:

ln (B/1-B) = 0.179 + 2.622**ln*(hares) – 6.777* *ln*(hares) – 0.588 if bobcat were present and *ln* (B/1-B) = 0.179 + 2.622**ln*(hares) if bobcat were absent. McFadden's ρ^2 for this

Table 3.3. Akaike Information Criterion (AIC) model selection results for 15 *a priori* candidate models compared using logistic regression to describe the relationship between five ecological variables and the detection of lynx tracks during snowtracking surveys conducted over 50 townships in northern Maine, U.S.A. from January-March, 2003-2005. K = number of estimable parameters, Loss = the maximized log-likelihood, AIC$_c$ = AIC value corrected for small sample size, w_i = Akaike weight.

Model (geographic range-scale)[a]	K	Loss	AICc	)AIC$_c$	w_i
H+B	4	-16.76	42.40	0.00	0.60
H+B+F	5	-16.65	44.66	2.25	0.20
H+B+H*B	5	-16.65	44.67	2.27	0.19
B	3	-23.48	53.47	11.07	0.00
F+B	4	-22.81	54.50	12.10	0.00
F+B+F*B	5	-21.84	55.04	12.64	0.00
H+B+F+E+S+H*B+H*S+H*F+B*F	11	-14.17	57.29	14.89	0.00
H+S	4	-29.67	68.23	25.83	0.00
CONSTANT	1	-33.20	68.49	26.09	0.00
H	3	-31.12	68.77	26.37	0.00
E	3	-31.40	69.33	26.93	0.00
S	3	-31.52	69.56	27.16	0.00
H+F	4	-30.75	70.40	28.00	0.00
H+S+H*S	5	-29.67	70.71	28.30	0.00
F	3	-32.59	71.71	29.31	0.00
H+F+H*F	5	-30.36	72.08	29.68	0.00

[a] H = mean estimated hare density (hares/ha); B = bobcat occurrence; F = mean fisher harvest (fisher/mi^2); S = maximum snow depth, 2004-2005 (cm); E = mean elevation (m). See methods for a more complete description of variables.

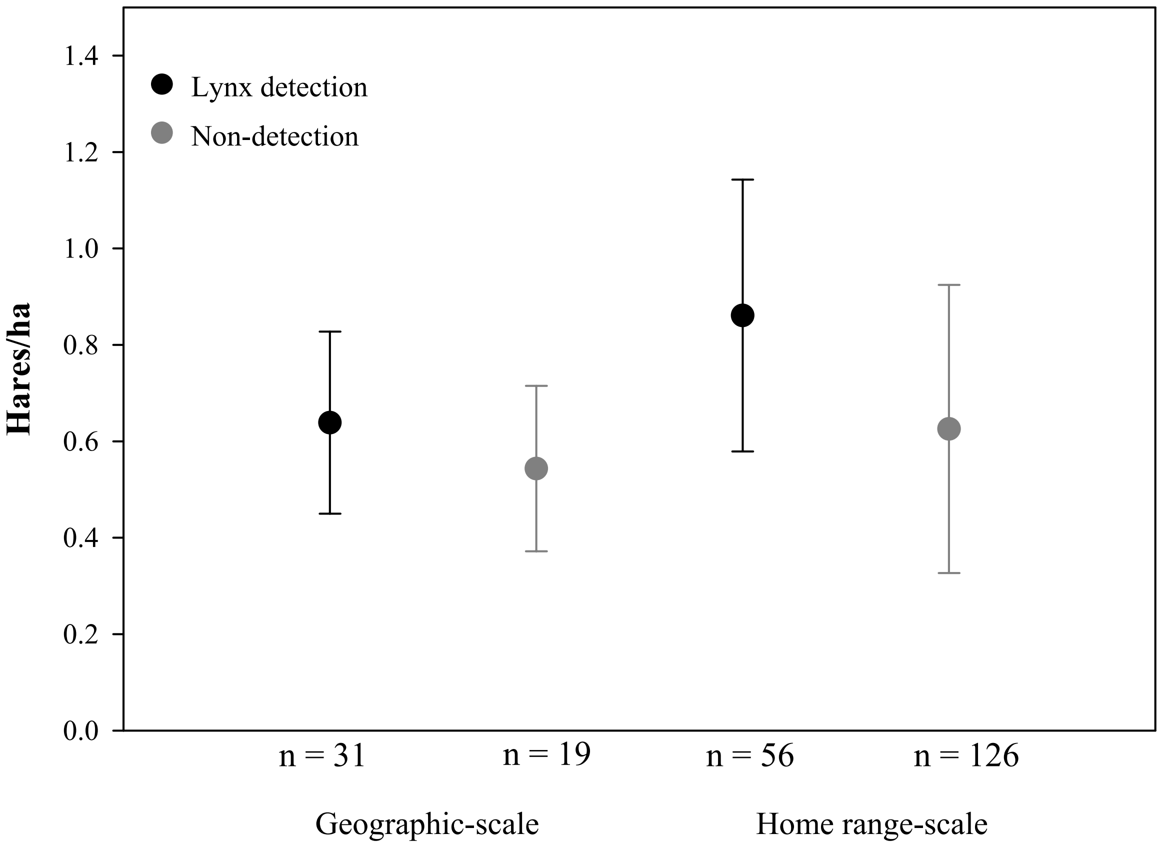

Figure 3.5. Mean hare densities (hares/ha) ± SD for townships and simulated core areas where lynx were and were not detected at the geographic- and home range-scales of analysis in northern Maine, U.S.A.

Table 3.4. Akaike Information Criterion (AIC) model selection results for 15 *a priori* candidate models compared using logistic regression to describe the relationship between five ecological variables and the occurrence of lynx for 3.15 km^2 simulated home ranges over 32 townships within the lynx range surveyed in northern Maine, U.S.A. from January-March, 2003-2005. K = number of estimable parameters, Loss = the maximized log-likelihood, AIC_c = AIC value corrected for small sample size, w_i = Akaike weight.

Model (home range-scale)[a]	K	Loss	AIC_c	)AIC_c	w_i
H+B+H*B	5	-91.73	193.81	0.00	0.89
H+B+F+E+S+H*S+H*B+H*F+B*F	11	-87.37	198.29	4.48	0.09
H	3	-98.70	203.54	9.73	0.01
H+S	4	-98.63	205.48	11.68	0.00
H+F	4	-98.68	205.58	11.77	0.00
H+B	4	-98.70	205.62	11.81	0.00
H+F+H*F	5	-97.98	206.30	12.49	0.00
H+S+H*S	5	-98.61	207.56	13.75	0.00
H+B+F	5	-98.68	207.69	13.88	0.00
CONSTANT	1	-112.34	226.70	32.89	0.00
B	3	-111.61	229.35	35.54	0.00
F	3	-112.10	230.34	36.53	0.00
F+B	4	-111.22	230.67	36.86	0.00
E	3	-112.32	230.78	36.98	0.00
S	3	-112.34	230.81	37.00	0.00
F+B+F*B	5	-110.97	232.29	38.48	0.00

[a] H = mean estimated hare density (hares/ha); B = bobcat occurrence; F = mean fisher harvest (fisher/mi^2); S = maximum snow depth, 2004-2005 (cm); E = mean elevation (m). See text for a more complete description of variables.

model was 0.183. In this model, H and H*B were statistically significant variables ($P < 0.01$ for both parameters), but neither the bobcat main effect nor the constant were statistically significant ($P = 0.47$ for the constant and $P = 0.42$ for the bobcat variable). The weight of evidence for the H+B+H*B model was 0.89, indicating that this model is the best of the candidate set (Table 3.4). Hosmer-Lemeshow results indicated that the both the H+B+H*B model ($P = 0.68$) and the global models ($P = 0.96$) met the assumptions of the logistic regression model (Kutner et al. 2005). Lynx detection buffers had a mean hare density of 0.86 hares/ha (SD = 0.28, n = 56), compared to the non-detection buffers which had a mean hare density of 0.63 hares/ha (SD = 0.30) (Figure 3.5).

POST HOC **ANALYSIS**

Both the geographic- and home range-scales of models identified hare density as important in describing lynx occurrence. Because hare density was generated using land cover classes, many of which are related to forest management, I wished to understand which of these classes were contributing most to this variable. Additionally, I wished to evaluate the form of the relationship between hare density and lynx occurrence to determine if this relationship was linear or if a density-dependent response was present in the data. I therefore evaluated a set of *post hoc* models to test the ability of alternative hare and land class variables to better explain the variance in lynx occurrence at both the geographic- and home range-scales. Variables studied were: 1) the square of hare density to evaluate density-dependence; 2) number of hares per buffer to represent total biomass of prey available to lynx (this variable was tested only on the home range-scale because townships encompassed different areas); 3) number of pixels in the regenerating clearcut class; 4) number of pixels in the partial harvest class; and 5) number of pixels in the mature class.

I used these variables in place of the H variable in the H+B for the geographic-scale data. At the home range-scale, lynx and bobcats co-occurred for only 13 of 182 cases and in the interest of identifying a better predictive model for the majority of the lynx range, I decided to drop these 13 cases from the *post hoc* analysis and to evaluate the performance of these variables without the confounding influence of the bobcat variable and H*B interaction term.

At the geographic-scale, the R+B model performed as well as the H+B model, with a)AIC < 2 and a w_i of 0.43 (versus 0.44 for the H+B model, Table 3.5), indicating that the regenerating clearcut class is able to explain the variance in lynx occurrence as well as the H variable at this scale (Table 3.5). Both variables were significant in the R+B model ($P = 0.004$ for R and $P < 0.001$ for B) and this model took the form:

$ln\ (B/1\text{-}B) = -1.986 + 0.039 * R^{½} - 5.823$ if bobcat are present and

$ln\ (B/1\text{-}B) = -1.986 + 0.039 * R^{½}$ if bobcat are absent.

At the scale of the home range, the hares model (H) was the best of the *post hoc* candidate models with a McFadden's $\rho^2 = 0.171$ and a w_i of 0.53 (Table 3.5). This variable was significant ($P < 0.001$) and the H model took the form:

$ln\ (B/1\text{-}B) = 0.179 + 2.622 * ln(\text{hares})$.

At both scales of analysis, the partial harvest and mature classes failed to explain variance in the response data. Additionally, the total number of hares did not perform as well as the mean density of hares (H) in the *post hoc* analyses. Density dependence did not appear significant in describing lynx occurrence at the geographic-scale, but was the

Table 3.5. Akaike Information Criterion (AIC) model selection results for *post hoc* candidate models compared using logistic regression to evaluate the relationship of alternative variables describing hare density, bobcat occurrence, and land cover classes to lynx occurrence detected during snowtracking surveys conducted in northern Maine, U.S.A. from January-March, 2003-2005. K = number of estimable parameters, Loss = the maximized log-likelihood, AIC$_c$ = AIC value corrected for small sample size, w_i = Akaike weight.

Model (geographic range-scale)[a]	K	Loss	AICc	)AIC$_c$	w_i
H+B	4	-16.76	42.40	0.00	0.44
R+B	4	-16.78	42.45	0.05	0.43
H+ H^2+B	5	-16.74	44.85	2.45	0.13
M+B	4	-22.86	54.62	12.21	0.00
PH+B	4	-23.47	55.83	13.43	0.00

Model (home range-scale)[a]	K	Loss	AICc	)AIC$_c$	w_i
H	3	-85.12	176.38	0.00	0.53
H+H^2	4	-84.60	177.44	1.06	0.31
R	3	-86.82	179.79	3.41	0.10
T	3	-87.41	180.97	4.59	0.05
M	3	-94.36	194.87	18.50	0.00
PH	3	-100.90	207.96	31.58	0.00

[a] H = mean estimated hare density (hares/ha); B = bobcat occurrence; R = pixels in regenerating clearcut class; M = pixels in mature class; PH = pixels in partial harvest class; T = total hares. See text for a more complete description of variables.

second ranked model on the home range-scale with a)AIC < 2. The squared term was not significant in this model ($P = 0.32$); thus, I cannot conclude with certainty that a density dependent relationship was present in these data. At both scales, the top models fit the assumptions of the logistic regression model based on Hosmer-Lemeshow tests using the same group sizes as in *a priori* models ($P = 0.43$ for geographic- and $P = 0.77$ for home range-scale).

MODEL VALIDATION

When bobcat occurrence was not considered at the home range-scale, the model with only the hare density variable (H) performed best in *post hoc* model comparisons. I used non-overlapping 3.15 km^2 buffers that were removed from the build dataset due to constraints on the number of buffers analyzed per township. Thus, the resulting validation dataset consisted of 10 detection buffers and 86 non-detection buffers (Appendix H). If the probability of lynx detection for a validation buffer was > 50% for a detection buffer or < 50% for a non-detection buffer, the observation was considered to be correctly classified (Fielding and Bell 1997).

The hares model was accurate in predicting lynx occurrence and absence for the 3.15 km^2 validation buffers. The model correctly predicted eight of ten lynx detections (80%) in the validation set with a mean occurrence probability of 64.9% (Table 3.6). This accuracy may be inflated, however, because seven of the ten validation buffers with lynx detection were taken from surveys of two townships on the Clayton Lake study site that have unusually high hare densities (Appendix H). The H model correctly predicted 46.0% of the detections in the build data. The model correctly predicted 89.9% of the non-detections used to build the model and 90.7% of the non-detection buffers in the

Table 3.6. Correct classification of lynx occurrence (based on a 50% probability) by a hare density logistic regression model for build and validation datasets using 3.15 km^2 simulated home ranges for lynx in northern Maine, U.S.A.

	Build data				Validation data			
Lynx occurrence	Number correctly classified	Total	Percent correct	Mean probability	Number correctly classified	Total	Percent correct	Mean probability
Detection	23	50	46.0	43.4	8	10	80.0	64.9
Non-detection	107	119	89.9	23.8	78	86	90.7	22.5
Total	141	169	83.4		86	96	89.6	

validation set (Table 3.6). Overall model accuracy was 83.4% for the build dataset and 89.6% for the validation dataset (Table 3.6).

DISCUSSION

Snowshoe hare density was an important variable describing lynx occurrence at both the geographic- and home range-scales. Although, this was expected given the reliance of lynx on hares during previous studies (Poole 1994, O'Donoghue et al. 1997), this relationship has never been investigated using field-derived estimates for hare densities at the 1st and 2nd order of resource selection (Johnson 1980). Hare densities were higher within the 3.15 km^2 simulated home ranges around lynx occurrences than across the townships within the geographic range of lynx (0.86 hares/ha versus 0.64 hares/ha), indicating that lynx are likely positioning their home ranges around areas of higher relative hare density (Figures 3.5, 3.6).

Modeling results of reintroduction efforts for lynx in the southern portion of the range estimated the minimum range of hare densities required for the persistence of a lynx population at 1.1-1.8 hares/ha (Steury and Murray 2004). The mean hare density within simulated home ranges around lynx occurrence in this study (0.86 hares/ha, SE = 0.04) is slightly lower than this range, but is consistent with Ruggiero et al. (2000) who concluded that the hare density needed for lynx persistence is > 0.5 hares/ha. Further, Krebs et al. (2001) reported decreases in lynx survival and increased emigration at hare densities of 0.3-0.8 hares/ha in Yukon, Canada.

The mean of 0.86 hares/ha was generated from simulated home ranges centered around lynx tracks and does not represent the range of hare densities used by resident

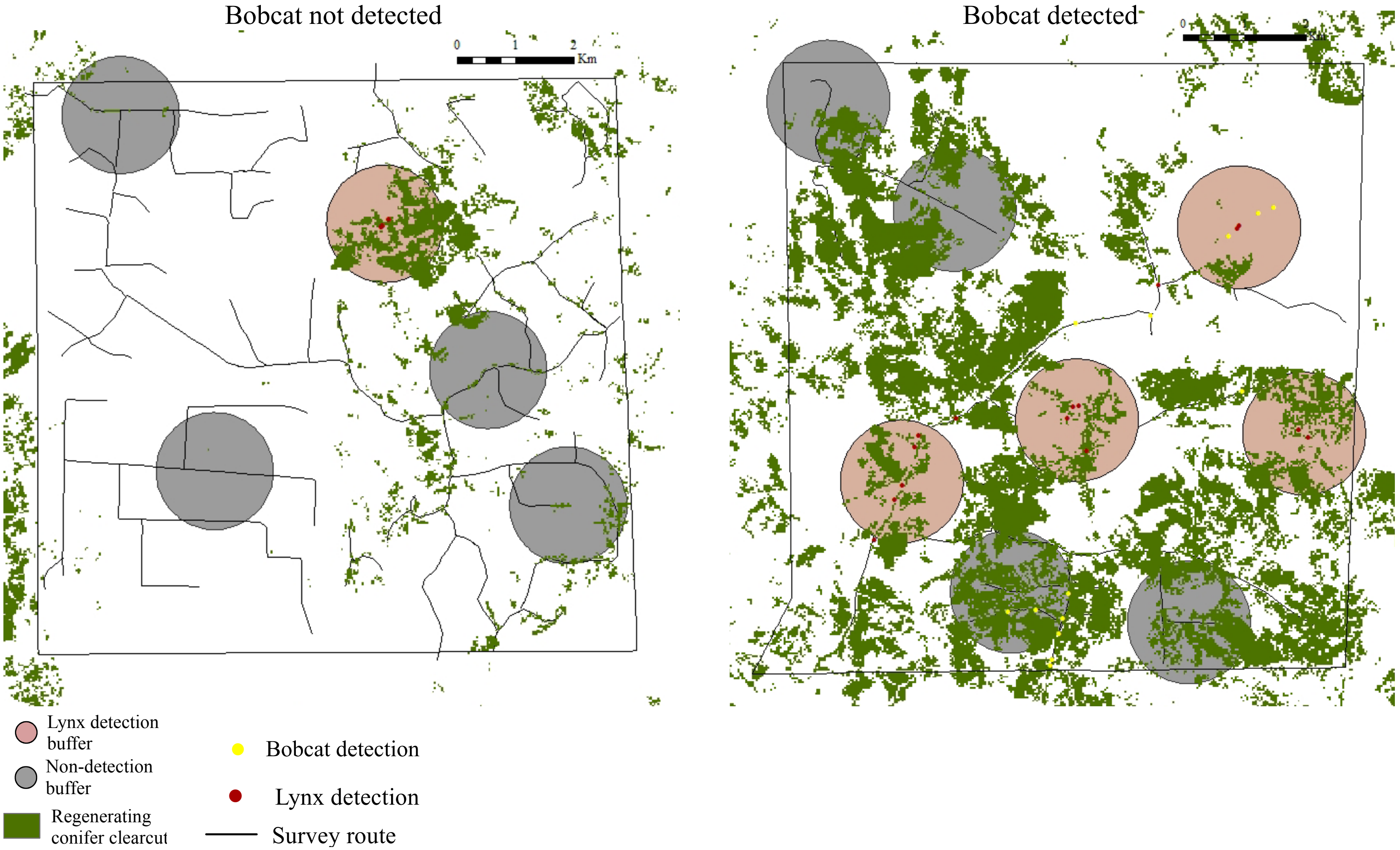

Figure 3.6. Placement of simulated detection and non-detection lynx buffers in a township without bobcat detection (left) and with bobcat detection (right) in northern Maine, U.S.A. Note that in a township without bobcats (left), lynx use areas of high hare density (i.e., regenerating clearcuts); whereas in townships with bobcat detections (right), lynx use areas with less regenerating clearcut (and therefore lower hare densities).

animals in known home ranges. A portion of lynx tracks detected during snowtracking surveys likely represented transient individuals traveling through “unsuitable” areas, which could lower the mean hare density in simulated lynx home ranges. Thus, the hare density needed to support reproducing resident animals may be higher than the mean of 0.86 hares/ha. Additionally, to estimate hare density over simulated lynx home ranges, a single hare density value was applied to land cover classes without consideration of the variance in these estimates. A median value of 0.8 hares/ha was applied to established partial harvests, but the partially harvested stands from which this median value was obtained varied widely in the hare densities they supported (0.26-1.65 hares/ha, Chapter 1). This variance was not incorporated in the modeling process and therefore, estimated hare densities in simulated lynx detection home ranges likely do not reflect the variance in hare densities in these areas. Finally, misclassification rates for the 2004 GAP map are unknown, but are likely high for the established partial harvest class given the error rate for this class in the 1993 map, and this may have further added to errors in hare density estimates. Hare densities were intended to be used in a relative manner to compare detection areas to non-detection areas. The mean of 0.86 hares/ha represents an estimate of relative hare density in simulated home ranges where lynx were detected and this value should not be used to estimate hare densities needed for lynx population persistence on the landscape.

At the geographic-scale, results of *post hoc* modeling indicate that the area of regenerating clearcuts describes the variance in lynx occurrence as well as hare density (Appendix J). Regenerating clearcuts support the highest hare density of all forest types studied in Maine (Fuller and Harrison 2005, Homyack 2006, Chapter 1) so the relationship between this cover class and lynx occurrence at the geographic-scale likely reflects use of areas of higher hare density by lynx. These results corroborate results of Hoving et al. (2004), who reported a positive association of lynx occurrences with extent of regenerating forest in northern Maine and other studies that have associated habitat use by lynx with dense understory conditions (Murray et al. 1994, Poole 1996, Paragi et al. 1997, Mowat and Slough 2003, Fuller 2006). Regenerating clearcut constituted 8.3% of the total area in the 2004 GAP map and these regenerating areas represent the large clearcuts made to salvage timber from the spruce budworm outbreak of the late 1970's to mid 1980's. Since 1989, however, the annual acres of forest that are clearcut have decreased from 145,357 to 18,779 in 2004 (Maine Forest Service 1990, 2005), an 87% decrease. Currently, clearcuts constitute < 4% of annual harvests, which may result in much less regenerating forest on the landscape in the future. Thus, a decrease in the amount of regenerating forest in northern Maine could have potentially negative implications for lynx conservation in the future if management objectives seek to maintain or increase densities relative to current levels.

The area in the partial harvest class was not statistically associated with lynx occurrence at the two scales studied. The partial harvest class in this study consisted of stands that were established longer than the partial harvests found to be negatively associated with lynx occurrence at the statewide scale (Hoving et al. 2004). Established partial harvest stands likely support higher hare densities than recent partial harvests (Fuller and Harrison 2005, Chapter 1); however, those higher hare densities (median = 0.74 hares/ha, range: 0.26-1.65 hares/ha, Chapter 1) are still substantially lower than has been reported for regenerating clearcuts (mean = 2.10 hares/ha, SE = 0.22, Chapter 1)

(Fuller and Harrison 2005, Homyack et al. 2006), were lower than the mean hare density observed in simulated lynx home ranges (0.86 hares/ha), and were lower than the landscape thresholds suggested in other studies (1.1 hares/ha; Steury and Murray 2004). Companion studies documented that established partial harvests were selected by 6 individual lynx within their home ranges (Fuller 2006). Thus, different responses by lynx to partial harvesting are emerging across different scales, highlighting the importance of considering scale when evaluating habitat relationships of lynx. The lack of statistical significance at the geographic- and home range-scales of lynx occurrences in this study does not prove that lynx are not associated with partial harvests in northern Maine. The partial harvest class had high rates of misclassification for the 1993 GAP classes (Hepinstall et al. 1999). Although accuracy may have improved slightly in the updated version (Legaard and Simons, University of Maine, Orono, *in prep*), the effect of misclassification on type II errors remains uncertain. Additionally, given the ubiquitous (Table 3.1) and dispersed (Appendix J) nature of partial harvests across northern Maine, most lynx would need to encompass much of this forest type within their home ranges (Fuller 2006) and further investigation is needed to more fully understand the relationships of partial harvesting to lynx occurrence.

The Hoving et al. (2004) model predicted the range of lynx to fall within the region of Maine that received total snowfall > 268 cm/year, but this overpredicted the current distribution of lynx. Overestimation was probably the result of Hoving's lack of detailed fine scale (i.e., township- or home range-scale) occurrence data for bobcats. Additionally, my results corroborated Hoving et al.'s (2004) findings that snow was not an important variable in determining the occurrence of lynx within northern Maine. The presence of snow as a dominant predictor variable at a regional scale (i.e., across eastern North America; Hoving et al. 2005), but not at a within-state (Hoving et al. 2004) or within-range (this study) scales suggests that snow may be a surrogate that describes broad-scale distributions of competitors of lynx (e.g., bobcats and fishers).

Despite the limited number of townships with bobcat occurrence within the geographic range of lynx in Maine, these data suggest both geographic range- and home range-scale allopatry between these two species. This is consistent with ecological theory predicting high competitive potential between species with high overlap in prey use, habitat use patterns, and body size, and suggests a competitive relationship between these two species (MacArthur 1972, Caughley and Sinclair 1994, Dayan and Simberloff 1996). Bobcat occurrence seemed to limit the distribution of lynx occurrence at the geographic-scale. As a single variable model, bobcat occurrence outperformed hare density in the analysis of the geographic-scale data ()AIC = 15.3, Table 3.3), suggesting that bobcat occurrence is the most important variable explaining the distribution of lynx occurrence in Maine. Alternatively, the significance of the bobcat variable in these models could be a result of the distribution of bobcat occurrences in the southern portion of the study area and the ability of this variable to explain the north-south trend in lynx occurrences, irrespective of competitive relationships. This alternative explanation is unlikely, however, given the significance of the interaction term between bobcat occurrence and hare density in the home range-scale models.

The interaction term between hares and bobcats was important at both scales, which further supports the hypothesis that these two species are competing for prey. On the geographic-scale, the H+B+H*B model had a)AIC$_c$ of only 2.27 compared with the top model (Table 3.3). The interaction term, however, was positive, indicating that the townships where lynx occur have a higher hare density in the presence of bobcats than without bobcats. The coefficient for this interaction term was not statistically significant at the geographic-scale, likely because only two of the 50 townships analyzed had both lynx and bobcat occurrence. In contrast, at the scale of the home range, the interaction term was significant and the coefficient was negative, indicating that in the absence of bobcats, lynx use areas with higher hare densities than in the presence of bobcats (Figure 3.6). One possible explanation for these discrepancies in the influence of the H*B interaction term is that, within a 100 km^2 township, bobcats are forcing lynx to use areas of lower hare density than those available. This could mean that lynx might co-occur with bobcats only in areas where hare densities were high enough to support both species. Competitive exclusion at the home range-scale may be the mechanism by which the bobcat population is limiting the distribution of lynx at the southern portion of their range in Maine. These results may be suggestive of the relationship between lynx and bobcats at the geographic range-scale, but more research is needed to understand the nature of the interaction between these species at the home range-scale.

Although bobcat occurrence may be limiting the southern distribution of lynx in Maine, it remains unclear what is limiting bobcat distribution to the north. It has been hypothesized that snow depth acts as a mediator of competition between lynx and bobcats. Bobcats have a higher foot loading than lynx and are unable to hunt hares as successfully in areas with deep, soft snow (Krohn et al. 2004, Hoving et al. 2005), and suffer energetically and exhibit high mortality when winters are severe (Litvaitis et al. 1986b). Neither maximum snow depth nor elevation were able to describe the variance in lynx occurrence at either scale of analysis; further, these variables were positively correlated with bobcat occurrence (Appendix K).

Bobcats occurred in only 13 of the 182 buffers used to build the home range-scale model and these conditions were not representative of the majority of the habitat within the lynx range. When these 13 cases were removed from the analysis during *post hoc* modeling, hare density best described the variance in home range-scale occurrences of lynx (McFadden's $\rho^2 = 0.183$ for the *a priori* model versus 0.171 for the *post hoc* model). I conclude that the model based on hare density (H) best describes the relationship between the ecological variables studied and lynx occurrence within the species' geographic range in Maine.

This study was designed to be descriptive; therefore, few data were reserved to validate the H model in favor of building stronger descriptive models. More rigorous validation of these results will be provided by future research and survey efforts. At the home range-scale, non-detection buffers outnumbered detection buffers two to one because non-detection buffers were simulated around random points and their numbers were limited only by distance constraints between buffers. The H model correctly classified non-detections better than detection buffers, which suggests that this model may be overfit to non-detections. If lynx were present in a township where they were not detected, then the variance in hare density would be expected to be higher for non-detections versus detections and the model might be expected to poorly classify non-detection buffers. This was not the case in this study (Table 3.6, Figure 3.5), suggesting that false negatives may have been rare in snowtracking surveys. Lynx detections likely included transient individuals; therefore this model can only be used to predict the occurrence of all lynx, regardless of residency status.

Detection/non-detection modeling leads to a comparatively high risk of type II error (not finding a difference when one is present) (MacKenzie 2005). This arises, in part, because the probability that a non-detection is truly an absence is unknown and areas of non-detection may actually be used by lynx (MacKenzie 2005, 2006). Additionally, small sample sizes may have contributed to reduced statistical power and may, therefore, have limited my ability to evaluate the relationships between predictor variables and lynx occurrence. Therefore, variables that were not significantly associated with lynx occurrence in these analyses may be indeed be important and I cannot conclude that fisher harvest density, maximum snow depth, elevation, partial harvests, mature forest, or total hares were not associated with lynx occurrence in Maine.

Several assumptions were made in the course of the GIS modeling that should be acknowledged in discussing results from these analyses. Snowtracking surveys were conducted over 3 years, but this annual variation, if present, was not incorporated in the analyses (Appendix E). In so doing, I assumed that no major fluctuations in the lynx population occurred over this time period that would affect the probability of lynx detection in a given township. Although lynx and hare populations in the northern boreal forest exhibit population cycles (Krebs et al. 2000), there is no evidence that lynx (J. Vashon, personal communication) or hare (Hodges 2000, D.J. Harrison, University of Maine, unpublished data) populations in the southeastern portion of their distributions undergo cyclic changes.

The logistic regression model assumes independence of observations and this assumption was likely violated in the home range-scale analyses. I employed a distance criterion (in the form of the simulated buffers) and a maximum for the number of buffers that could be analyzed from the same survey to minimize these effects. Lynx are known to make long-distance movements up to 1,100 km (Poole 1997), which could decrease the likelihood that snow-tracking surveys represent independent observations if detections included transient individuals as a substantial portion of the sample.

Modeling lynx occurrences across the landscape of northern Maine using a GIS is a very coarse approach. Datasets for each predictor variable are likely to include inaccuracies. In applying stand-scale estimates of hare density to land cover classes, I am not considering the effects of landscape scale processes on these estimates. Additionally, field data were not available for every land cover class used in the analyses, forcing me to infer a hare density for these classes from the available literature. Snow depth data were used for only 10 dates during 2004 and 2005, and may not have included periods of high snowfall that may have melted between the dates used to index snow depths. The relationships between lynx occurrence and the ecological variables studied are specific to this study area and cannot be assumed to apply to other areas of North America. Thus, others should be cautious when extrapolating these findings beyond the Acadian forest.

CONCLUSIONS

Snowshoe hare density was an important variable describing lynx occurrence at both scales studied. Hare densities were higher within the 3.15 km^2 home ranges simulated around lynx occurrences than across the townships within the geographic range of lynx (0.86 hares/ha versus 0.64 hares/ha), indicating that lynx are likely positioning their home ranges around areas of higher relative hare density within the lynx range in northern Maine. At the scale of the geographic range, the area of regenerating clearcuts was a comparable surrogate for hare density in describing patterns of lynx occurrence. Regenerating clearcuts support the highest hare density of forest types studied in Maine and the relationship between this cover class and lynx occurrence likely reflects use of areas of higher hare density by lynx. A decreasing trend in the amount of clearcuts that are created each year may result in less regenerating forest on the landscape in the future, which could have potentially negative implications for lynx conservation efforts aimed at maintaining current numbers of lynx or increasing future populations.

Despite the limited number of townships with occurrence of both bobcats and lynx, these data suggest geographic- and home range-scale allopatry and a competitive relationship between these two species. Bobcat occurrence seemed to limit the distribution of lynx occurrence at the geographic-scale and the interaction of bobcat occurrence and hare density was significant at the home range-scale, suggesting a competitive mechanism for this allopatric distribution.

Bobcat occurrence was rare within the range of lynx occurrence, thus I recommend hare density as the best variable for describing the relationship between the ecological variables studied and lynx occurrence within the species' geographic range in Maine. The model predicting home range-scale occurrences of lynx based on hare density accurately predicted non-detections, but was less successful at correctly classifying detections. This model had an overall accuracy of 83.4% for build data (n = 169) and 89.6% (n = 96) for validation data.

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APPENDICES

APPENDIX A

Vegetation characteristics in 36 forest stands measured in northern Maine during the leaf-on season, 2005.

Table A.1. Vegetation characteristics measured in 36 forest stands (21 partially harvested stands and 15 regenerating conifer clearcuts) in northern Maine, U.S.A. during the leaf-on season, 2005. Stand numbers relate to Figure 1.1.

			Variable							
Stand number	Stand ID[a]	Stand type[b]	Percent canopy closure[c]	Basal area (m^2/ha)[d]	Visual obstruction (m)[e]	Logs/ha[f]	Conifer trees/ha[g]	Deciduous trees/ha[g]	Dead trees/ha[g]	Average DBH trees (cm)[h]
1	AF1	PH	92.5	32.7	3.71	1400	25	600	25	15.9
2	AF2	PH	82.7	34.8	3.04	750	350	575	50	16.3
3	AF3	PH	96.0	37.7	2.12	825	375	525	125	16.8
4	AF4	PH	81.5	28.7	2.36	1875	275	475	100	16.4
5	AF5	PH	80.6	27.3	2.35	2080	240	700	200	16.1
6	AF7	PH	88.4	30.6	2.33	2375	300	425	75	14.3
7	CLSH1	PH	91.6	36.2	1.79	850	375	500	100	12.7
8	CLSH2	PH	74.4	19.2	2.15	1452	95	167	95	21.3
9	CLSH3	PH	88.1	24.3	2.28	1525	25	400	50	16.6
10	CLSH4	PH	90.6	31.9	3.35	1400	300	675	25	13.6
11	CLSH5	PH	90.9	30.5	4.60	1100	0	1100	50	13.0
12	S11	PH	56.2	26.1	4.52	2075	525	75	275	14.3

Table A.1. Continued.

			Variable							
Stand number	Stand ID[a]	Stand type[b]	Percent canopy closure[c]	Basal area (m^2/ha)[d]	Visual obstruction (m)[e]	Logs/ha[f]	Conifer trees/ha[g]	Deciduous trees/ha[g]	Dead trees/ha[g]	Average DBH trees (cm)[h]
13	S12	PH	60.0	29.6	3.72	2850	750	150	100	11.8
14	S13	PH	35.4	16.0	2.76	325	475	0	25	12.4
15	S14	PH	57.4	28.2	2.00	1825	500	0	200	16.0
16	S15	PH	68.0	27.5	1.60	2600	275	50	125	13.2
17	S16	PH	59.0	28.9	3.63	875	1100	0	100	17.5
18	S17	PH	69.9	33.5	1.59	1425	475	75	100	13.9
19	S21	PH	41.5	15.0	5.54	2400	375	200	25	22.5
20	S22	PH	79.5	37.4	2.66	1075	1100	350	75	13.9
21	S23	PH	74.7	24.9	2.51	1850	425	550	25	10.7
	PH median		79.5	28.9	2.51	1452	375	400	95	14.3
	(range)		(60.6)	(22.7)	(3.95)	(2525)	(1100)	(1100)	(250)	(11.9)

Table A.1. Continued.

			Variable							
Stand number	Stand ID[a]	Stand type[b]	Percent canopy closure[c]	Basal area (m^2/ha)[d]	Visual obstruction (m)[e]	Logs/ha[f]	Conifer trees/ha[g]	Deciduous trees/ha[g]	Dead trees/ha[g]	Average DBH trees (cm)[h]
22	CLREG1	REG	68.2	29.9	2.07	450	1100	100	150	10.2
23	CLREG2	REG	66.0	34.1	0.92	1550	450	50	50	17.7
24	CLREG3	REG	71.8	24.6	1.25	850	1150	0	0	9.3
25	CLREG4	REG	55.7	32.9	1.87	1250	750	100	0	8.6
26	JH01C	REG	79.0	46.6	2.81	550	2050	100	50	10.4
27	JH02C	REG	87.0	51.9	3.33	1600	1850	150	0	10.6
28	JH03C	REG	83.5	43.5	1.91	450	1600	0	50	10.0
29	JH04C	REG	85.5	43.2	1.66	1150	1650	100	100	12.0
30	JH05C	REG	82.9	41.6	3.63	1150	1900	350	100	11.3
31	JH54C	REG	78.2	36.5	2.53	600	2050	100	100	11.3
32	JH56C	REG	78.6	48.2	2.04	650	1900	0	0	11.4
33	SM4B	REG	88.8	55.4	1.24	1000	1800	100	150	13.9

Table A.1. Continued.

			Variable							
Stand number	Stand ID[a]	Stand type[b]	Percent canopy closure[c]	Basal area (m^2/ha)[d]	Visual obstruction (m)[e]	Logs/ha[f]	Conifer trees/ha[g]	Deciduous trees/ha[g]	Dead trees/ha[g]	Average DBH trees (cm)[h]
34	SM4C	REG	90.3	48.7	1.65	1250	1000	450	100	12.7
35	SM4D	REG	68.6	31.8	1.31	800	600	0	150	18.0
36	SM4E	REG	82.4	43.8	1.62	1150	1200	150	100	11.0
Conifer regen. median			79.0	43.2	1.87	1000	1600	100	100	11.3
(range)			(34.5)	(30.8)	(2.71)	(1150)	(1600)	(450)	(150)	(9.4)

Table A.1. Continued.

			Variable							
Stand number	Stand ID[a]	Stand type[b]	Conifer stems > 1.5m/ha	Deciduous stems >1.5m/ha	Dead stems >1.5m/ha	Total stems >1.5m/ha	SCU >1.5m/ha	Stumps/ha[i]	Average stump diameter (cm)	Basal area removed (m^2/ha)[j]
1	AF1	PH	200	9650	1150	11000	10250	375	21.9	14.1
2	AF2	PH	2800	9725	425	12950	18125	400	28.2	24.9
3	AF3	PH	1075	9925	750	11750	13150	250	21.4	9.0
4	AF4	PH	3150	13150	550	16850	22600	425	22.9	17.5
5	AF5	PH	720	13720	500	14940	15880	440	23.6	19.2
6	AF7	PH	3950	19825	2725	26500	31675	750	23.7	33.0
7	CLSH1	PH	1625	16475	3175	21275	21350	375	34.0	34.1
8	CLSH2	PH	929	16310	595	17833	19095	476	33.2	41.3
9	CLSH3	PH	0	15275	1100	16375	15275	350	35.0	33.7
10	CLSH4	PH	625	9075	1450	11150	10950	400	26.3	21.8
11	CLSH5	PH	3350	4800	1125	9275	14850	525	20.6	17.5
12	S11	PH	10975	3150	250	14375	36075	675	17.2	15.7

Table A.1. Continued.

Stand number	Stand ID[a]	Stand type[b]	Variable Conifer stems > 1.5m/ha	Deciduous stems >1.5m/ha	Dead stems >1.5m/ha	Total stems >1.5m/ha	SCU >1.5m/ha	Stumps/ha[i]	Average stump diameter (cm)	Basal area removed (m^2/ha)[j]
13	S12	PH	4300	6600	1550	12450	19500	400	23.0	16.6
14	S13	PH	4825	3450	325	8600	17925	450	19.7	13.7
15	S14	PH	15975	5525	950	21975	53450	475	15.5	9.0
16	S15	PH	19050	2175	725	21700	59325	450	18.5	12.1
17	S16	PH	3875	4625	450	8725	16250	200	19.0	5.7
18	S17	PH	24825	2600	3950	31375	77075	425	25.8	22.3
19	S21	PH	1500	1550	625	3675	6050	375	32.7	31.4
20	S22	PH	8250	6075	6475	20800	30825	325	27.5	19.3
21	S23	PH	5575	5125	2075	12675	21850	175	28.4	11.1
	PH median		3350	6600	950	14375	19095	400		17.5
	(range)		(24825)	(18275)	(6225)	(27700)	(71025)	(575)	23.6 (19.5)	(35.6)

Table A.1. Continued.

			Variable							
Stand number	Stand ID[a]	Stand type[b]	Conifer stems > 1.5m/ha	Deciduous stems >1.5m/ha	Dead stems >1.5m/ha	Total stems >1.5m/ha	SCU >1.5m/ha	Stumps/ha[i]	Average stump diameter (cm)	Basal area removed (m^2/ha)[j]
22	CLREG1	REG	12500	2200	4250	18950	39700	550	24.7	26.4
23	CLREG2	REG	25350	3500	1800	15325	79550	600	18.5	16.1
24	CLREG3	REG	11050	800	350	12200	33950	450	23.3	19.1
25	CLREG4	REG	15300	4750	1350	21400	50650	750	24.0	33.9
26	JH01C	REG	8200	1050	2600	11850	25650	800	16.6	17.3
27	JH02C	REG	7050	2500	7950	17500	23650	1100	16.4	23.3
28	JH03C	REG	11850	2500	3000	17350	38050	650	26.9	36.8
29	JH04C	REG	11250	1800	6050	19100	35550	1000	19.5	29.7
30	JH05C	REG	4100	3550	6700	14350	15850	500	19.8	15.4
31	JH54C	REG	8850	2000	1050	11900	28550	400	18.6	10.8
32	JH56C	REG	6800	2450	3700	12950	22850	450	26.5	24.9
33	SM4B	REG	16700	4100	6150	26950	54200	200	29.6	13.8

Table A.1. Continued.

			Variable							
Stand number	Stand ID[a]	Stand type[b]	Conifer stems > 1.5m/ha	Deciduous stems >1.5m/ha	Dead stems >1.5m/ha	Total stems >1.5m/ha	SCU >1.5m/ha	Stumps/ha[i]	Average stump diameter (cm)	Basal area removed (m^2/ha)[j]
34	SM4C	REG	13500	5450	10000	28950	45950	300	36.0	30.5
35	SM4D	REG	15500	1050	1000	17550	47550	500	23.4	21.5
36	SM4E	REG	15400	1450	5350	22200	47650	200	20.5	6.6
Conifer regen. median			11850	2450	3700	17500	38050	500		21.5
(range)			(21250)	(4650)	(9650)	(17100)	(63700)	(900)	23.3 (19.5)	(30.2)

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[a] Stand ID, AF = stands surveyed by A. Fuller in 1997-1998, CLSH = stands selectively harvested 8-12 years prior to survey located at Clayton Lake, S = conifer-dominated partial harvested stands located in northern Maine, CLREG = regenerating conifer stands treated with herbicide, 20-30 years post harvest located at Clayton Lake, JH = stands surveyed by J. Homyack in 2001-2002, SM = stands surveyed by S. Mullen in 2001-2003.

[b] Stand type, PH = partially harvested stands (see Table 1.2 for further descriptions of partial harvest stands), REG = regenerating conifer stands treated with herbicide, 20-30 years post harvest.

[c] Percent canopy closure measured with a spherical densitometer at 1m.

[d] Basal area measured with a $2m^2/ha$ wedge prism and includes live and dead trees.

[e] Visual obstruction measured as a continuous variable as the distance to obstruction over 1m.

[f] Logs were counted if >1m intersected the plot boundary and sound.

[g] Trees were counted if >half of the tree intersected the plot boundary.

[h] DBH = diameter at 1.37m.

[i] Stumps were counted and measured if sound and >half of the stump intersected the plot boundary.

[j] Basal area removed = $\pi*(1/2*\text{mean stump diameter})^2$ * mean number of stumps/stand.

APPENDIX B

Photographs of partially harvested study stands in northern Maine.

Figure B.1. Photographs of selection harvest stands described in Table 1.2. Stands shown are AF2 (upper left), CLSH2 (upper right), AF5 (leaf-on, lower left), and AF5 (leaf-off, lower right).

Figure B.2. Photographs of shelterwood stands described in Table 1.2. Stands shown are S11 (upper left and right), S16 (lower left), and S17 (lower right).

APPENDIX C

An assessment of potential observer and substrate bias in counts of snowshoe hare pellets.

The objectives of this pilot study were to evaluate two assumptions made in estimating hare density from pellet counts:

1. Each observer will detect the same number of pellets at a given plot.
2. The ability of observers to detect pellets does not change in different types of substrate.

METHODS

To evaluate the validity the 2 assumptions above, I tested for observer bias and the effect of substrate on pellet counts. I chose 4 ground types that were common in my study: “needles,” “leaf litter,” “raspberries/debris,” and “sphagnum moss.” I established 10 adjacent pellet plots in areas that represented each of these ground types. To assess observer bias, two full-time technicians and I counted each of the 10 plots at each site, leaving all pellets on the plot for the next observer to count. I scattered previously collected pellets over the plots to ensure that no plot would receive a zero count. Each observer was instructed to count every other pellet that intersected the plot boundary and a time limit of 10 minutes/plot ensured relatively equal counting effort across plots. Each observer attached a string to the two stakes demarcating the plot boundaries because the string placement can affect the number of pellets counted and is a potential source of bias. See Chapter 1 for pellet count methods. This resulted in a sample size of 40 plots for each observer (n = 120 total).

After each plot was counted by each observer, we cleared each plot of all pellets and attached strings to plot stakes. I then placed a number of pellets on each plot ranging from 10 to 45 and recorded this number without revealing it to the observers. Both observers counted the pellets on each of the 10 plots, leaving pellets in place for the next observer. Nine of the 20 observations for the leaf litter site (9 of 80 total observations) were excluded from the analysis due to the possibility that these plots had not been sufficiently cleared of pellets before counting.

To statistically evaluate the presence of observer bias, I used a one-way Analysis of Variance (ANOVA) model to test the effect of observer on pellet count. Pellet counts did not appear normally distributed in a dot density plot and I therefore transformed this response variable for this analysis using a natural log transformation. I used a Generalized Linear Model (GLM) to compare detectability between the four ground types and the two observers. In these models, I used the number of pellets planted as a covariate because this variable is directly related to the number of pellets counted at each plot. To ensure that no observer bias confounded detectability results, I included the observer in the GLM as a predictor variable and tested for a main effect of this variable in addition to interaction effects with ground type. I also included a squared term for the number of pellets planted to determine if the relationship between the number of pellets detected changed with increasing number of pellets planted. I used a Tukey test for pairwise comparisons to compare the detectability of pellets between ground types on a *post hoc* basis.

The ANOVA and GLM models assume that the error terms are normally distributed with constant variance and no outliers are present in the data. I used a scatterplot of the semi-studentized residuals to assess the constancy of variance and to evaluate the presence of outliers. To further test for non-constancy in the error terms, I used a Brown-Forsythe test. I created normal probability plots to test the correlation of the semi-studentized residuals with their expected values under normality.

RESULTS

No significant difference in log transformed pellet count existed between the three observers studied (*F* = 0.04, *P* = 0.96), indicating that trained observers were similar in their ability to detect pellets. A scatterplot of semi-studentized residuals against fitted values for this analysis did not indicate outliers or non-constant variance. The Brown-Forsythe test did not find non-constant variance among the three observers (F = 0.07, *P* = 0.94); however error terms were non-normally distributed (correlation coefficient for normal probability = 0. 98).

Substrate type was significant as a main effect in the GLM (*F* = 30.31, *P* < 0.01) and a *post hoc* Tukey test found that the number of pellets detected in "sphagnum" plots was significantly lower than "raspberry/debris" plots (*P* < 0.01), which was significantly lower than "needles" and "leaf litter" plots (*P* = 0.03), which did not differ from each other (*P* = 0.65) (Figure A.1). Observer was not significant as a main effect in this analysis (*F* = 1.19, *P* =0.28) nor was the interaction effect between ground types and observers (*F* = 0.41, *P* = 0.74). The number of pellets counted at each plot did not change with increasing number of pellets planted (*F* = 0.28, *P* = 0.60), indicating that the ability of observers to detect pellets did not change at higher pellet densities.

A scatterplot of the semi-studentized residuals showed a relatively constant variance with only one outlier. A Brown-Forsythe test at $\alpha = 0.05$ could not find a difference between count variances of the four substrate types (*F* = 1.24, *P* = 0.30). A normal

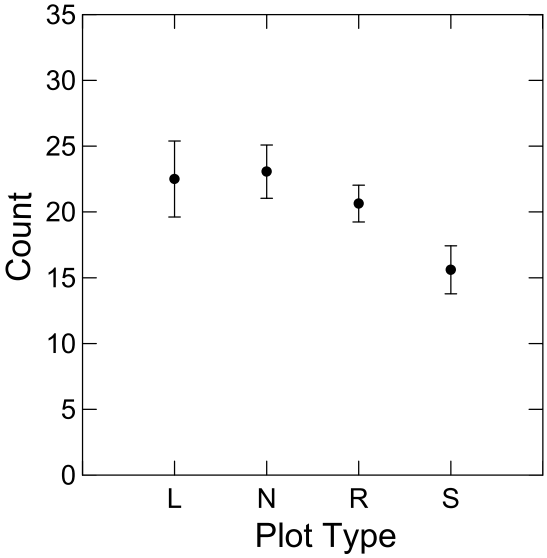

Figure C.1. Mean counts of snowshoe hare pellets (± SE) in four substrate types to evaluate the effects of substrate on the detectability of pellets. L = leaf litter, N = needles, R = raspberries/debris, S = sphagnum moss. All groups except L and N were statistically different from the other ($P < 0.05$).

probability plot showed a significant correlation between residuals and expected values (coefficient of correlation = 0.99), thus validating the use of the GLM.

CONCLUSIONS

These analyses did not find an effect of observer on pellet counts, but did find that substrate could significantly affect the observer's ability to detect pellets. This type of study has an inherent risk of type II error (not detecting a difference when one is present) that increases with decreasing sample size. I therefore attempted to collect a sample sufficient to detect differences between observers if they are present. I conclude with some confidence that substrate type did affect our ability to detect pellets. This was a pilot study under controlled conditions and further study is needed to assess the magnitude of these substrate effects and their potential influence on the estimation of hare density from pellet counts.

APPENDIX D

Pellet densities and estimated hare densities measured in 36 forest stands in northern Maine during the leaf-off seasons, 2005 and 2006 and the leaf-on season, 2005.

Table D.1. Snowshoe hare pellet densities (pellets/ha/day) and estimated hare densities (hares/ha) (using the equation presented in Homyack et al. 2006a) among 21 partial harvests and 15 regenerating clearcut stands in northern Maine during the leaf-off (October – April) seasons for 2005 and 2006 and the leaf-on (May-September) season, 2005. See Table 1.2 for a description of stands.

			Year and season					
Stand Number	Stand ID[a]	Stand type[b]	2005 leaf-off pellets/ha/day	2005 leaf-off hare density (hares/ha)	2005 leaf-on pellets/ha/day	2005 leaf-on hare density (hares/ha)	2006 leaf-off pellets/ha/day	2006 leaf-off hare density (hares/ha)
1	AF1	PH	93.07	0.44	187.62	0.74	47.71	0.30
2	AF2	PH	456.26	1.54	239.97	0.90	176.44	0.69
3	AF3	PH	148.15	0.61	135.79	0.58	43.76	0.29
4	AF4	PH	35.66	0.27	115.27	0.51	33.88	0.26
5	AF5	PH	147.56	0.61	55.47	0.33	32.73	0.26
6	AF7	PH	437.02	1.48	627.79	2.09	127.99	0.55
7	CLSH1	PH	487.62	1.63	325.13	1.16	370.66	1.28
8	CLSH2	PH	126.65	0.54	42.14	0.29	67.62	0.36
9	CLSH3	PH	37.59	0.27	24.35	0.23	53.09	0.32
10	CLSH4	PH	346.11	1.21	209.38	0.80	148.94	0.61
11	CLSH5	PH	192.35	0.74	94.32	0.45	201.75	0.77
12	S11	PH	244.79	0.90	191.43	0.75	189.44	0.73
13	S12	PH	134.66	0.57	159.09	0.65	247.25	0.91

Table D.1. Continued.

Stand Number	Stand ID[a]	Stand type[b]	Year and season					
			2005 leaf-off pellets/ha/day	2005 leaf-off hare density (hares/ha)	2005 leaf-on pellets/ha/day	2005 leaf-on hare density (hares/ha)	2006 leaf-off pellets/ha/day	2006 leaf-off hare density (hares/ha)
14	S13	PH	31.37	0.25	85.50	0.42	46.15	0.30
15	S14	PH	278.55	1.00	190.70	0.75	399.98	1.37
16	S15	PH	216.12	0.81	289.45	1.05	140.22	0.58
17	S16	PH	89.40	0.43	197.59	0.77	149.81	0.61
18	S17	PH	480.06	1.61	395.78	1.38	505.30	1.69
19	S21	PH	230.17	0.86	82.30	0.41	98.56	0.46
20	S22	PH	314.92	1.11	128.13	0.55	456.42	1.54
21	S23	PH	328.89	1.15	259.28	0.95	433.93	1.47
22	CLREG1	REG	1005.52	3.20	471.31	1.61	833.33	2.68
23	CLREG2	REG	1012.67	3.22	602.68	2.01	1055.83	3.35
24	CLREG3	REG	576.89	1.90	455.40	1.56	456.52	1.54
25	CLREG4	REG	1325.05	4.17	962.86	3.12	1271.93	4.01

Table D.1. Continued.

Stand Number	Stand ID[a]	Stand type[b]	Year and season					
			2005 leaf-off pellets/ha/day	2005 leaf-off hare density (hares/ha)	2005 leaf-on pellets/ha/day	2005 leaf-on hare density (hares/ha)	2006 leaf-off pellets/ha/day	2006 leaf-off hare density (hares/ha)
26	JH01C	REG	439.37	1.49	405.27	1.40	529.24	1.76
27	JH02C	REG	308.02	1.09	520.05	1.76	342.99	1.20
28	JH03C	REG	954.80	3.05	757.35	2.49	579.15	1.91
29	JH04C	REG	399.19	1.37	458.65	1.57	354.83	1.23
30	JH05C	REG	531.07	1.77	856.18	2.79	488.85	1.64
31	JH54C	REG	542.08	1.80	331.54	1.18	387.94	1.33
32	JH56C	REG	727.60	2.36	493.03	1.68	827.69	2.66
33	SM4B	REG	593.96	1.96	159.36	0.65	447.39	1.51
34	SM4C	REG	597.11	1.97	312.54	1.12	368.29	1.27
35	SM4D	REG	1075.09	3.41	286.06	1.04	515.12	1.72
36	SM4E	REG	400.34	1.37	196.42	0.76	282.34	1.01

[a] Stand ID: AF = stands surveyed by Fuller (2005) in 1997-1998; CLSH = stands selectively harvested 8-12 years prior to survey located near Clayton Lake; S = conifer-dominated partial harvested stands located in northern Maine; CLREG = regenerating conifer stands at 20-30 years post-harvest and treated with herbicide and located near Clayton Lake; JH = stands surveyed by Homyack (2006) in 2001-2002; SM = stands surveyed by Mullen (2003) in 2001-2003.

[b] Stand type: PH = partially harvested stands; REG = regenerating conifer stands at 20-30 years post-harvest and treated with herbicide.

APPENDIX E

Townships surveyed via snowtracking for Canada lynx tracks in northern Maine, 2003-2005.

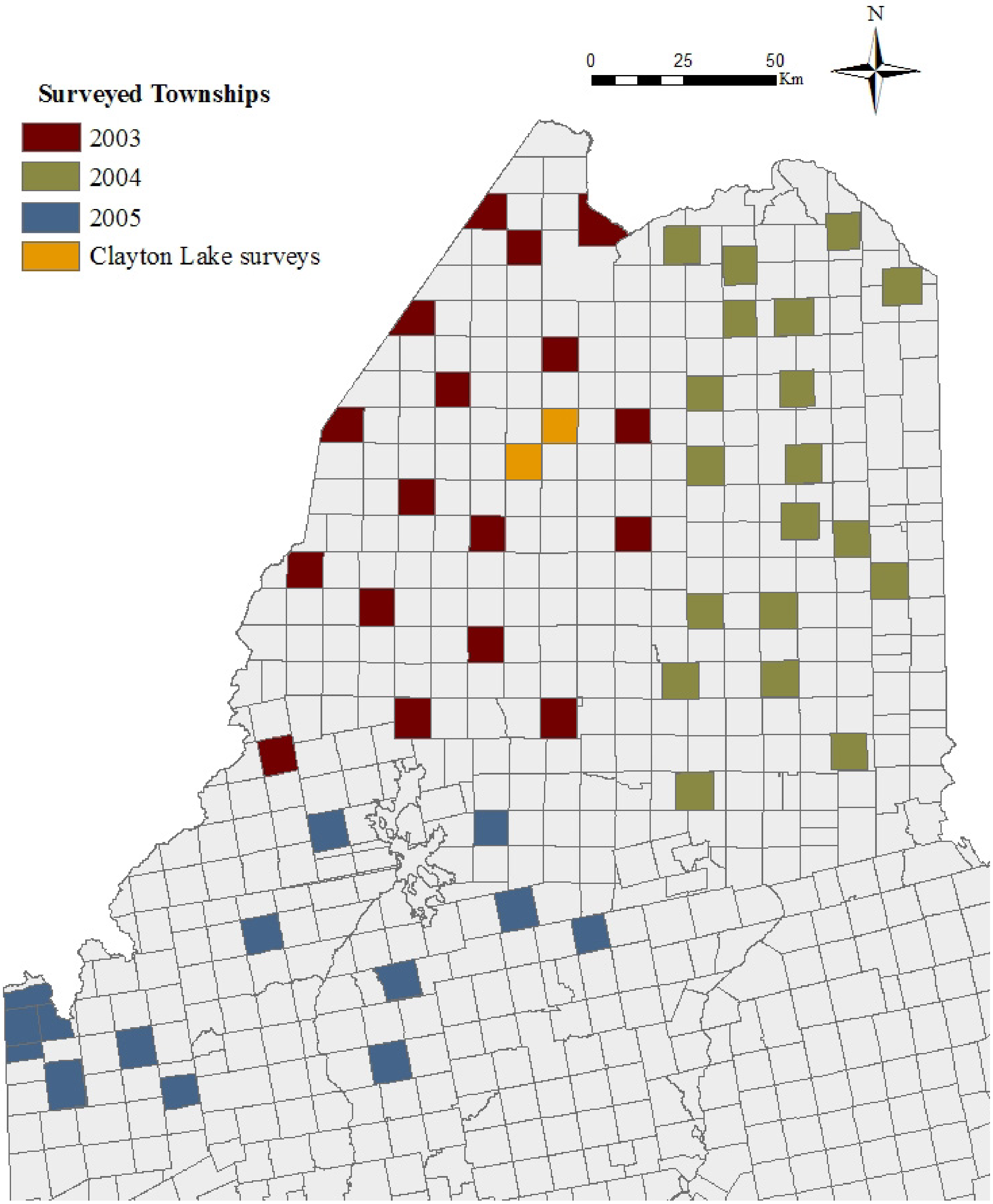

Figure E.1. Townships by year where snowtracking surveys were conducted by the Maine Department of Inland Fisheries and Wildlife for Canada lynx tracks in northern Maine from January to March, 2003-2005. Clayton Lake surveys were conducted in 2001 and 2004.

APPENDIX F

Maximum snow depths during February-March, 2004-2005.

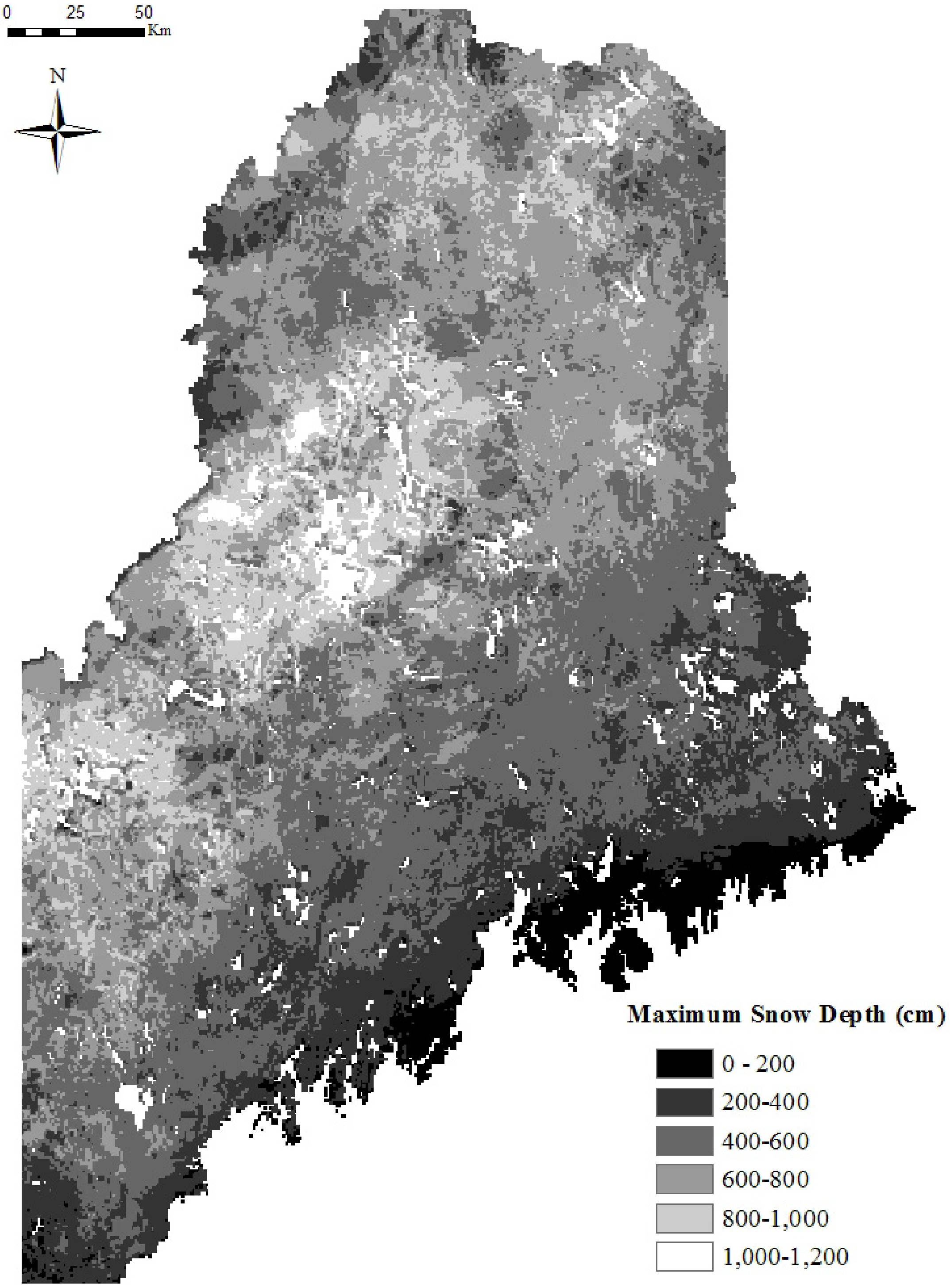

Figure F.1. Mean of maximum snow depth over five dates from February 1-April 1 in 2004 and 2005. Data from the National Oceanic and Atmospheric Administration National Weather Service's National Operational Hydrologic Remote Sensing Center.

APPENDIX G

Mean density of fishers harvested per township, 1995-2004.

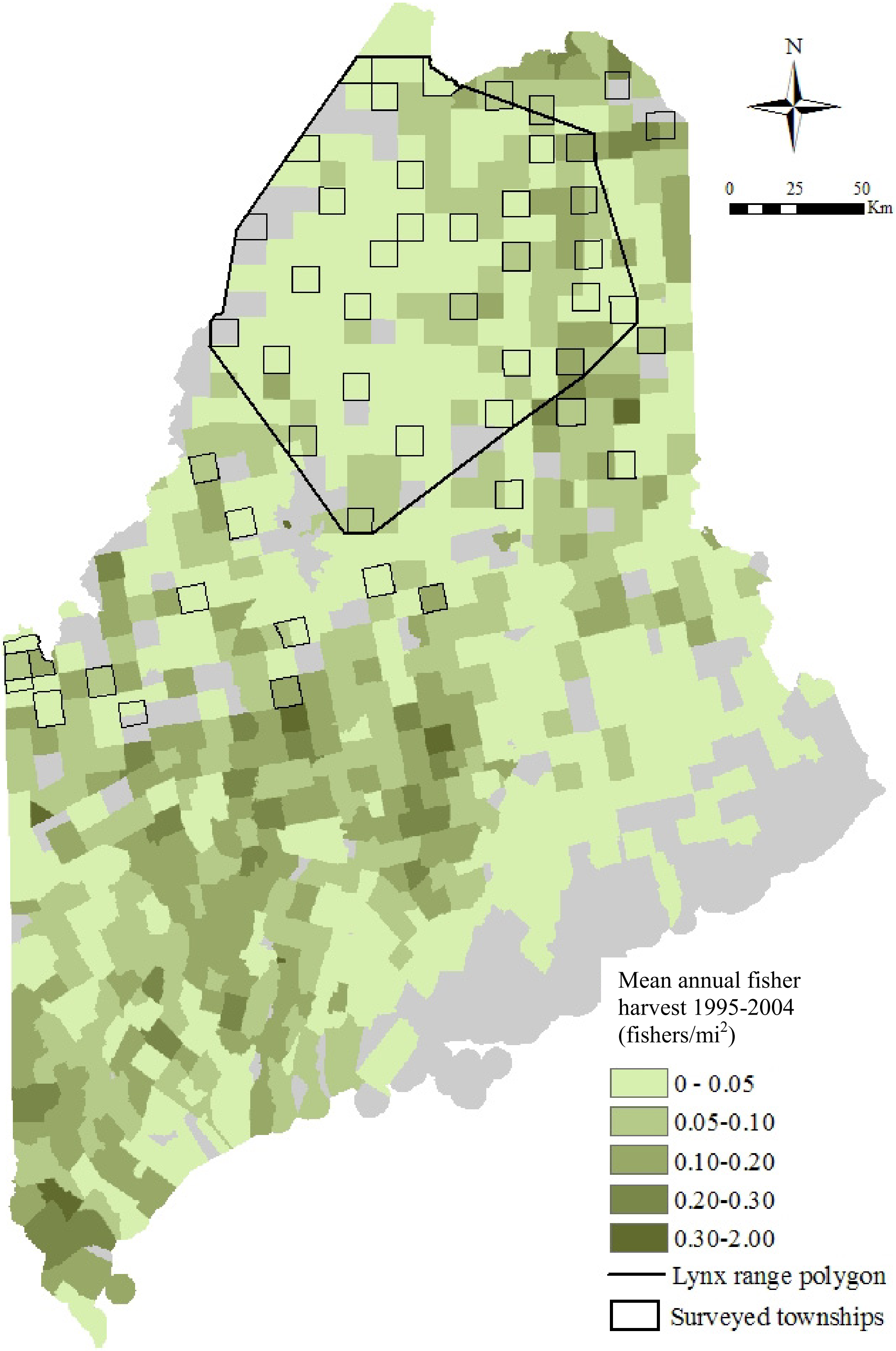

Figure G.1. Mean annual fisher harvest per township (fisher/mi^2), for the trapping seasons 1995-2004 in relation to townships surveyed for Canada lynx tracks in northern Maine from January to March, 2003-2005. Gray represents missing data. Data courtesy of the Maine Department of Inland Fisheries and Wildlife.

APPENDIX H

Locations of 3.15 km^2 buffers used to validate predictions of a
logistic regression model predicting the occurrence
of Canada lynx from snowshoe hare density.

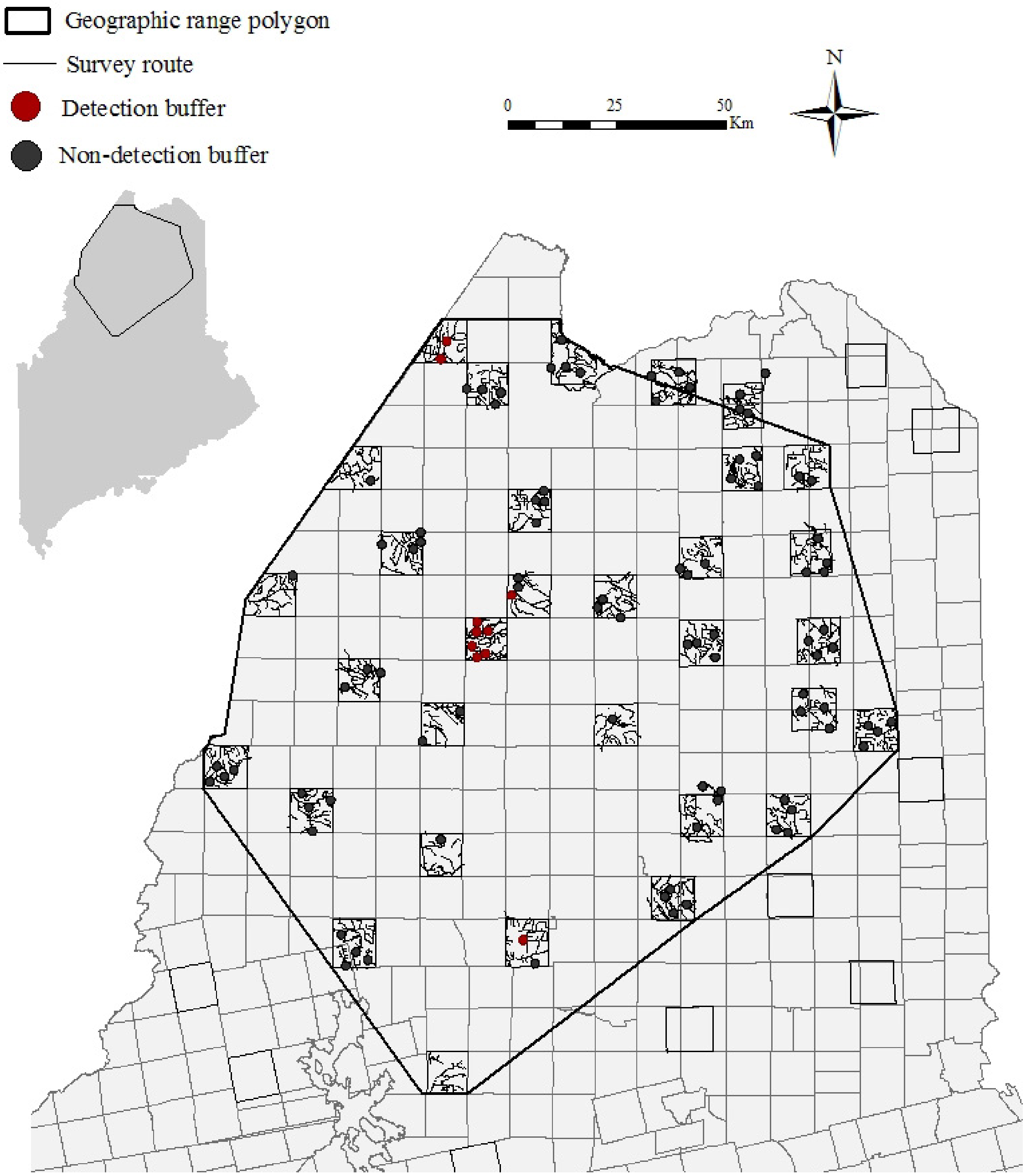

Figure H.1. Locations of buffers used for validating a logistic regression model predicting the occurrence of Canada lynx in northern Maine, U.S.A. (10 detections, 86 non-detections) from snowshoe hare density.

APPENDIX I

Digital elevation model for Maine, U.S.A.

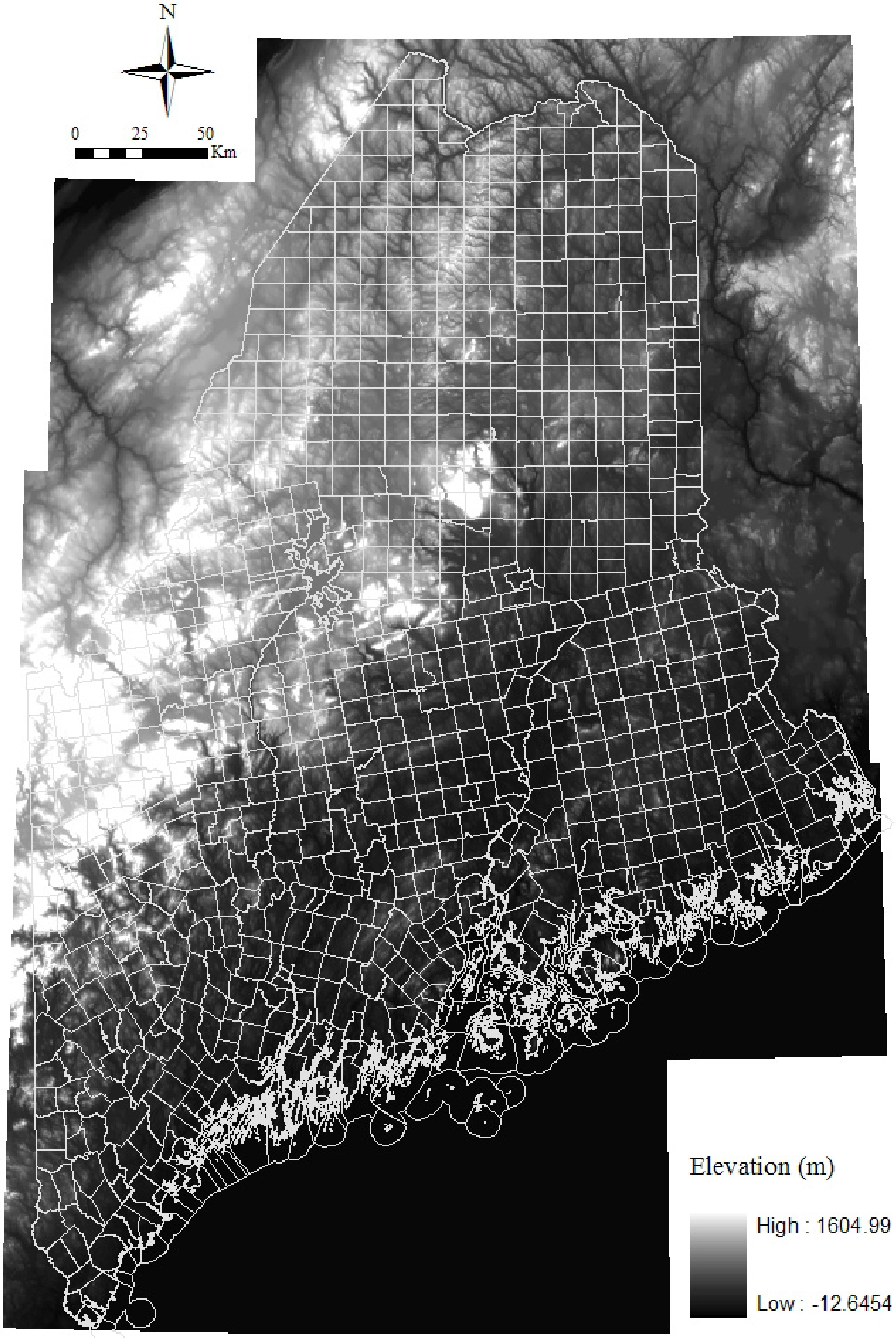

Figure I.1. Digital elevation model for Maine, U.S.A. (data from U.S. Geological Survey).

APPENDIX J

Distribution of forest classified as regenerating clearcut and partial harvest based on remotely-sensed satellite imagery.

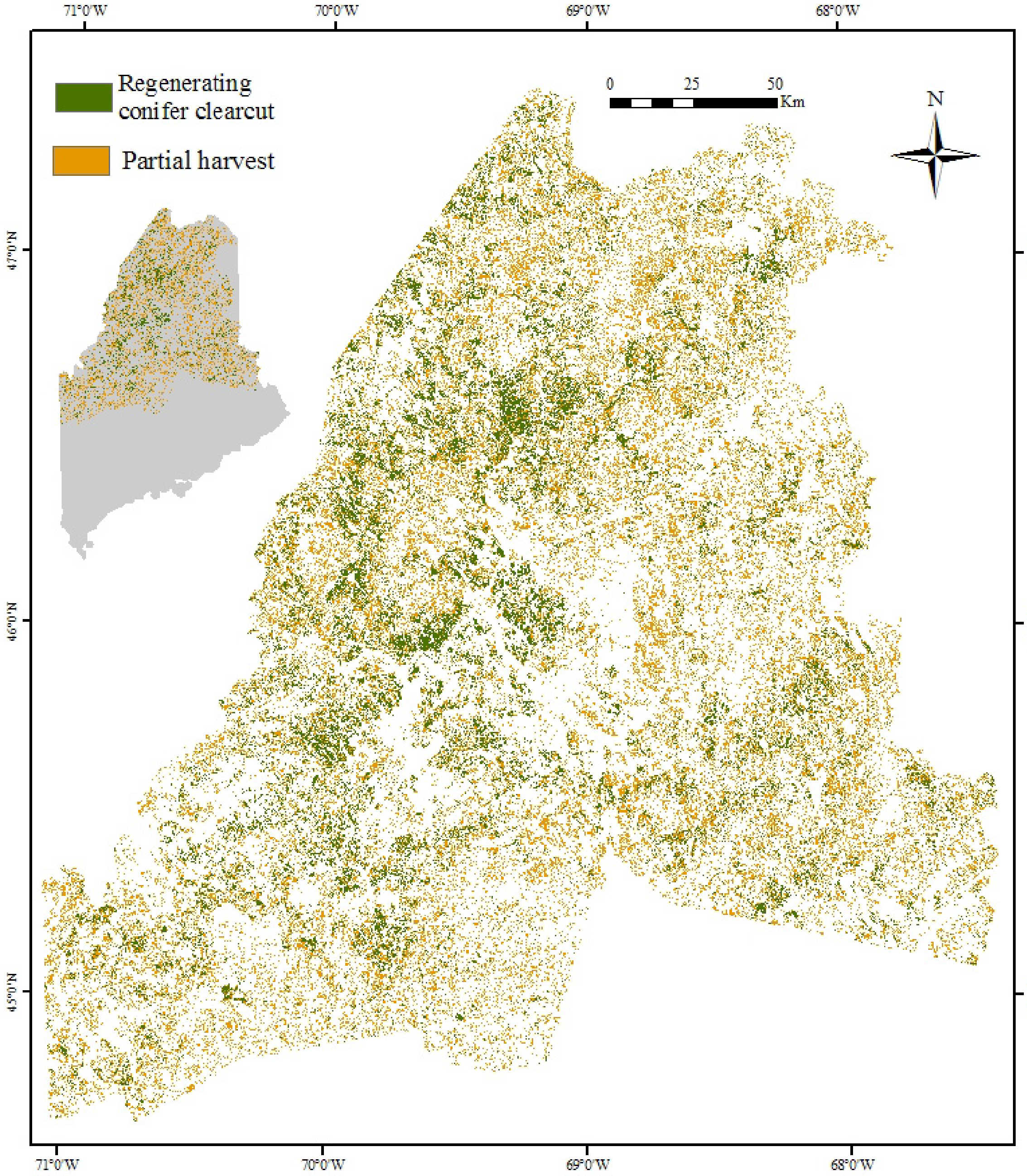

Figure J.1. Regenerating clearcut and partially harvested areas as classified by a 2004 updated GAP map.

APPENDIX K

Coefficients of correlation between predictor variables used in *a priori*
logistic regression models predicting the
occurrence of Canada lynx.

Table K.1. Coefficients of correlation between five predictor variables used in logistic regression models of lynx occurrence in northern Maine, U.S.A. during the winters of 2003-2005 based on 100 km^2 townships (n = 50).

	Variable				
Variable	Snow	Bobcat	Elevation	Fisher	Hares
Snow	1.00				
Bobcat	0.25	1.00			
Elevation	-0.08	0.29	1.00		
Fisher	0.18	0.14	-0.32	1.00	
Hares	-0.08	0.25	0.22	-0.09	1.00

Table K.2. Coefficients of correlation between five predictor variables used in logistic regression models of lynx occurrence in northern Maine, U.S.A. during the winters of 2003-2005 based on 3.15 km^2 simulated home ranges (n = 182).

	Variable				
Variable	Snow	Bobcat	Elevation	Fisher	Hares
Snow	1.00				
Bobcat	0.40	1.00			
Elevation	0.32	0.38	1.00		
Fisher	-0.14	-0.01	-0.27	1.00	
Hares	-0.09	0.15	0.14	-0.12	1.00

BIOGRAPHY OF THE AUTHOR

Laura Lee Robinson was delivered by her father on July 30, 1977 in a trailer park in rural northeastern Washington. She grew up in central Washington and misspent her youth hiking the desert hills, rock climbing, swimming in the river, and snowboarding the mountains. She graduated from Wenatchee High School in 1995 and graduated *magna cum laude* with a B.S. in biology with minors in chemistry and Spanish from Western Washington University in 1999. She then packed up and moved to northern California to work in an environmental lab for a couple of years. After deciding that this life was not for her, she traveled extensively within and abroad to find her path. Wildlife ecology had always seemed fascinating to her and in pursuit of a career in this coveted field, she endured a baking summer in the deserts of southern California, studying burrowing owls as a field technician. She then moved to New York state where she spent a year radio tracking coyotes, foxes, and fishers and using fecal genetics to identify carnivores. She has earned a few scholarships and some recognition in her time, but her true accomplishments include mastering (almost) the spanish language, learning to play the piano, guitar, and didgeridoo, making really good bread from scratch, finishing a New York Times Friday crossword, and maintaining relationships with wonderful people. Laura is a candidate for the Master of Science degree in Wildlife Ecology from the University of Maine in August, 2006.