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Effects of Precommercial Thinning on Snowshoe Hares, Small Mammals, and Forest Structure in Northern Maine

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EFFECTS OF PRECOMMERCIAL THINNING ON SNOWSHOE HARES, SMALL MAMMALS, AND FOREST STRUCTURE IN NORTHERN MAINE

By

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B.S. West Virginia University, 1999

A THESIS

Submitted in Partial Fulfillment of the
Requirements for the Degree of
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(in Wildlife Ecology)

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EFFECTS OF PRECOMMERCIAL THINNING ON SNOWSHOE HARES, SMALL MAMMALS, AND FOREST STRUCTURE IN NORTHERN MAINE

By Jessica A. Homyack

Thesis Co-Advisors: Dr. Daniel J. Harrison and Dr. William B. Krohn

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
Degree of Master of Science
(in Wildlife Ecology)
May, 2003

The extent of precommercial thinning (PCT) to manipulate stand density in overstocked, regenerating stands and to accelerate growth, yield, and the rate of development of crop trees has been increasing within the Acadian forest of northeastern North America. Although the silvicultural responses of crop trees to thinning are well studied, few studies have evaluated the effects of PCT on forest-dependent wildlife and their habitat. I investigated the effects of PCT and stand succession on snowshoe hares, small mammals, and forest structure on 38 stands (25 treated with PCT, 13 unthinned stands) from 1 to 16 years post-treatment within 7 townships in the commercial forests of northern Maine. Forest stands were clearcut from 1967-1983, treated with an aerial herbicide during 1977-1988, and treatment stands were manually thinned from 1984-1999.

Densities of snowshoe hares were examined by establishing approximately 46 km of pellet transect across 30 stands and live-trapping a subset of 8 stands to determine the relationship between densities of pellets and estimated densities of hares. Densities of hares were linearly related to pellet densities from 0–3 hares/ha ($P < 0.001$). Two similar pellet × hare density regressions developed outside Maine did not perform well ($AIC_c >$ 10) and predictions from these regressions underestimated densities of hares. Unthinned stands had approximately 2× greater densities of hares than similar stands treated with PCT across stand age-classes, 2 years of sampling, and during leaf-off (October – May) and leaf-on (June – September) seasons ($P < 0.10$). Although densities of hares were lower in stands treated with PCT, thinned stands still maintained densities greater than stands managed using some alternative silvicultural regimes.

I examined the temporal effects of PCT on small mammals by live-trapping within 37 stands (24 treated with PCT) during June-August 2000 and 2001. Thinning increased [red-backed voles (*Clethrionomys gapperi*), $P = 0.008$; masked shrews (*Sorex cineus*), $P < 0.001$] or produced no detectable effect [deer mice (*Peromyscus maniculatus*), $P = 0.544$; short-tailed shrews (*Blarina brevicauda*), $P = 0.517$] on the 4 most abundant species of small mammals captured on my study areas; therefore, PCT was compatible with maintaining or enhancing densities of common species of forest-dwelling small mammals in regenerating conifer stands.

Dominant changes in forest structure were described from 1 to 11 years post-treatment between herbicide treated clearcuts with and without PCT, to predict wildlife responses to thinning and stand succession. During summers 2001 and 2002, 29 structural characteristics were quantified across 30 forest stands (17 treated with PCT).

Variables with either significant effects of treatment or thinning class were incorporated into a principal components analysis (PCA) to reduce the dimensionality of data. Near-ground cover, overhead cover, and understory structure described approximately 80% of variation between thinned and unthinned stands. Horizontal cover, an overstory to understory contrast, and a gradient of herbaceous vegetation accounted for 75% variation in forest structure among thinning classes of stands. Wildlife associated with dense, early successional habitat, such as snowshoe hares, have been negatively affected by PCT, but thinning could positively influence species that use more mature forest with a more open understory (i.e. red-backed voles).

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PREFACE

The Acadian forest is located in the transitional zone between deciduous forest to the south and coniferous forest to the north, and extends from northern New England east through the maritime provinces of Canada (Seymour and Hunter 1992). The Acadian forest is further identified as the region of geographic overlap between the distributions of balsam fir (*Abies balsamea*), primarily a boreal species, and red spruce (*Picea rubens*), an Appalachian species. The region has received widespread disturbance by the eastern spruce budworm (*Choristoneura fumiferana*), which reached outbreak status about every 30-50 years in the last century (Irland et al. 1988). The most recent budworm outbreak in the region occurred during the 1970's-1980's, with large areas of susceptible conifer forest having widespread mortality. Spruce budworm kills spruce and fir trees by defoliating them for several years and reducing vigor or causing direct mortality. Landowners of commercial forest responded to the budworm outbreak by conducting extensive salvage operations and accelerating rates of pre-salvage clearcutting to minimize loss of fiber (Maine Forest Service, unpublished data).

During the end of the outbreak (1985) and the 5 years following (1985 to 1990), an average of 46,921 ha were clearcut each year in Maine (Maine Forest Service, unpublished data), and > 420,000 ha were clearcut across Maine, New Brunswick, Quebec, and Nova Scotia (Canadian Council of Forest Ministers 2002). In the following decade (1991-1999), Maine's average number of ha harvested annually by clearcutting dropped to 17,927, but clearcutting remained a dominant silvicultural practice over much of eastern Canada. The large land area of regenerating forest created during a relatively short period of time contributed to an age class unbalance with a preponderance of young, regenerating stands (Seymour 1985). A few years after harvesting (from 1985-1995), an average of 19,184 ha a year (Maine Forest Service, unpublished data) of young clearcuts were treated with an aerial herbicide (i.e. Glyphosate or Triclopyr) to promote softwood regeneration in Maine. Herbicide treatments, prolific seeding of shade-tolerant conifers, and abundant precipitation yielded sapling stands that were often stocked with > 37,000 conifer stems per hectare (Gadzik 1999). Overstocked conifer stands often result in a reduced growth rate and fiber loss to mortality, via self-thinning (Wilson et al. 1999). Many companies responded by exploring new methods, including precommercial thinning (PCT), to reduce competition to accelerate the growth of residual trees in young, overstocked stands and to minimize the effects of an imbalance in age structure across the landscape (Seymour 1999).

Within commercially managed forests, PCT has been used to manipulate stand density in stands 10-20 years after harvest when crop trees typically average 1.5-3.0-m height. A typical example of this high-yield silvicultural system includes a progression of a complete overstory removal followed by herbicide application 2-5 years later to control competing vegetation (Seymour and Hunter 1992). Next, at about age 15, stands are thinned with motor manual brush saws to about 2,000-2,500 trees per hectare to reduce the density of overstocked sapling stands and remove competing deciduous trees (Seymour 1999).

Large shifts in the dominant silvicultural practices in Maine have occurred over the last 15 years. Whereas clearcutting was once the dominant silvicultural regime, partial harvesting now accounts for about 96% of the annual total area harvested in the state. The passage of the Maine Forest Practices Act in 1989 (Title 12 MRSA Chapter

805) placed a regulatory disincentive on large clearcuts. This act resulted, in part, from a negative public perception of clearcutting (Bliss 2000) and contributed to a substantial decline in the number of ha clearcut each year from the late 1980's to 2002 (Figure P.1). In contrast, the number of ha precommercially thinned each year has shown a slow, but steady increase from about 2,428 ha in 1987 to > 8,499 ha in 2001. Over 8,000 ha of regenerating softwood stands are treated with PCT each year in Maine and at this current rate approximately 131,000 ha (or 2% of Maine's commercial timberland) will have been spaced by 2005. The increased prevalence of PCT on forested landscapes is not unique to Maine. From 1990-2000, the annual land area treated with PCT increased 2.7x in New Brunswick and 4.3x in Quebec (Canadian Council of Forest Ministers 2002), indicating that much of the Acadian forest has experienced this silvicultural trend.

Although area clearcut (< 3.0% in 2001) and thinned (3.5% in 2001) annually in Maine only account for a small portion of the total silvicultural activity, these practices may have significant effects on species that reach their highest densities in regenerating, early successional habitat. During both 2000 and 2001, a greater number of ha of forest were treated with PCT than were clearcut (Figure P.1), emphasizing the trend towards thinning of overstocked stands and a move away from even-aged management. The effects of these changes on the management of Maine's forests and on wildlife species that are dependent upon early-successional forests are unknown.

Wildlife generally respond to forest structure rather than stand-age (Carey and Johnson 1995, Hayes et al. 1997), and the post-treatment changes that occur in stand structure following forest management may have strong effects on a suite of forest-dependent wildlife. For example, understory structure and diversity provides foraging,

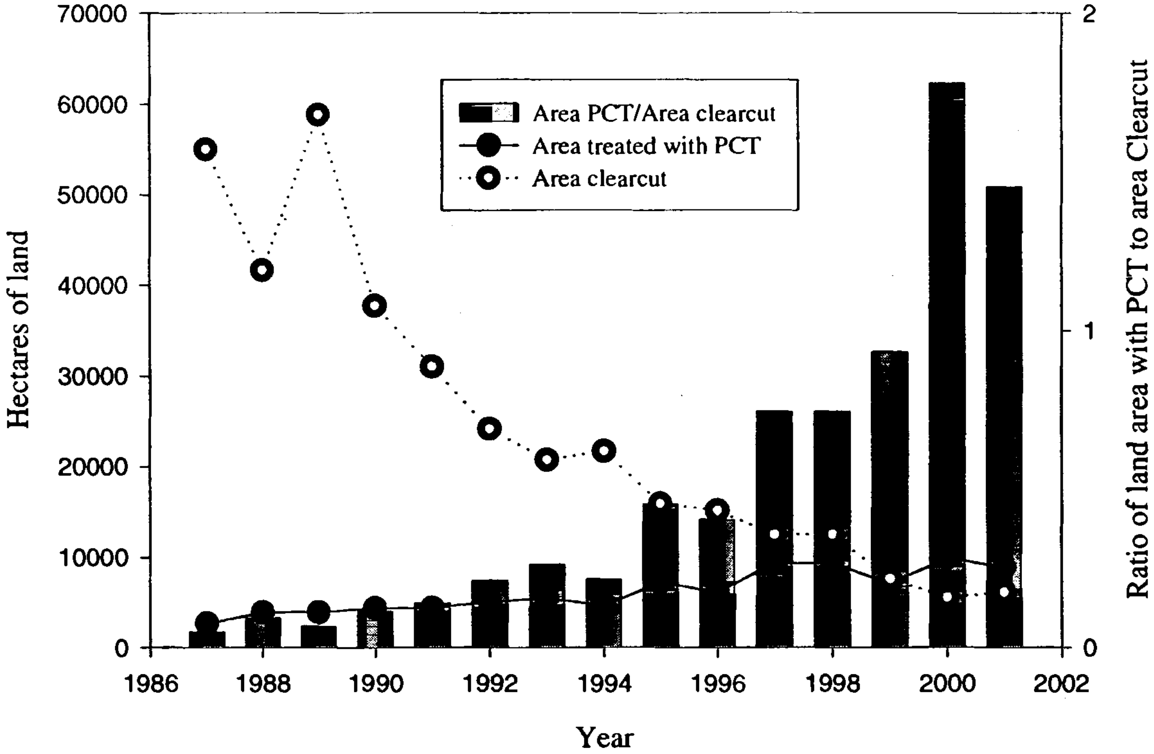

Figure P.1. Changes in the annual number of acres clearcut and precommercially thinned in Maine, 1987 to 2002 (Data from the Maine Forest Service).

nesting, and perching substrate for numerous species of songbirds (MacArthur and MacArthur 1961, Woodcock et al. 1997), thermal cover and protection from predators for small herbivores (Wolff 1980, Pietz and Tester 1983, Litvaitis 1993, Litvaitis et al. 1985, Fuller 1999), and browse for ungulates (Doerr and Sandburg 1986, Newton et al. 1989, Lautenschlager et al. 1999). A structurally diverse canopy layer may function as escape cover and rest sites for meso-carnivores (Buskirk 1984, Payer and Harrison 2000) and gallinaceous birds (Allan 1985, Kilpatrick et al. 1988, Chamberlain et al. 2000), protection from extreme weather for ungulates (Ozoga and Gysel 1972), and nesting and foraging sites for songbirds (MacArthur and MacArthur 1961, Sharpe 1996). Lastly, coarse woody debris and snags contribute subnivian access for small predators (Sherburne and Bissonette 1994), nesting and foraging sites for cavity nesters (Hunter 1990, Sharpe 1996), escape cover from predators, habitat for invertebrate prey, and mediation of microclimate for small mammals (Hayes and Cross 1987, Carey and Johnson 1995, Hagan and Grove 1999), and herpetofauna (Whiles and Grubaugh 1993, deMaynadier and Hunter 1995). Therefore, human alteration of structural characteristics of forested ecosystems may have varied effects upon the vertebrate species whose geographic distribution includes commercially managed forest.

The purpose of this thesis was to examine the effects of PCT on wildlife species, with special emphasis on the primary prey of the federally threatened (US Department of the Interior 2000) Canada lynx (*Lynx canadensis*) (O'Donoghue et al. 1998). Specifically, I studied the effects of PCT on snowshoe hares (*Lepus americanus*) (Chapter 2), an early successional species that may be important to the recovery of Canada lynx (Hickenbottom et al. 1999), small mammals (Chapter 3), which are important prey items for a diverse group of forest carnivores (Dibello et al. 1990, Cumberland 2001), and on the within-stand and structural attributes of regenerating clearcut stands that result following herbicide application and PCT (Chapter 4). Further, I developed a predictive relationship for estimating density of snowshoe hares based on counts of fecal pellets and determined the utility of this method for predicting numbers of hares (Chapter 1).

CHAPTER 1

QUANTIFYING DENSITIES OF SNOWSHOE HARES IN NORTHERN MAINE USING PELLET PLOTS

ABSTRACT

Snowshoe hare (*Lepus americanus*) have important community-level roles throughout their range as prey for numerous species of wide-ranging carnivores and as a dominant herbivore. Monitoring populations of hares across landscapes requires surveys that are efficient and accurate. Predictive relationships between densities of fecal pellets and snowshoe hares have been reported for boreal forests in northwestern Canada and for Idaho; however the authors recommended further testing of the pellet-survey technique across the geographical range of hares. I developed a functional relationship of hare densities in relation to pellet densities in northern Maine and evaluated the utility of using previously published regression coefficients to predict densities of hares in Maine. I estimated pellet densities by establishing 1.6 km of transect in each of 8 forest stands and by counting the number of pellets deposited by hares during leaf-off seasons (Oct.-May 2000-2001 and 2001-2002). Further, I live-trapped hares on those stands during May-June 2001-2002 to estimate densities. Minimum number of hares known alive were a linear function of pellet densities ($P < 0.001$) to 31,000 pellets/ha/month (3.04 hares/ha) for the 8 stands that I sampled; this equation best balanced goodness of fit with statistical parsimony ($\Delta AIC_c = 0.00$). However, a previously developed regression for Maine ($\Delta AIC_c = 2.77$) performed similarly well ($r = 0.93$) and had the advantage of predicting actual densities of hare. In contrast, regressions reported for the Yukon Territory, Canada ($\Delta AIC_c = 29.03$) and northern Idaho ($\Delta AIC_c = 32.79$) did not perform well and

underestimated densities of hares (mean differences -0.40 and -0.42 hares/ha, respectively) when compared to predicted densities in Maine. I suggest that future research be directed towards documenting functional relationships between pellet densities and hare densities during the leaf-off season to avoid potential biases resulting from pooling data across seasons. My data suggest that predictive relationships between number of fecal pellets and densities of snowshoe hare are region-specific. Therefore, caution should be exercised when regression equations developed to estimate density of hares from one ecoregion are applied within other ecoregions.

INTRODUCTION

The ecology of snowshoe hares has been extensively studied, partly because of this species' role as prey for numerous wide-ranging mammalian and avian predators. Hares are a prevalent prey item for Canada lynx (*Lynx canadensis*) (O'Donoghue et al. 1998), American marten (*Martes americana*) (Soutiere 1979, Cumberland et al. 2001), coyotes (*Canis latrans*), fishers (*Martes pennanti*), bobcats (*Lynx rufus*) (Dibello et al. 1990), goshawks (*Accipiter gentilis*), broad-winged hawks (*Buteo platypterus*), barred owls (*Strix varia*), snowy owls (*Nyctea scandiaca*) and great horned owls (*Bubo virginianus*) (Mendall 1944, Rohner and Krebs 1996). Snowshoe hares are also a primary consumer within the northern forest ecosystem (Krebs et al. 2001a) and can cause dramatic decreases in the available biomass of woody stems (Pease et al. 1979), especially during cyclic population "peaks." Snowshoe hares browse and girdle woody stems (Pease et al. 1979, Radvanyi 1987, Bergeron and Tardif 1988); therefore, they may also play an important role in nutrient cycling (Krebs et al. 2001a).

Ecologists and managers are often interested in densities of snowshoe hare across large areas because of direct and indirect interactions with many other wide-ranging species via predation, competition, and herbivory. Further, concern about the habitat relationships of snowshoe hare under various forest management scenarios has increased since the federal listing of Canada lynx as a threatened species in the contiguous United States in March 2000 (United States Department of the Interior 2000). Accurate and expedient methods to indirectly estimate snowshoe hare populations are needed to evaluate and monitor temporal, successional, and human-induced changes in hare densities across large areas.

Conventional mark-recapture techniques are labor intensive, costly to employ, and are usually constrained to relatively small areas (Litvaitis et al. 1985b, Krebs et al. 2001b). Counts of fecal pellets of snowshoe hares on numerous small plots provide a quicker and more cost-effective measure of abundance of hares, and have been shown to accurately predict population densities within the regions where they are developed (Krebs et al. 1987, Long 1995, Krebs et al. 2001b, Murray et al. 2002). Krebs and others (2001b) recently recalculated the relationship between observed densities of hares and pellet densities for the Kluane region of northwestern Canada and assessed the temporal generality of the regression. They cautioned against making management recommendations with this regression outside of the Kluane boreal forest region, and questioned the spatial generality of hare-pellet regression equations throughout the species' geographic range. Murray et al. (2002) examined the utility of the regression developed in the Yukon for estimating hare densities in Idaho and concluded that the equation predicted hare densities moderately well at higher densities (≈ 0.50 hares/ha), but underestimated hares when pellet densities were close to zero.

The objectives of my study were to develop a predictive equation of observed snowshoe hare densities based on fecal pellet densities in northern Maine, to examine the evidence supporting that predictive model relative to hare pellet-density relationship models reported for western and eastern Maine (Litvaitis et al. 1985a, Long 1995), the Yukon Territory (Krebs et al. 2001b), and Idaho (Murray et al. 2002), and to evaluate whether a regional-specific model is required to estimate densities of hare in the northeastern United States.

STUDY AREA

Four townships (T 4 R 11 WELS, T 5 R 11 WELS, T 1 R 13 WELS, and T 1 R 14 WELS) spanning 50 km north to south and 43 km east to west in Piscataquis County, Maine comprised the study area (Figure 1.1). Two industrial forest owners (i.e. Great Northern Paper, Inc., Millinocket, Maine and Plum Creek Timber Company, Fairfield, Maine) managed the lands for pulpwood and sawtimber.

Each of the 8 study sites in the 4-township area were located in the transitional zone between the sub-boreal spruce-fir and northern hardwoods ecosystem (Seymour and Hunter 1992). Average annual temperature for the region during 1970 to 1999 was 3.78° C and average annual precipitation was 101 cm, with 276 cm falling annually as snow (Garoogian 2000). Stands were dominated by balsam fir (*Abies balsamea*) and spruce (*Picea spp.*), and had minor components of white pine (*Pinus strobus*), northern white cedar (*Thuja occidentalis*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), paper birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*).

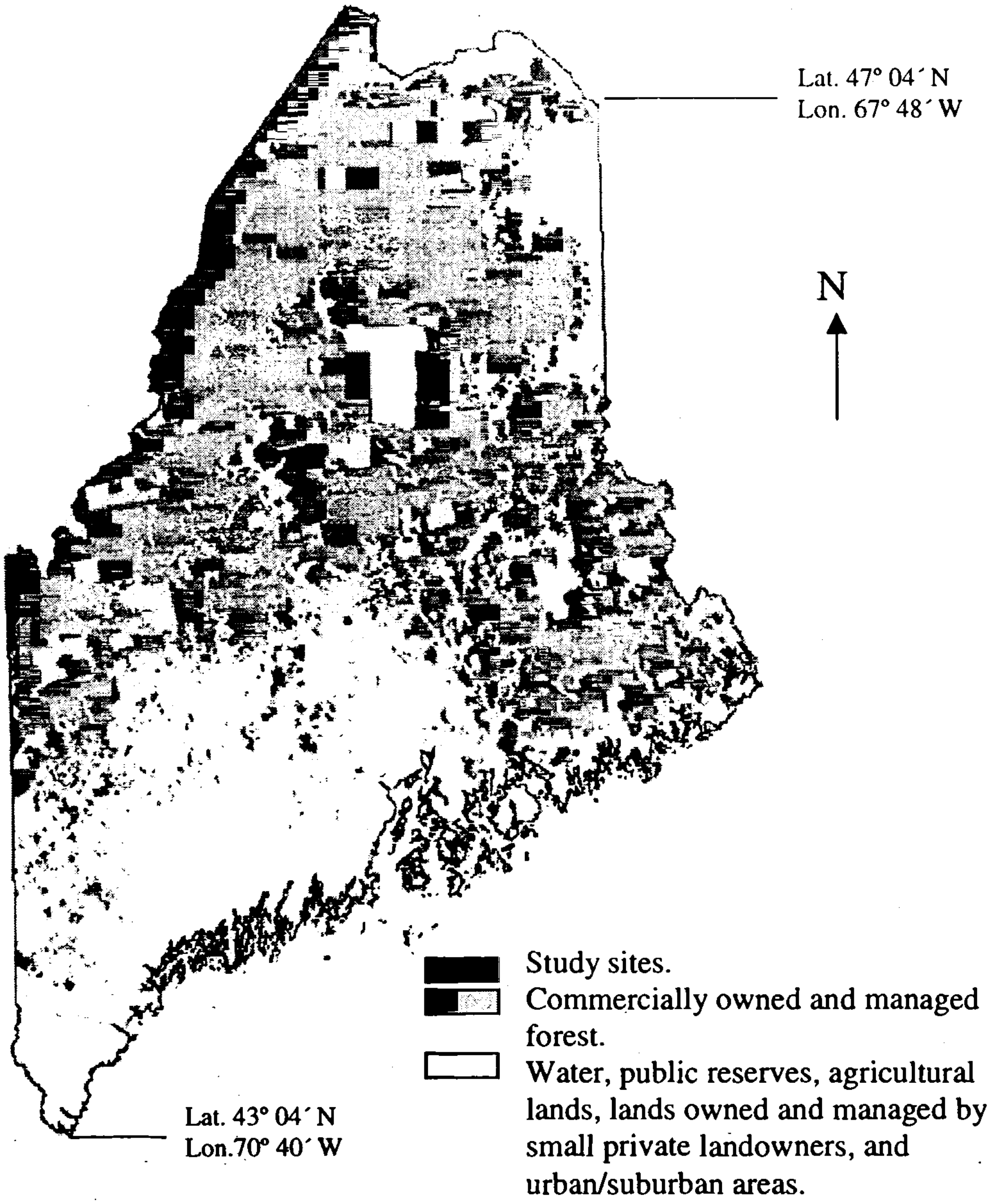

Figure 1.1. Location of study sites containing 8 stands where hare pellet-density relationships were investigated within 4 townships in the commercially owned and managed forests of north-central Maine, 2000-2002.

I selected 8 forest-stands within the study area that had been clearcut (timber harvesting resulting in residual basal area of acceptable growing stock trees > 11.43 cm dbh of < 20.66 m^2/ ha) 1974-1983 and treated with an aerial herbicide (e.g. Glyphosate at ≈ 1.68 kg/ha acid equivalent) 1983-1988 to reduce competing deciduous vegetation; 4 of the 8 stands had been manually thinned 2 to 13 years previously using brushsaws (Seymour et al. 1984). Stands were selected across a range of stand ages and with different thinning treatments to maximize the range of hare densities encountered because I was interested in developing a generalized predictive equation of hare density versus pellets across the range of hare densities typically encountered in northern Maine. The 8 stands were chosen to have flat to gently sloping topography, relatively uniform within-stand conditions, and area > 10 ha (range 11.6 to 66.4 ha).

METHODS

Pellet transects

I established transects to measure snowshoe hare pellets and absolute densities of hares on 8 forest stands. The stand was considered the unit of replication because home ranges of individual hares in Maine average 4.8 ha for females and 7.4 ha for males (Litvaitis 1984), which was approximately 3,200 to 4,900x greater than the area of individual pellet plots. Each replicate had 1.6 km of pellet transects placed > 50 m from the stand boundary to minimize samples from hares that were not resident within the stand and to minimize edge-effects (Harris 1988, Fraver 1994). Within each of 7 stands I established 4 parallel, 400-m transects and separated transects by 65 m (Figure 1.2). In the remaining stand I established 3, parallel 540-m transects to conform to the long and narrow shape of that stand.

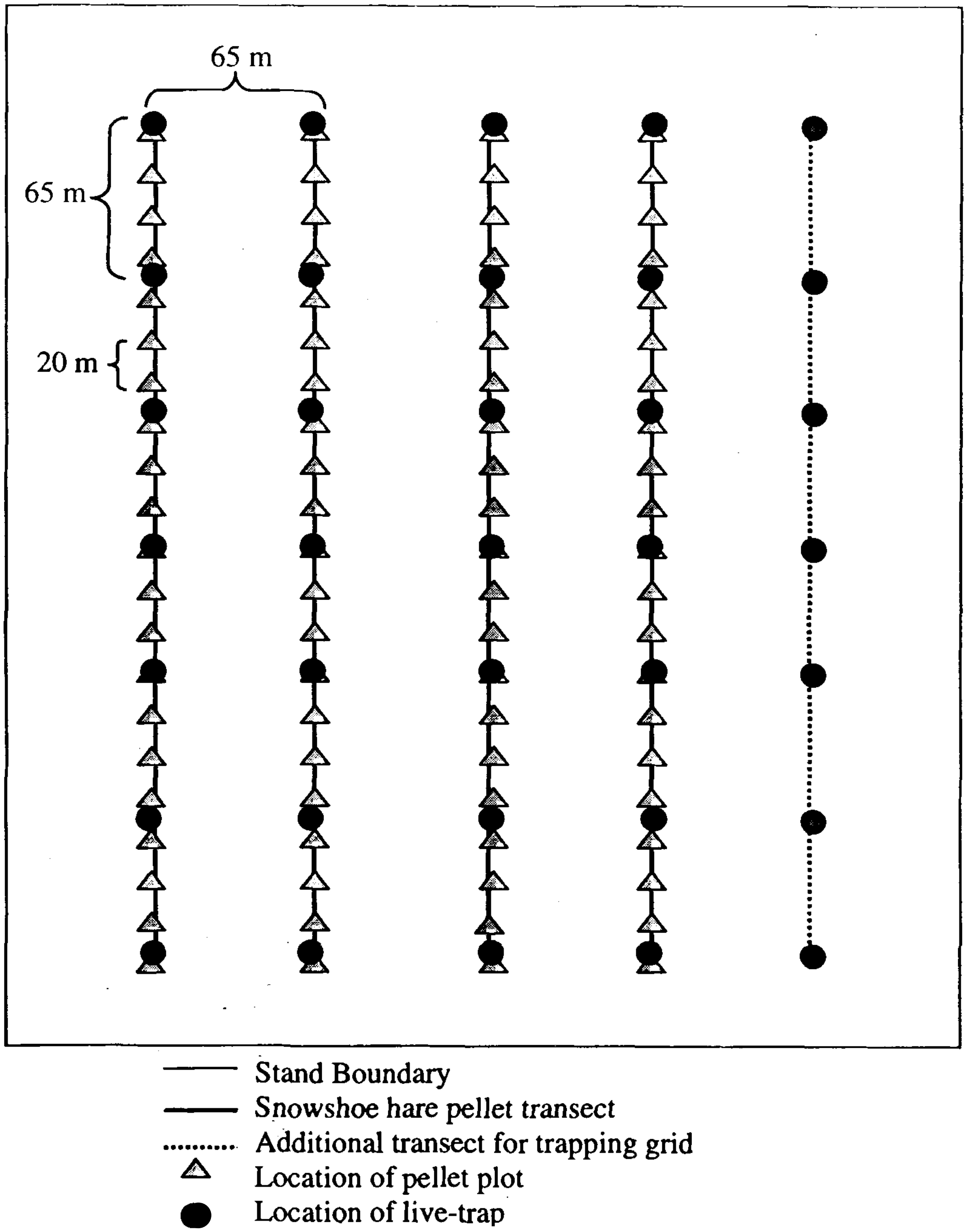

Figure 1.2. Position of 84 snowshoe hare pellet plots on 4 parallel transects and live-trapping grid within each of 7 stands in northcentral Maine, USA. An eighth stand was surveyed with an arrangement of 3 parallel 540 m transects because the standard survey dimensions did not fit within 50 m of stand boundaries. Figure not drawn to scale.

I marked 5 m by 30 cm (1.5 m^2) randomly oriented quadrats at 20-m intervals along transects for a total survey of 84 pellet plots (126 m^2) sampled per stand. I cleared all pellets from plots during 18 – 25 October, 2000 and during 13 – 29 September, 2001; therefore, only pellets deposited during the leaf-off season (October – May) were counted in subsequent surveys. I counted and removed the pellets deposited on the plots in the leaf-off season during 17-23 May, 2001 and during 10-24 May, 2002; counts were conducted prior to leaf-out of deciduous trees (ca. 20 May – 10 June) to represent winter abundance and habitat use of snowshoe hares (Litvaitis et al. 1985). I rigorously trained all technicians and minimized the number of individuals who counted pellets to reduce observer bias.

Live-trapping

I live-trapped hares within 4 stands during 8 May-15 June, 2001 and within the remaining 4 stands during 4 May-4 June, 2002. I established a 390 × 260 m trapping grid in each stand on the pellet transects and added a fifth, parallel transect to maximize the grid size and total number of captures (Figure 1.2). One stand had a 585 × 130-m grid because the standard survey dimensions would not fit within 50 m of the stand boundary. I placed 1 single-door 66 x 22 x 22 cm collapsible Tomahawk trap (Model 205) (Tomahawk Live Trap Co., Wisconsin, USA) at 65-m intervals, 1-2 m from the transect, for a total of 35 traps per stand (30 traps for the stand with a 585 × 130-m grid). Traps were baited with dried alfalfa cubes and covered with moss, leaves, and bark to provide shelter from wind and rain and cover from predators. I set traps in each stand for 13-18 consecutive nights and traps were checked once daily. The Institutional Animal Care and Use Committee at the University of Maine approved the trapping and handling protocol.

Hares were restrained in a cloth handling-bag and were marked with numbered, self-piercing tags (Monel no. 1 or Monel no. 3; National Band and Tag Co., Newport, KY) in each ear, or behind the intercapitular ligaments of the interdigital webs of each hind foot (Keith et al. 1968). Hare were sexed and the right hind foot length was measured. Individual hares were examined for reproductive condition by noting obvious testes for males, and the presence or absence of swollen mammaries, large nipples, and matted hair around nipples to indicate lactation for females. I used live-trapping to estimate population sizes at the end of the leaf-off season; therefore, only adult hares were marked. Leverets (< 2 months of age) were easily distinguished from adults (> 6 months of age) during our trapping period (early May – mid-June) by physical characteristics and were released unmarked. Hind foot measurements of hares have often been used to separate juveniles from adult hares (Litvaitis 1990, Rohner and Krebs 1996). Leverets had hind foot measurements of < 8 cm and adult hares had hind feet ≥ 12.0 cm. After handling, all hares were released at the capture site.

Pellet density – hare density relationship

I converted the mean number of pellets/plot for each stand into pellets/ha/month based on the number of days elapsed since a grid had been cleared of pellets. I attempted to produce population estimates using the mark-recapture data using closed models in Program MARK; however, the number of individual hares captured per grid and the capture and recapture probabilities were too small to produce meaningful or accurate population estimates (White and Burnham 1999). Thus, I considered the minimum number alive (MNA) of hares as a minimum density estimate for developing density × pellet relationships. First, I examined the average inter-capture distance per stand in case movement distances of study animals were dependent on density or habitat. Next, I calculated the effective trapping area as the area of the trapping grid plus a buffer whose dimensions were one-half the average recapture distance for that specific stand (Mean = 104.4 m, 95% CI 96.7 to 112.1 m) (Litvaitis et al. 1985a). Then, I calculated minimum density estimates as the MNA divided by the stand-specific effective trapping area (Otis et al. 1978). I conducted a linear regression with pellets/ha/month as the predictor variable and estimated density (minimum) of hares/ha as the response variable to evaluate the relationship between pellet densities and densities of snowshoe hares on my northern Maine study sites. I tested the assumptions of the model by examining the data for normal errors with a normal probability plot and Lilliefor's test, and for constant variance with a modified Levene's test (Neter et al. 1996).

Next, I compared this linear regression to a similar relationship developed by Long (1995) adapted from data collected in eastern and western Maine, 1981-1983, by Litvaitis et al. (1985a); however, the regression first needed to be recalculated because the y-intercept was forced through the origin. Many statisticians advise against regression through the origin under most circumstances (Bissel 1992, Neter et al. 1996). Forcing the y-intercept to equal zero causes the coefficient of determination (r^2) to be uninterpretable and examining the fit of the data to a model is more difficult. For these reasons, I recalculated the regression equation for predicting hare densities from pellets reported by Long (1995), so that it was not forced through the origin.

I examined the strength of my model for predicting snowshoe hare densities in Maine to those reported for other regions in the geographic distribution of the snowshoe hare. Examining the information lost by applying several models to a single data set is a model-selection problem. I utilized an information-theoretic framework using Akaike's Information Criteria (AIC) to examine the relative strength of evidence for each model when applied to my 8 stands in northern Maine. AIC is an alternative to traditional hypothesis testing that uses an important relationship between Kullback-Leibler information and maximum likelihood to rank multiple hypotheses (models), and the model with the lowest AIC value is considered to best balance statistical parsimony with goodness of fit for the empirical data (Burnham and Anderson 2001). I followed the guidelines of Burnham and Anderson (2002) for the methods to compute AICs and model weights, and to make inferences from these values.

I calculated AIC corrected for a small sample size to parameter ratio (AIC_c) and compared relative AIC values among 4 models when applied to the data that I collected in northern Maine. The 4 models evaluated were: a linear equation for minimum hare density × pellets based on my 8 stands in northern Maine, the recalculated Litvaitis-Long model for actual hare densities × pellets from eastern and western Maine (1995), a published hare × pellets density relationship reported for the Yukon Territory, Canada (Krebs et al. 2001b), and a published pellet-density regression for Idaho (Murray et al. 2002). I converted my pellet data from pellets/ha/month to pellets/$0.155m^2$ plot/year as reported by Krebs et al. (2001b) and Murray et al. (2002) and computed AIC_c for those models when applied to the hare density × pellet data for my 8 sites. Murray et al. (2002) presented both linear and exponential functions for various plot sizes and shapes used to predict hare density × pellets in Idaho. I fit the linear function reported for rectangular plots because the plot shapes were most similar to my methods and because the authors discussed several advantages of the linear regressions over the exponential versions.

Murray et al. (2002) examined hares at low densities and added 1/6 to his number of pellets counted per 0.155 m^2 plot to remove zero values. Hare densities were considerably higher on my study sites. Only 8.59% (inter-quartile range 0.89 to 10.12%) of my plots had zero values; therefore, I did not adjust those values.

The Krebs et al. (2001b) and the Murray et al. (2002) equations included $\log_e$ transformations of the predictor and response variables, whereas the regressions developed in Maine did not require these transformations of predictor or response variables based on the results from the modified Levene's test. Burnham and Anderson (2002) warn that estimation of Kullback-Leibler information cannot be directly compared across a model set with both transformed and untransformed response variables. I resolved this difficulty by calculating the likelihood function for the lognormal distribution instead of the Gaussian distribution, which is normally used to calculate AIC values in this setting. The $\log_e$-$\log_e$ models estimated AIC values using this lognormal distribution and can be validly compared to AIC values from the normal regression models (W. Halteman, University of Maine; and D. Anderson, Colorado Cooperative Fish and Wildlife Research Unit; pers. comm.).

RESULTS

I captured 128 hares (69 M, 59 F) 308 times during May-June 2001 and 114 hares (64 M, 49 F, 1 unknown) 464 times during 2002. Average recapture distances of hares were similar across the range of densities sampled (Figure 1.3). Hare densities based on MNA ranged from 0.555 to 3.037 hares/ha among the 8 stands; pellet densities ranged from 1,934.5 to 31,314.6 pellets/ha/month.

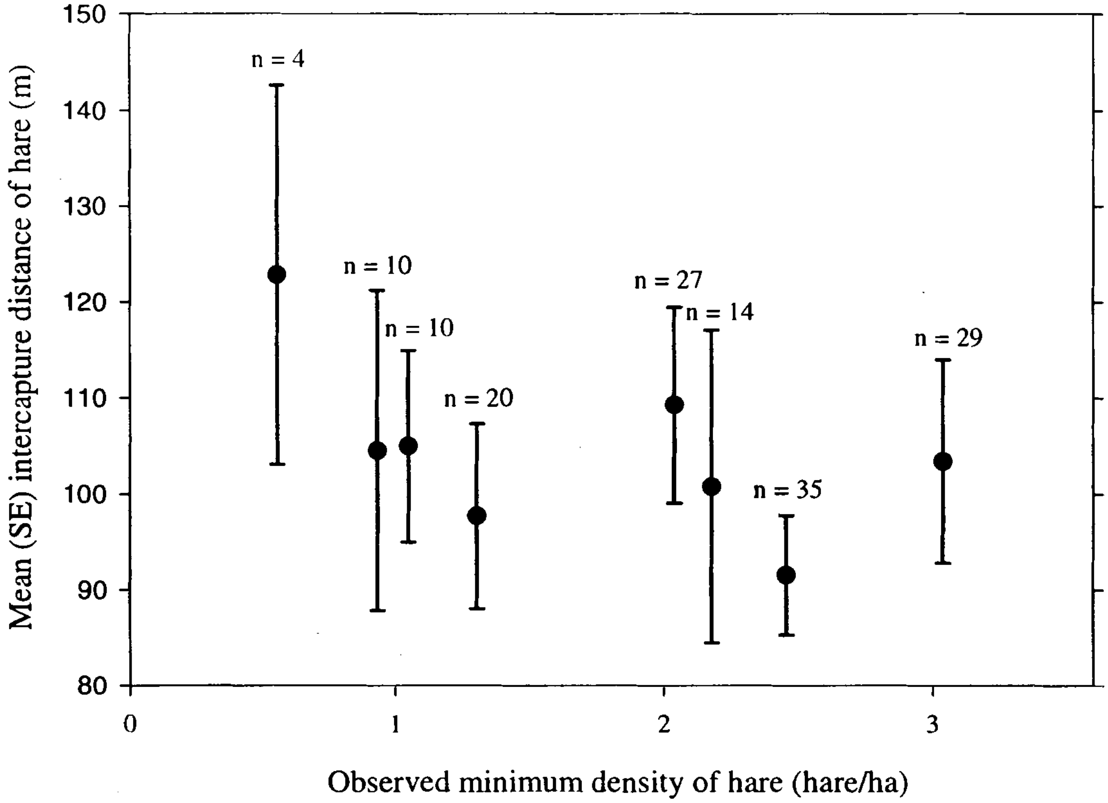

Figure 1.3. Relationship between mean inter-capture distance (SE) and density of snowshoe hare within 8 forest stands in north-central Maine, 2001-2002 (n = number of hares with > 1 capture). Inter-capture distance was defined as the average distance that hares (per stand) traveled between successive captures.

There was a positive relationship between pellets/ha/month and hares/ha ($r^2 = 0.89$, $n = 8$, $P < 0.001$) on my study sites in northern Maine (Figure 1.4). Errors were normally distributed (Lilliefors, $P = 0.225$) and variance was constant (Modified Levene's, $P = 0.718$). The relationship between hare densities appeared to be linear for densities ranging from 0.555 to 3.037 hares/ha in Maine. The slope of the line was 0.00008 with a standard error of 0.000011. The regression equation describing this relationship is:

$$\text{Hares/ha} = 0.281 + 0.00008\ (\text{pellets/ha/month}).$$

Recalculating the Long-Litvaitis relationship caused a small reduction of the slope, from 0.000116 (95% CI 0.000093, 0.000139) to 0.00010 (95% CI 0.000061, 0.000140); however, this relationship was still highly significant ($r^2 = 0.87$, $N = 8$, $P < 0.001$). The equation for this relationship is:

$$\text{Hares/ha} = 0.145 + 0.00010\ (\text{pellets/ha/month}).$$

Similar to previous studies conducted in northwestern Canada (Krebs et al. 2001b), western U.S.A. (Murray et al. 2002), and elsewhere in eastern and western Maine (Litvaitis et al. 1985, Long 1995), densities of hares were strongly correlated ($r = 0.94$) across a range (1,935-31,315 pellets/ha/month) of pellet densities in north-central Maine (Table 1.1). The model developed for northern Maine on my 8 study sites had the lowest AIC_c value ($\Delta AIC_c = 0.00$) and the Litvaitis-Long model also received support ($\Delta AIC_c = 2.77$), but these data did not support models developed outside of Maine ($\Delta AIC_c > 25.00$) (Table 1.1). Based on the Akaike weights, there was > 99% probability that the 2

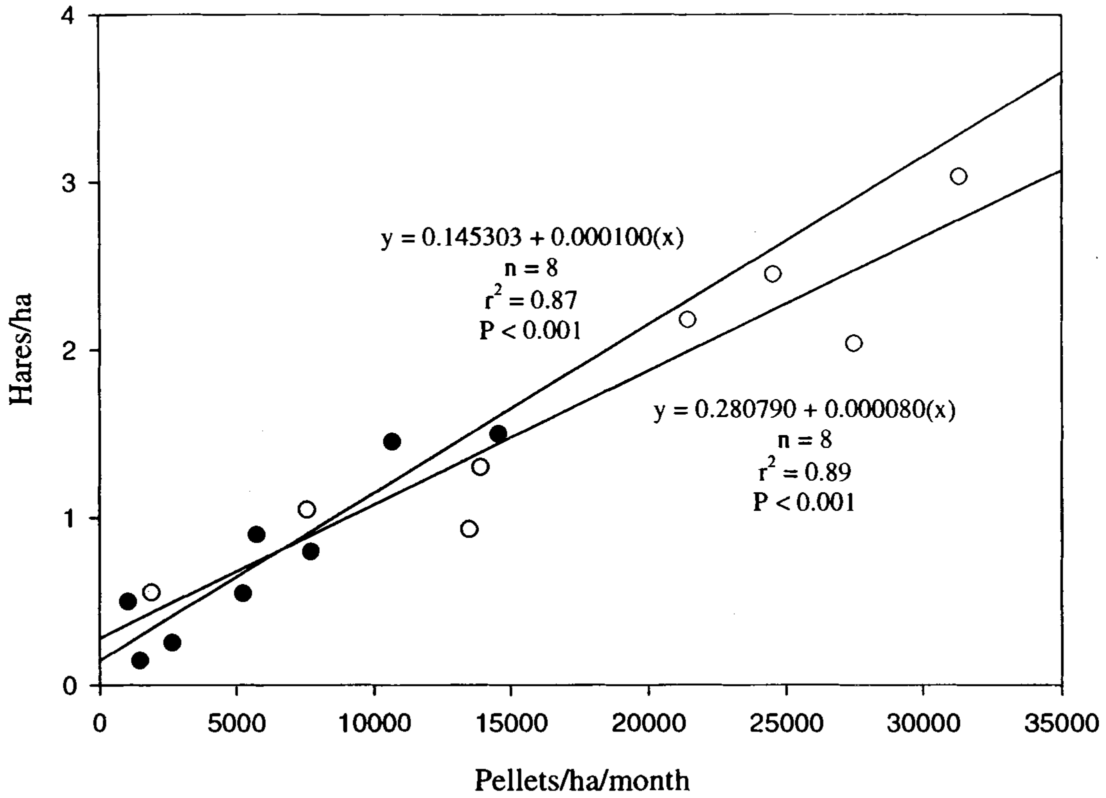

Figure 1.4. Relationships between density (hares/ha) of snowshoe hares and pellet density (pellets/ha/month) using mark-recapture estimates of hare densities as reported by Long 1995 (adapted and recalculated from Litvaitis et al. 1985) (closed circles) and minimum densities based on minimum number alive (open circles) in Maine. The model reported by Long (1995) was recalculated to avoid forcing the relationship through the origin.

Table 1.1. Reported correlation coefficients (r) and relative strength of evidence (Δ AIC$_c$, w_i) to support 4 area-specific predictive relationships of snowshoe hare densities from pellet densities based on pellet counts conducted in northern Maine, 2000-2002. The 4 predictive relationships are from northern Maine (this study), eastern and western Maine (Litvaitis et al. 1985, Long 1995), the Yukon Territory, Canada (Krebs et al. 2001), and Idaho (Murray et al. 2002).

Model	Region of study	Reported correlation coefficient (r)	K	AIC$_c$	Δ AIC$_c$	Akaike weights (w_i)
Homyack[a]	Northern Maine, USA	0.94	3	2.781	0.000	0.800
Litvaitis-Long[b]	Eastern & Western Maine, USA	0.93	3	5.551	2.770	0.200
Krebs et al. 2001a[c]	Yukon Territory, Canada	0.76	3	31.811	29.030	0.000
Murray et al. 2002[d]	Northern Idaho, USA	0.87	3	35.570	32.789	0.000

[a] Model given by: hares/ha = 0.281 + 0.000080(pellets/ha/month).

[b] Model given by: hares/ha = 0.145 + 0.00010(pellets/ha/month).

[c] Model given by: $\log_e$(hares/ha) = -1.203 + 0.899 $\log_e$(mean number of pellets/plot).

[d] Model give by: $\log_e$(mean number of hares) = 1.569 + 1.133 $\log_e$(mean number of pellets/plot).

models developed in Maine fit the data better than either of the models from the Yukon or Idaho.

DISCUSSION

Not surprisingly, the linear regression developed with the 8 data points from northern Maine was the strongest ($\Delta AIC_c = 0.00$) of the candidate model set, but the Litvaitis-Long model developed in Maine also described the data well. Models with a ΔAIC_c of ≤ 2 have substantial support, a $\Delta AIC_c > 3$ and < 7 have less support, and models with a $\Delta AIC_c > 10$ have virtually no support (Burnham and Anderson 2002). The Akaike weights (w_i) are conditional on both the data and *a priori* models and describe the approximate probability that a model is the "best" model (Anderson et al. 2000). If all models were similar and explained the hare density × pellet density relationship for northern Maine similarly, then all models would have had small Δ_i values and the Akaike weights would have been nearly equal. However, the regression model developed from this study received 0.80 of the model weight, and the remaining weight (0.20) was attributable to the Long-Litvaitis regression. Thus, predictive relationships of hare densities developed outside of Maine were not appropriate to explain the observed variation in these data.

The information-theoretic framework strongly advises towards biological significance trumping statistical significance. This approach does not rely heavily on arbitrary cutoffs to determine whether a model is "significant." Instead, the approach favors biological interpretation of results and only presents rough guidelines to gauge the appropriateness of a model (Burnham and Anderson 2002). Although these guidelines based on the relative strength of evidence and model weights (w_i) suggested that the site-specific regression developed for these data was the strongest model, I believe that the modified Litvaitis-Long model developed from data in eastern and western Maine should be considered the most biologically meaningful model. My goal was not to find the best fit for my data, but to determine a predictive relationship for future researchers to translate pellet densities into hare densities. Because of insufficient numbers of captures and recaptures of hares per sampling grids during my study, I was unable to obtain actual density estimates from multiple mark-recapture population models. Therefore, I used the minimum number of hares known alive within each stand (MNA) to derive my regression model for predicting hare densities. In contrast, Litvaitis (1990) captured a greater number of hares (496 hares 1,060 times) on larger trapping grids (49 ha) and was able to produce closed-capture population estimates for his grids; thus the Litvaitis-Long regression equation was based on estimates of actual densities. Therefore, I believe that equations that predict estimated densities of hares are superior to my conservative estimates of densities based on MNA.

Mark-recapture models take into account behavioral and temporal factors such as trap-happiness, trap shyness, and time dependent recapture rates to estimate the number of animals present in the population that were never captured (White et al. 1982). Thus, it is not surprising that a regression equation derived from mark-recapture population estimates did not receive most of the model weight when fit to observed MNA densities × pellet densities. However, the densities of hares estimated based on the modified Litvaitis-Long (1995) equation differed little from the MNA-based densities computed from live trapping data obtained from my 8 sites. Average hare densities predicted based on my regression equation averaged 2.5% lower than densities estimated based on the

Litvaitis-Long equation. The recalculated Long-Litvaitis equation predicted densities 0.22 (range –0.22 to 0.85) hares/ha greater than observed densities calculated based on MNA across my 8 stands in north-central Maine. The apparent repeatability of the separate experiments at different times, places, using different methods, and by different researchers suggests that there were not great differences between the 2 functional relationships (Johnson 1999). Further, Long and Litvaitis developed their linear regression using observed pellet densities that ranged from only 1,000–15,000 pellets/ha/month (0.15-1.50 hares/ha). Despite the limited range of data used to develop the model, it reasonably predicted hare densities from 1,000 to 31,000 pellets/ha/month during my study (0.15-3.04 hares/ha). Therefore, I considered the modified Litvaitis-Long equation have greater biological relevance than the other 3 models.

Although regression models developed outside of Maine were inferior for predicting hare densities on the 8 stands that I sampled, I also wished to estimate the effect size, or how poorly these models predicted hare densities in Maine. I used the 8 pellet densities from stands sampled during this study and the 8 pellet densities recorded for stands sampled in eastern and western Maine (Litvaitis et al. 1985a) to predict hare densities using regression coefficients from the Yukon Territory, Canada (Krebs et al. 2001b) and Idaho (Murray et al. 2002). I then compared these estimates with hare densities predicted using the most biologically relevant model developed for Maine (i.e., modified Litvaitis-Long equation). Hare densities for the 16 sites from eastern, western, and northern Maine calculated using the regression model from the Yukon (Krebs et al. 2001b) were substantially lower than densities predicted by the regression model

Table 1.2. Comparison of predicted densities of snowshoe hares calculated from an equation developed in Maine with those predicted using reported relationships from the Yukon Territory, Canada (Krebs et al. 2001) and northern Idaho (Murray et al. 2002).

Predicted densities (hares/ha)[a]	Densities estimated with Krebs et al. 2001b equation (hares/ha)[b]	% Difference between predicted and Krebs et al. 2001	Densities estimated with Murray et al. 2002 (hares/ha)[c]	% Difference between predicted and Murray et al. 2002	Source of pellet densities
0.30	0.15	-49.29	0.08	-71.47	Litvaitis et al. 1985[c]
0.41	0.25	-39.06	0.16	-60.76	Litvaitis et al. 1985
0.25	0.11	-56.33	0.57	-77.34	Litvaitis et al. 1985
0.67	0.46	-31.29	0.35	-48.25	Litvaitis et al. 1985
0.92	0.65	-28.99	0.54	-41.50	Litvaitis et al. 1985
0.72	0.50	-30.62	0.38	-46.65	Litvaitis et al. 1985
1.21	0.87	-28.12	0.77	-36.10	Litvaitis et al. 1985
1.60	1.15	-28.04	1.10	-31.18	Litvaitis et al. 1985
2.29	1.63	-28.72	1.71	-25.38	This study
1.49	1.08	-27.98	1.01	-32.39	This study
0.90	0.64	-29.06	0.53	-41.80	This study
3.28	2.29	-30.00	2.62	-19.93	This study
0.34	0.19	-44.62	0.11	-66.96	This study
1.53	1.10	-28.01	1.05	-31.92	This study
2.89	2.04	-29.50	2.26	-21.79	This study
2.60	1.84	-29.12	1.99	-23.43	This study

[a] Hare densities were predicted with recalculated Long-Litvaitis equation, given by: hares/ha = 0.145303 + 0.0001 (pellets/ha/month)

[b] Relationship reported in Krebs et al. (2001) is given by: $\log_e$(hares/ha) = -1.203 + 0.899 $\log_e$(mean number of pellets/plot). Multiply final estimates by 1.567, a correction factor for the log-log relationship.

[c] Relationship reported in Murray et al. (2002) is given by: $\log_e$(mean number of hares) = 1.569 + 1.133 $\log_e$(mean number of pellets/plot). Multiply estimates by 1.41, a correction factor for the log-log relationship. Divide final estimates by 19 ha for a conservative density estimate. I did not add (1/6) to data as reported in Murray et al. (2002) because I found few zero pellets/plot.

[d] Litvaitis et al. (1985) estimated hares densities that were reported in Long (1995).

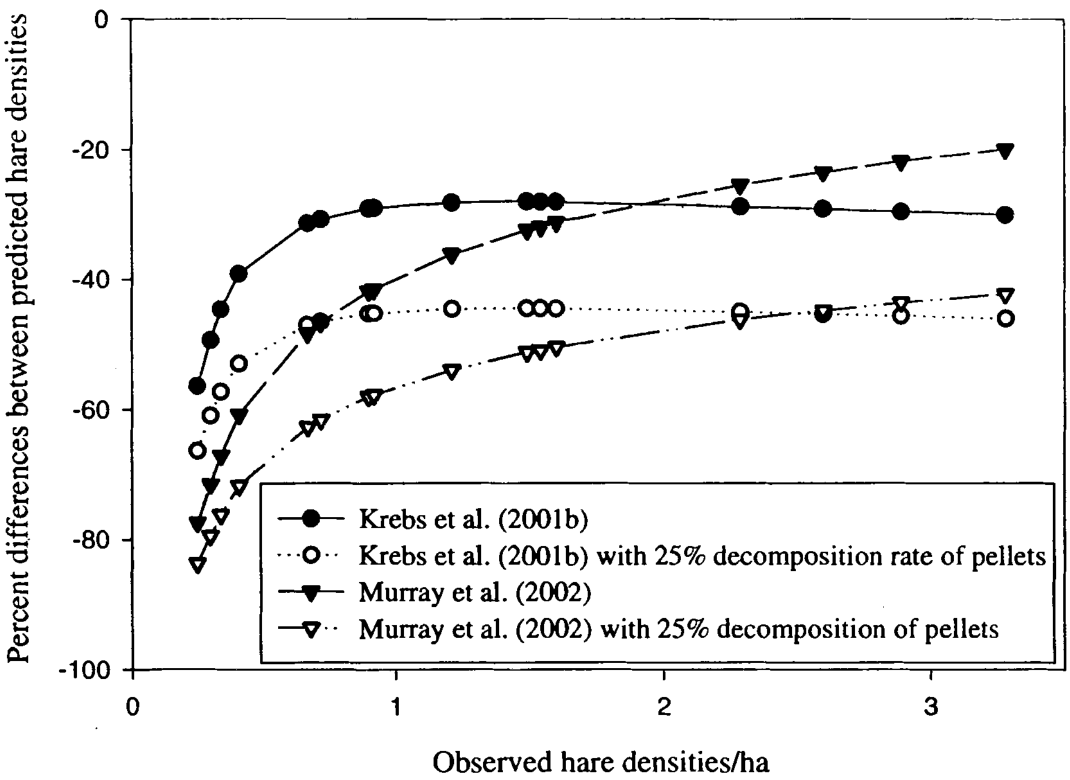

Figure 1.5. Percent difference between observed densities of snowshoe hares predicted using the best model from Maine (modified Litvaitis-Long equation) and densities predicted with models developed by Krebs et al (2001b) and Murray et al. (2002), with and without reducing pellet densities for decomposition. Pellet densities were based on 16 stands surveyed in Maine during 1981-83 (n = 8) and 2000-02 (n = 8). For open symbols, pellet densities were reduced by a decomposition rate of 25% to account for field observations of Murray et al. (2002).

developed for Maine (i.e., modified Long-Litvaitis equation, Table 1.2, Figure 1.5). The mean difference between densities estimated from the Maine versus the Yukon model was -0.40 hares/ha (95% CI -0.26 to -0.55). Similarly, densities predicted from regression coefficients for Idaho (Murray et al. 2002) were also less than predicted densities of hares for the 16 sites in Maine based on the modified Litvaitis-Long model (Table 1.2, Figure 1.5). The estimates for the Idaho model were lower by an average of -0.42 hares/ha (95% CI -0.34 to -0.50).

Geographic variation in relationships between densities of hares and pellets may result from variation in the number of pellets produced by snowshoe hares over time (Hodges 1999), and from differences in digestibility and chemical composition of primary foods (Sinclair et al. 1988). Thus, regional differences in diet quality of hares and species composition of available browse may impair estimates of density based on pellet × density relationships developed in other ecoregions. For example, wild-caught snowshoe hares from the Yukon Territory produced a greater number of pellets/day than captive hares in Vancouver, British Columbia fed similar diets (Hodges 1999). Further, cottontail rabbits (*Sylvilagus floridanus*) fed similar diets had large variation in daily numbers of pellets produced among individuals that was not explained by sex or size of rabbits (Cochran and Stains 1961). Pellet production rate is inversely related to the quality of food eaten, so that lagomorphs eating higher quality forage produce fewer pellets (Arnold and Reynolds 1943, Sinclair et al. 1988, Cochran and Stains 1961). Available forage for hares in Maine may have higher average digestibility than that of northwestern Canada and northern Idaho, which might account for a smaller number of pellets produced per hare per unit of time.

Diets of hares during the leaf-off season are dominated by low-quality woody browse and conifer needles, while in the summer, diets change dramatically to consist of herbaceous vegetation of with low fiber content (Wolff 1978, Larter 1999). Murray et al. (2002) suggested that pellets produced from higher-quality foods deposited during the leaf-on season may degrade more quickly than the larger and more fibrous pellets deposited during winter. Cochran and Stains (1961) reported that cottontail rabbit pellets produced from a high-quality commercial food decayed faster than pellets produced from low-quality diet of sumac (*Rhus spp.*). I noticed obvious differences in pellet size and color between seasons, with leaf-on pellets being smaller in size and darker in color. Both Krebs et al. (2001b) and Murray et al. (2002) only counted pellets once yearly during late spring (i.e. annual estimate of density), whereas I cleared pellets from plots in fall and counted pellets in spring (i.e. winter estimate of density). Persistence of pellets may have been greater for the larger, lighter-colored and more fibrous pellets deposited by hares during the leaf-off season, and annual estimates of density conducted in spring may have occurred after pellets from the leaf-on season had weathered and decayed. Failure to count some pellets deposited by hares during leaf-on season because of decomposition may explain discrepancies among relationships of densities of pellets and hares.

Others have raised concerns about potentially large biases arising from variations in pellet deposition rates caused by seasonal variation in forage quality and losses of pellets to decomposition (Orr and Dodds 1982, Angerbjorn 1983, Murray 2002). Murray et al. (2002) was unable to detect a difference in persistence of snowshoe hare pellets between recent clearcuts and mature forest, but Angerbjorn (1983) reported that pellets deposited by mountain hares (*Lepus timidus*) decayed more quickly in grass than other cover types and Cochran and Stains (1961) suggested that decomposition of pellets varies with cover type, food quality and weather. I avoided confounding seasonal effects of deposition and decomposition rates by calculating the relationship of snowshoe hare pellets deposited during the leaf-off season (Oct.–May) to densities of adult hares surviving the following May-June. Average monthly temperatures in northern Maine during this period ranged from only -10.17 to 13.33° C (National Oceanic and Atmospheric Administration 2000, 2001, 2002), which would slow decomposition of pellets.

It is unlikely that pellets would decompose during 8-9 months of cool and subfreezing temperatures during the leaf-off season throughout most of the geographic range of hares. Pellets from cottontail rabbits decomposed quickly during the summer months, but most persisted through winter in Illinois (Cochran and Stains 1961). Thus, if decomposition did occur, weathering would most likely affect pellets deposited by hares during leaf-on seasons (June–September). Murray et al. (2002) reported that only 75% of fresh pellets ($n = 540$ pellets) placed on plots survived an entire year in Idaho, suggesting that decomposition may reduce pellet densities in a year or less. To examine this hypothesis further, I compared predicted hare densities in Maine to those predicted by Krebs et al. (2001b) and Murray et al. (2002) after pellet densities were reduced by the 25% decomposition rate. Accounting for decomposition of hare pellets in Maine did not explain the underestimation of hare numbers by regressions outside of Maine ($P < 0.001$); in fact, a 75% persistence rate widened the gap between observed and predicted densities, but still in a nonlinear fashion (Figure 1. 5). These results indicate that decomposition of hare pellets does not explain the discrepancy between observed hare densities in Maine and densities predicted using regressions from the western United States and Canada.

Although decomposition of pellets may not explain geographic variation in predicted hare densities, there are still biologically important reasons to survey seasonal pellet densities rather than annual counts. Association of leaf-off season pellet densities with densities of hares during early spring should be conservative because spring corresponds with the fewest hares. I excluded leverets in density estimates so that all marked individuals were > 8 months in age. Snowshoe hares select cover types based on understory cover in winter, but in summer occupy open habitats with more herbaceous vegetation (Wolff 1980, O'Donoghue 1983). Seasonal changes in habitat use by hares coupled with variation in pellet deposition rates caused by forage of different quality, may confound estimates of pellet densities based on annual counts. Further, winter is thought to be the limiting season for snowshoe hares (Pease et a. 1979, Pietz and Tester 1983) and estimates of densities of adult hares surviving at the end of the critical limiting season may more accurately depict differences in habitat quality by incorporating aspects of population performance such as over-winter survival (Van Horne 1983).

Whereas MNA densities of snowshoe hare from northern Maine were strongly correlated ($r = 0.94$) to pellet densities from the previous leaf-off season, leaf-on season pellet densities explained considerably less ($r = 0.65$) variation in numbers of hares. The weaker relationship between leaf-on season (June-September) pellet densities and number of hares residing in stands in early spring (May-June) suggests that counts of pellets that include the summer months, when hares are more like habitat generalists (Wolff 1980, O'Donoghue 1983) and forage primarily on herbaceous vegetation (Wolff

1978, Larter 1999), produce more variable predictions of hare densities than leaf-off season counts. Therefore, I suggest that counts of pellets during leaf-off seasons be used to predict densities of hares to avoid these potential biases and produce more biologically meaningful estimates of hare numbers.

Krebs et al. (2001b) and Murray et al. (2002) reported that a $\log_e$-$\log_e$ relationship best fit their data because variances increased with the observed mean number of both pellets and hares. I hypothesized several explanations for why a log-log relationship was needed to describe pellet densities as a function of hare density for data from northern Canada and the western United States, but not Maine. First, variances may have increased with the mean in northern Canada when densities changed significantly within a year. It is well documented that hares undergo dramatic population cycles in northern Canada and densities can widely fluctuate, even within a year (Hodges 2000). Krebs et al. (2001b) only counted pellets once yearly and related those pellet densities to hare densities estimated from live trapping that began the previous year. Or, perhaps data sets for my model and the modified Litvaitis-Long model were too small and had little power to detect heteroscedasticity (Krebs et al. 2001b, $n = 85$; Murray et al. 2002, $n = 24$; Long 1995, $n = 8$; this study, $n = 8$). To ensure that a $\log_e$-$\log_e$ relationship was not a better fit to my data than the 4 *a priori* models, I computed the AIC_c for a model with my 8 MNA hare density × pellet density points from northern Maine with the predictor and response variables $\log_e$ transformed. This model was added after my *a priori* models were developed; therefore interpretation of this model can only be considered exploratory (Burnham and Anderson 2002). The $\log_e - \log_e$ model developed for northern Maine ($\Delta AIC_c = 4.704$) received less support than the other models from Maine (Table 1.1).

Further, the recalculated Akaike model weights (w_i) from greatest to smallest were as follows: the linear model from northern Maine ($w_i = 0.743$), the Litvaitis-Long model from eastern and western Maine ($w_i = 0.186$), the $\log_e - \log_e$ model developed for northern Maine ($w_i = 0.071$), the Krebs et al. (2001b) model from western Canada ($w_i < 0.001$), and the Murray et al. (2002) model from Idaho ($w_i < 0.001$). The approximately 2.6× more weight given to the linear model from eastern and western Maine than the post hoc $\log_e - \log_e$ model developed for northern Maine indicate that the hare density × pellet density relationship for northern Maine was better fit by a linear function than a log-normal function.

CONCLUSIONS

Although a functional relationship between pellet densities and densities of hares was established in the Yukon Territory, Canada, the relationship may differ for hares near the southern periphery of their range. Observed relationships of pellet × hare density during 2000-2002 in northern Maine were similar to relationships observed in 1981-1983 for eastern and western Maine. Thus, the linear relationship between densities of pellets and hares may be stable through time and across a range of habitat types in the eastern spruce-fir, northern hardwood forests, and within a range of 0-3 hares/ha. My estimated relationship between MNA density and pellet density was consistent with a previously derived relationship for Maine; however hare densities estimated using regression equations developed for the Yukon Territory, Canada (Krebs et al. 2001b) and northern Idaho (Murray et al. 2002) underestimated predicted densities for north-central, eastern, and western Maine.

I suggest that densities of snowshoe hares in northeastern North America be estimated from pellet counts using the modified linear regression (i.e. not forced through the origin) model derived by Long (1995) which was adapted from data collected by Litvaitis et al. (1985) for eastern and western Maine. Previous investigators conducted yearly pellets counts (Krebs et al. 2001b, Murray et al. 2002); however, densities of hares estimated based on pellets deposited during the leaf-off season may be more biologically meaningful and might avoid potential biases arising from the dynamic summer-winter diets of hares, differential losses of pellets to decomposition during summer and winter months, and to seasonal shifts in habitat use by hares.

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CHAPTER 2

TEMPORAL EFFECTS OF PRECOMMERCIAL THINNING ON SNOWSHOE HARES IN MAINE

ABSTRACT

Snowshoe hares (*Lepus americanus*) are an important prey species and dominant herbivore across much of their North American range, and forestry practices that degrade habitat for hare may have community-wide effects. Further, the effects of precommercial thinning (PCT) on hares have been questioned in relation to indirect effects on recovery of the Federally threatened Canada lynx (*Lynx canadensis*). I examined the effects of PCT on snowshoe hares, from 1-11 years post-treatment in the commercial forests of northern Maine. I established > 46 km of pellet transect across 13 unthinned, regenerating conifer stands, and 17 regenerating conifer stands treated with PCT. Hare pellets were counted and cleared along transects twice a year during 2001 and 2002, and stand-level vegetation characteristics previously documented as correlates with hare density were measured in all stands. Densities of snowshoe hares were consistently lower in stands treated with PCT than in similar unthinned stands across all thinning classes and seasons during both years of the study ($P < 0.10$). Stands treated with PCT supported hare densities approximately ½ those observed in untreated stands when averaged across seasons and 2 years of sampling. In general, hare density was greatest in stands in the 1-year thinning class when compared to 6 and 11-year thinning classes, but a statistical difference ($P < 0.10$) among thinning classes was evident only during leaf-off seasons. Several habitat characteristics previously reported to be important positive correlates of hare densities, such as understory stem densities and horizontal cover, were

lower in thinned versus unthinned stands. PCT was associated with densities of snowshoe hare that were lower than those in similar unthinned stands; however, thinned stands may retain densities of hares greater than stands managed using other forest harvesting regimes (e.g., some types of partial harvests).

INTRODUCTION

In March 2000, the U.S. Fish and Wildlife Service (USFWS) listed Canada lynx as threatened under the Endangered Species Act (ESA) (United States Department of the Interior 2000). Lynx are specialized predators (O'Donoghue et al. 1998) of snowshoe hares and density of hares is positively and exponentially associated with stands with high densities of conifer saplings (Litvaitis et al. 1985a). Maine has the only verified population of resident lynx in the northeastern USA and the relationships among lynx, habitat, and forestry practices are not thoroughly understood (Aubry et al. 2000). At a statewide scale, large areas of regenerating conifer stands are a habitat variable that is positively associated with both occurrence of lynx and relative abundance of snowshoe hares in Maine (Hoving 2001). Thus, extensive areas of regenerating forest may promote persistence of the only verified population of lynx in the northeastern USA. However, little is known about the temporal effects of stand succession on densities of snowshoe hare at the southern periphery of their range, particularly after intensive management of vegetation.

Thirteen environmental organizations, including Defenders of Wildlife and the Biodiversity Legal Foundation, legally challenged the ESA listing of lynx as threatened in the contiguous United States. They alleged that the listing of lynx as endangered and designation of critical habitat was necessary to ensure survival and recovery. If USFWS designates critical habitat, it is likely, because lynx are strongly tied to high densities of hares (O'Donoghue et al. 1998, Mowat et al. 2000), that foraging habitat will be designated as "critical." Because large areas of regenerating conifers are known to support high densities of snowshoe hares, forestry practices that degrade habitat for hares may be questioned under ESA.

Precommercial thinning (PCT) is a silvicultural technique that decreases stem density and may reduce densities of hares relative to unthinned, regenerating stands (Sullivan and Sullivan 1988). Further, the biological assessment of the effects of U.S. National Forest land and resource management plans on Canada lynx suggested that forest thinning might reduce foraging habitat of lynx in the northeastern USA (Hickenbottom et al. 1999). During 1993 to 2001, greater than 67,000 ha (167,000 acres) of forest were precommercially thinned in Maine (Maine Forest Service 1994-2002). Because total acreage of PCT is projected to increase, forest managers will be asked to justify this practice based on maintaining wildlife habitat and biodiversity.

Limited information about the effects of precommercial thinning on snowshoe hares has indicated that thinning reduces density of hare for 3-4 years after treatment (Sullivan and Sullivan 1988), but how long after treatment abundances of snowshoe hares continue to be lower relative to unthinned stands is unknown. It is also unknown how the acceleration of stand development associated with PCT affects snowshoe hares compared to untreated stands. Further, previous studies of hares and thinning included non-herbicided stands that were released with brushsaws (Sullivan and Sullivan 1988, de Bellefeuille et al. 2001). In Maine, stands treated with PCT are first aerially sprayed with herbicides (e.g., Glyphosate or Triclopyr) and later manually thinned; the combination of these treatments may have different effects on densities of hares than in stands treated solely with brushsaws.

Investigators have consistently related high densities and relative abundances of snowshoe hares to mid-successional habitats with high stem densities of saplings (Wolff 1980, O'Donoghue 1983, Pietz and Tester 1983, Litvaitis et al. 1985a, Litvaitis et al. 1990, Koehler 1990, Fuller 1999, Hoving 2001). Thus, it would be expected that a forest practice that decreases the stem density of regenerating forest stands and promotes rapid growth of crop trees would decrease densities of snowshoe hare. Therefore, I hypothesized that PCT would reduce snowshoe hare densities relative to similar untreated stands, and that these changes would be related to reduced densities of coniferous and deciduous stems.

The objectives of this study were to: 1) determine if precommercial thinning with brush-saws decreases abundances of snowshoe hare on herbicide treated clearcuts, from 1-11 years post-treatment; 2) determine the magnitude of differences in hare densities between unthinned and PCT stands; and 3) describe the differences in vegetation characteristics preferred by hares between thinned and unthinned clearcut stands from 1–11 years after treatment.

STUDY AREA

I selected 6 townships (Hersey, T4 R 11 WELS, T 5 R 11 WELS, T4 R 12 WELS, T1 R 13 WELS, and Spencer Bay) in the commercial forests of northern Maine that fall within the historical distribution of Canada lynx (Hoving 2001) as my study area (Figure 2.1). Hersey Township is located in Aroostook County, Maine whereas the other

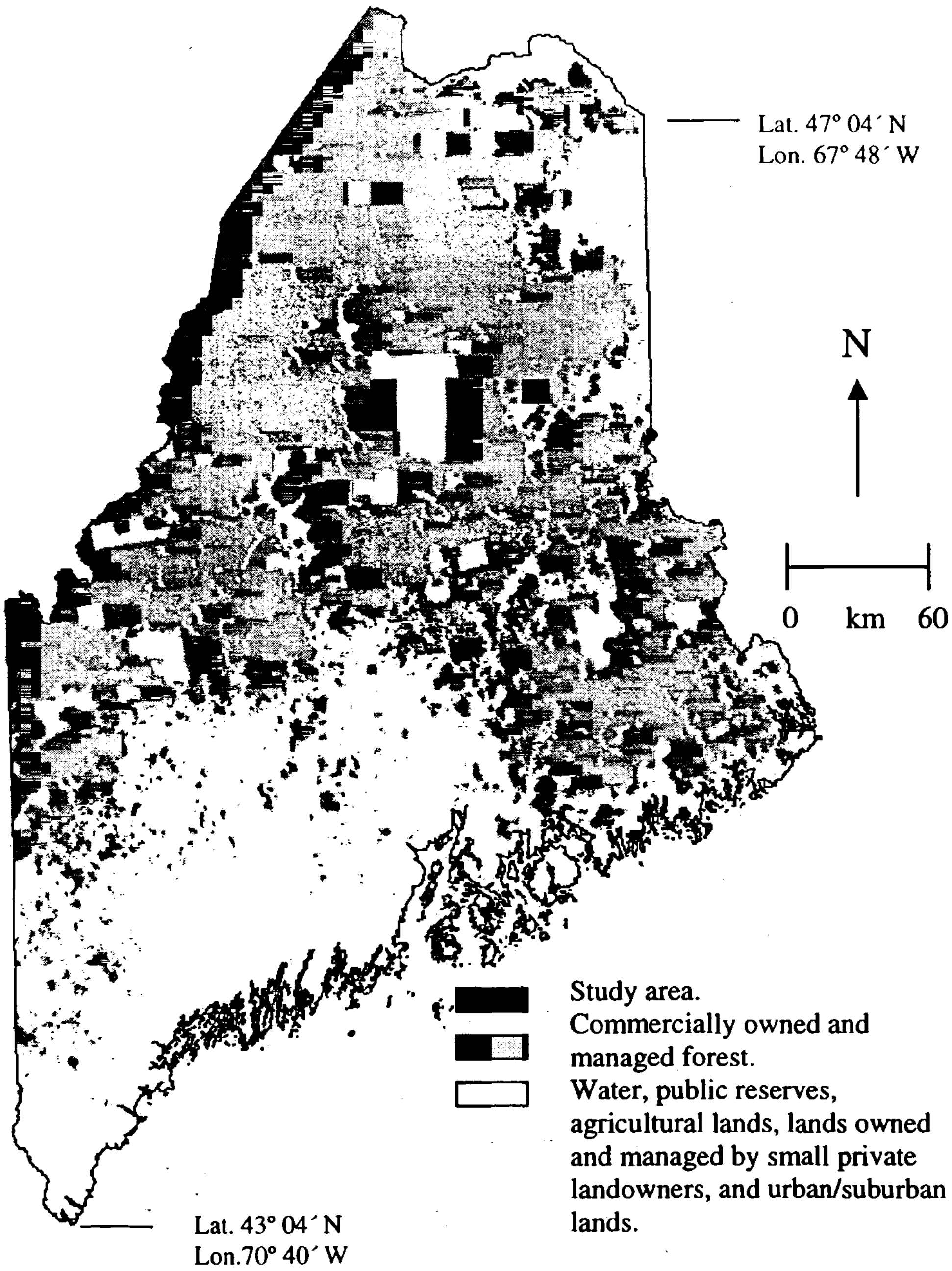


Figure 2.1. Location of study areas within 6 townships in the commercially owned and managed forests of north-central Maine.

5 townships are located in Piscataquis County, Maine. These towns range from 102 km east to west and from 49 km north to south. Great Northern Paper Company, Millinocket, Maine; Plum Creek Timber Company, Fairfield, Maine; and International Paper Company, Costigan, Maine managed the study areas for pulp and sawtimber production.

The study areas occur within the ecotone between the northern boreal forest and the eastern deciduous forest that is referred to as the sub-boreal Acadian forest (Seymour and Hunter 1992). Balsam fir (*Abies balsamea*) and spruce (*Picea spp.*) dominate the study sites, but stands also have minor components of white pine (*Pinus strobes*), northern white cedar (*Thuja occidentalis*), larch (*Larix laricina*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), paper birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*). The annual mean temperature in this region was 3.78 °C and the area received an average of 101 cm of precipitation annually, with 276 cm of snowfall (Garoogian 2000). Stands (n = 30) surveyed on the study areas were chosen based on flat to gently sloping topography, and ranged from 8.5 to 74.3 ha in size (Median = 22.2 ha).

METHODS

I examined site quality, tree density, diameter breast height (dbh) of dominant trees, and size and spatial independence of stands before selecting them as study sites. I estimated site quality of stands with 4 to 6 soil cores taken throughout the stand with a soil auger. Stands were assigned a drainage value from 1 (highly productive) to 5 (unproductive) according to Brigg's (1994) scale of forest tree productivity.

Treatment stands were clearcut (timber harvesting resulting in residual basal area of acceptable growing stock trees > 11.43 cm dbh of < 20.66 m^2/ ha) 1968-1982, aerially herbicided (e.g. Glyphosate at ≈ 1.68 kg/ha acid equivalent) 1982-1988, and precommercially thinned with motor-manual brush-saws from 1989-1999. Unthinned stands were clearcut 1974-1982 and herbicided (e.g. Glyphosate at ≈ 1.68 kg/ha acid equivalent) 1982-1988 (Table 2.1). Stands were divided into blocks based on date of precommercial thinning. The study design included 17 treatment stands at 5-year intervals since thinning (1-2 year post-thinning, n = 5; 6-7 years, n = 5; 11-12 years, n = 7) and 13 stands with management histories and site quality similar to treated stands, but that were not thinned (1-2 year, n = 5; 6-7 years, n =5; 11-12 years, n = 3). I allowed some latitude (1-2 years) in separating stands into thinning class categories based on the date of silvicultural treatments. When selecting study sites, I paired a treatment stand with an unthinned stand with a similar year of clearcut, year of herbicide, and site quality to avoid any large differences between treatment and unthinned stands within a thinning class. This was a retrospective study; therefore stands were not paired in a statistical sense and were analyzed as unpaired replicates.

Pellet counts

Fecal pellet counts can be a reliable estimate of snowshoe hare abundance (Krebs et al. 1987, Long 1995, Krebs et al. 2001, Murray et al. 2002, Chapter 1) and are more practical than live-trapping over large areas because indirect estimates of abundance are more economical and less labor intensive than typical mark-recapture techniques (Litvaitis et al. 1985b). I established 46.68 km of pellet transect across the 30 stands. The stand was considered the unit of replication because the median stands size was 3.6 ×

Table 2.1. Stand history, location, and site quality of 17 PCT and 13 unthinned stands in northern Maine. (T = stand treated with PCT, C = unthinned stand). Site quality ranged from 1 (well drained, productive) to 5 (poorly drained, unproductive) according to Briggs (1994) classification guidelines.

Site number	Year of Clearcut	Year of Herbicide	Year of PCT	Township	Site Quality
1-1-T	1982	1988	1999	T 4 R 11	4+
1-2-T	1980	1983	1999	T4 R 12	3-
1-3-T	1977	1983	1999	T4 R 11	4+
1-4-T	1982	1988	1999	T4 R 11	4
1-5-T	1976	1983	1999	T4 R 12	4
6-1-T	1979	1988	1994	Hersey	3+
6-2-T	1979	1988	1994	Hersey	2-
6-4-T	1974	1982	1994	T 5 R 11	3-
6-5-T	1976	1985	1995	T 5 R 11	3-
6-6-T	1979	1982	1994	T 5 R 11	3-
11-1-T	1975	1983	1989	T 1 R 13	3
11-2-T	1968	1987	1990	Spencer Bay	3-
11-3-T	1975	1983	1989	T 1 R 13	2-
11-4-T	1975	1986	1990	T 1 R 13	3
11-5-T	1975	1983	1989	T 1 R 13	2
11-6-T	1975	1984	1991	T 1 R 13	2-
11-7-T	1975	1986	1989	Spencer Bay	2-
1-1-C	1982	1988	n/a	T 4 R 11	4
1-2-C	1979	1983	n/a	T 4 R 11	3-
1-3-C	1981	1984	n/a	T 4 R 11	4+
1-4-C	1983	1988	n/a	T 5 R 11	4+
1-5-C	1976	1985	n/a	T 4 R 11	3-
6-1-C	1979	1988	n/a	Hersey	3+
6-2-C	1981	1988	n/a	Hersey	3+
6-4-C	1974	1982	n/a	T 5 R 11	4
6-5-C	1974	1985	n/a	T 4 R 12	3
6-6-C	1976	1983	n/a	T 4 R 11	4
11-1-C	1976	1982	n/a	T 5 R 11	3
11-3-C	1976	1982	n/a	T 5 R 11	3+
11-4-C	1974	1985	n/a	T 5 R 11	3

greater than the average home range size of hares in Maine (Litvaitis 1984). I established 1.6 km of transect in 28 stands and the remaining two stands had 1.18 km and 1.34 km of transect resulting from their size and irregular shape. I placed transects greater than 50 m from stand boundaries to minimize edge-effects (Harris 1988, Fraver 1994). When possible, I established 4 parallel, 400 m transects in a stand and separated transects by 65 m. I marked 5m by 30 cm pellet plots at 20 m intervals along transects for a total of 84 plots per stand and a total of 2,480 pellet plots for the study. I randomly oriented pellet plots along transects and marked them with orange wooden stakes at either end of the plot.

I cleared all plots of hare pellets during October 18-25, 2000 so that only pellets deposited after leaf-off were counted during spring 2001. Subsequently, I counted and cleared pellets 4 times during the remainder of the study: May 17-June 14, 2001, September 13-29, 2001, and May 10-June 17, 2002, and September, 13-October 13, 2002. I averaged the number of pellets/plot for each stand and converted it to a value of pellets/ha/day. I divided the year into 2 seasons, leaf-off season and leaf-on season. Thus, spring pellet counts (May-June) were used to estimate abundance during the previous winter (defined as leaf-off season, October-May) whereas fall pellet counts (September-October) were used to estimate abundance during the previous summer (defined as leaf-on season, June-September).

Live-trapping

I live-trapped hares within the core portions of 2 thinned stands and 2 untreated stands during May-June, 2001 and in 2 different thinned and 2 different untreated stands during May-June 2002 to evaluate the relationship between pellet densities and estimated densities of snowshoe hares. I also evaluated whether there were any differences in sex ratios or lactation rates among stands treated with PCT and unthinned stands. Greater densities of animals in a particular cover type may not necessarily indicate higher habitat quality (Lidicker 1975, Van Horne 1983); thus, I examined the sex ratios and lactation rates as additional indicators of the habitat quality for hares in thinned and unthinned stands. Chapter 1 provides a detailed description of methods used to trap, mark, sex, and determine lactation status of hares.

Habitat sampling

Across their geographical range, snowshoe hares respond numerically to stand structure and densities of hares are consistently related to a few key stand-level habitat characteristics, including positive associations with understory stem density (O'Donoghue 1983, Sullivan and Sullivan 1988, Litvaitis et al.1985a, Monthey 1986, Koehler and Brittell 1990, Long 1995, Fuller 1999), woody debris (Conroy et al. 1979, Scott and Yanhner 1989, Ferron et al. 1998), and horizontal vegetation density (Wolfe et al. 1982, Pietz and Tester 1983, de Bellefeuille et al. 2001, Wirsing et al. 2002). Therefore, differences among stand structure between PCT and untreated stands (low hare-density and high hare-density stands) may explain some variation in hare numbers among my study sites in northern Maine.

I selected 6 forest structural variables *a priori* based on previous studies of habitat relationships of snowshoe hares, including measures of overstory, understory, woody debris, and horizontal cover. I measured those stand-scale habitat characteristics on fixed area nested plots placed along the pellet transects. Five plots per 400 m of transect were established at random distances on the pellet transects for a total of 20 plots per stand. I measured vegetation within 25 m^2 plots in thinned stands and within 10 m^2 plots in unthinned stands. Larger plots were established on thinned stands because stem density was reduced in these stands, and I wished to sample approximately 100 crop trees per stand.

I quantified the number of coniferous trees (≥ 7.6 cm dbh, >1 m height, alive) within the plot and measured the number and type (coniferous or deciduous) of all understory stems (< 7.6 cm dbh, >1 m height, alive) within the plot. I quantified the number of stem cover units ((3 × number of understory conifer stems) + number of understory deciduous stems) (Litvaitis et al. 1985a) per/ha. Horizontal vegetation structure was measured as a continuous variable using a 2.0 m cover pole with alternating 0.1 m red and white bands (Griffith and Youtie 1988). Visual obstruction was measured in opposite directions from the center point following a random compass bearing. The distance from the center point where ≥ 25% of all bands were visually obstructed was recorded. I estimated the volume of downed logs with a modified version of the planar intersection method used by Payer and Harrison (2000). I established a 20-m randomly oriented transect with the midpoint at each sampling station and quantified the number of logs that crossed the transect and were ≥ 1.0 m length, ≥ 7.6 cm diameter (at the point of intersection), and ≤ 45° from the ground. I considered only sound to moderately decayed logs, so that extremely decayed logs were excluded from sampling. I also measured overhead canopy cover with a spherical densiometer (Lemmon 1956) to simulate the cover perceived by hares during the winter on top of snowpack. Four readings in the 4 cardinal compass directions at 1.0 m height were taken at the center of each plot and averaged to a single value for each plot.

Statistical analyses

I examined pellet densities separately during leaf-off and leaf-on seasons to avoid confounding effects of seasonal change in diets and shifts in habitat use that might contribute to variation in pellet deposition rates by hares. I conducted a repeated measures two-way Analysis of Variance (ANOVA) for the observed densities of pellets during the leaf-off season to determine if there were any differences among thinning classes (1, 6, 11 years since treatment), treatment (stands treated with PCT, unthinned stands), year of sampling (2000-2001 leaf-off season, 2001-2002 leaf-off season) and any interactions (Zar 1999). Similarly, I conducted a repeated measures two-way ANOVA for the observed pellet densities during the leaf-on season to determine if there was any differences among thinning classes, treatments, or years of sampling. I examined normality of error terms with normal probability plots and Lilliefor's test. I examined the data for constant variance with the modified Levene's test and plots of the residuals. I examined any significant differences among thinning classes *a posteriori* with Tukey's Honest Significant Difference Tests (Zar 1999).

Densities of snowshoe hare pellets were highly correlated with and linearly related to densities of hares on my northern Maine study sites (Chapter 1). Thus, observed differences in pellet densities directly correspond with differences in absolute densities of hares. All statistical comparisons were conducted using pellet densities; however, estimated densities of hares are also presented to enhance biological interpretations from statistical conclusions. I used the modified Litvaitis-Long model (hares/ha = 0.145303 + 0.0001 (pellets/ha/month)) to predict hare densities from pellet densities (Chapter 1).

Differences in proportions of males versus females and number of lactating females versus non-lactating females in PCT and unthinned stands were tested using a Z-test (Zar 1999). I pooled the data across years of sampling and stands within a treatment to maximize statistical power.

I used the mean of each habitat variable for each stand to descriptively analyze differences in stand structure among thinning classes and treatments by conducting a Two-way ANOVA on the means of each habitat variable (averaged across 20 plots within each stand) with thinning class (1, 6, 11 years since treatment) and treatment (stands treated with PCT and unthinned stands) as factors. I examined error terms for normality with a Lilliefor's test and probability plots and conducted a Modified Levene's test to examine the data for constant variance. Non-normal habitat variables were transformed using $\log_e$ transformations (Neter et al. 1996).

RESULTS

Pellet densities

Residual errors of pellet densities for the leaf-off seasons were normally distributed ($P > 0.10$) and variance was constant ($P > 0.10$), suggesting that the effects of treatment, thinning class, and year of sampling could be appropriately evaluated using parametric ANOVA. Previously herbicided clearcuts treated with PCT had lower pellet densities relative to similar unthinned stands during the leaf-off seasons ($F = 17.881$, $P < 0.001$) (Figure 2.2, Table 2.2). Unthinned stands had 1.97- and 2.01-fold greater densities of pellets than stands that were treated with PCT during both the 2000-2001 and 2001-2002 leaf-off seasons, respectively. Further, there was an effect of thinning class on pellet densities during the leaf-off season ($F = 3.451$, $P = 0.048$). In 2000-2001

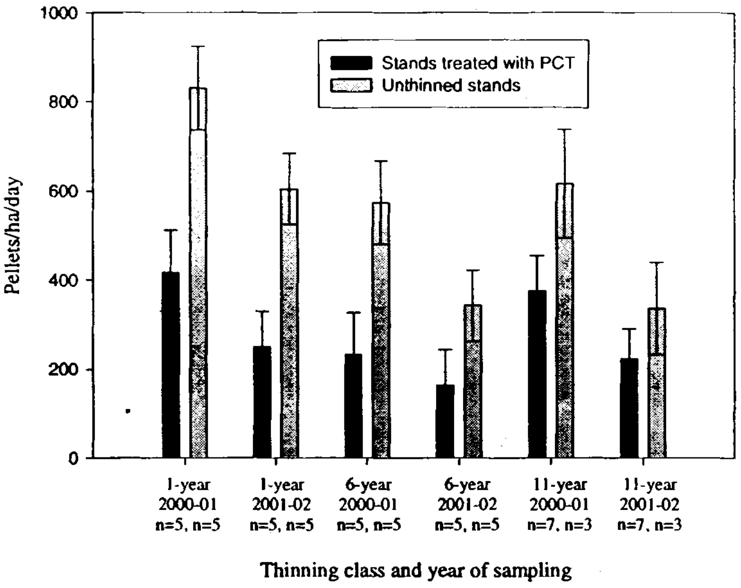
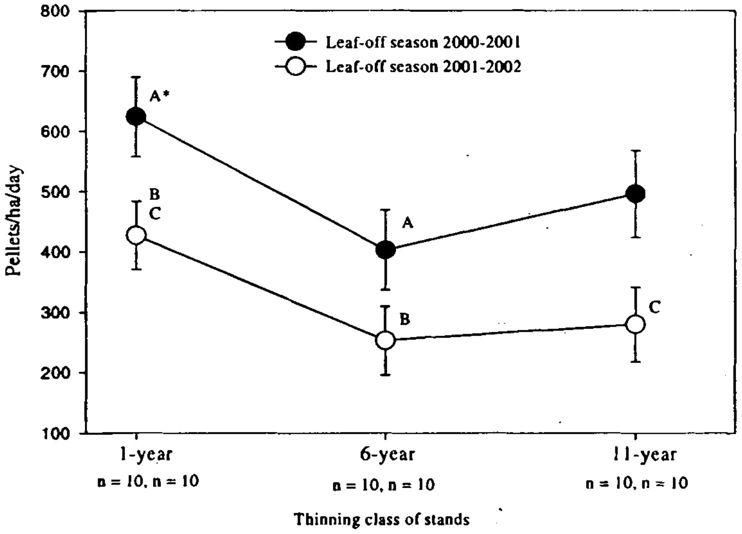


Figure 2.2. A comparison of mean (SE) number of snowshoe hare pellets/ha/day between PCT stands and similar unthinned stands in northern Maine during leaf-off seasons, 2000-2002.



* Statistical significance at p < 0.10 level denoted by like letters

Figure 2.3. Mean (SE) pellets/ha/day averaged across stands treated with PCT and unthinned stands during the leaf-off seasons, from 1-11 years post-treatment in northern Maine; 1 = treated in 1999, 6 = treated in 1994, 11 = treated in 1989-1990. Statistical significance at P < 0.10 level is denoted by like letters.

Table. 2.2. Effects of treatment, thinning class, and year of sampling on pellet density and estimated density[a] of snowshoe hares within 30 stands (17 treated with PCT, 13 unthinned) and among leaf-off (October – May) and leaf-on (June-September) seasons in northern Maine, 2000-2002.

Season	Factor	F-Statistic	P-value	Pellets/ha/day (SE)	Hares/ha (SE)
Leaf-off, 2000-02	**Treatment**	**17.881**	**< 0.001**		
	PCT			227.36 (30.41)	0.83 (0.24)
	No-PCT			562.38 (52.83)	1.80 (0.30)
	Thinning class	**3.451**	**0.048**		
	1-year			525.91 (68.92)	1.72 (0.35)
	6-year			328.63 (47.71)	1.13 (0.29)
	11-year			352.46 (48.48)	1.31 (0.29)
	Year	**29.825**	**< 0.001**		
	2000-2001			491.82 (49.87)	1.62 (0.29)
	2001-2002			312.84 (39.86)	1.08 (0.26)
Leaf-on, 2001-02	**Treatment**	**21.231**	**< 0.001**		
	PCT			116.30 (12.07)	0.49 (0.18)
	No-PCT			261.27 (36.70)	0.93 (0.26)
	Thinning class	0.173	0.842		
	1-year			205.92 (38.93)	0.76 (0.26)
	6-year			167.79 (32.23)	0.65 (0.24)
	11-year			163.67 (30.62)	0.73 (0.24)
	Year	**93.346**	**< 0.001**		
	2001			256.30 (32.08)	0.91 (0.24)
	2002			101.94 (10.49)	0.45 (0.18)

[a] Hare densities were estimated from pellet densities using the most appropriate regression model (Chapter 1). The equation used: Hares/ha = 0.145303 + 0.0001 (pellets/ha/month).

the 1-year thinning class had greater numbers of pellets than the 6-year thinning class ($P < 0.005$), but the 1-year and 11-year stands did not differ significantly ($P < 0.10$) (Figure 2.3, Table 2.2). During 2001-2002, however, the 1-year thinning class supported greater ($P < 0.05$) densities of pellets than either the 6-year or 11-year thinning classes. Pooled across both years, the 1-year thinning class had 1.6 times greater pellet densities than the 6-year and 1.4 times greater pellet densities than the 11-year thinning class. The 2000-2001 leaf-off season had 1.57 × greater pellet densities than the 2001-2002 leaf-off season ($F = 28.825$, $P < 0.001$).

Residual errors were not normally distributed ($P = 0.01$) and variance was not constant ($P < 0.10$) for pellet densities during the leaf-on season. Therefore, I $\log_e$ transformed pellet densities to correct for these violations of the parametric assumptions of ANOVA. After transformation, errors were normally distributed ($P > 0.10$) and variance was constant ($P > 0.10$). Stands treated with PCT had lower densities of snowshoe hare pellets than similar unthinned stands during the leaf-on seasons ($F = 19.499$, $P < 0.001$) (Table 2.2, Figure 2.4). Unthinned stands had 2.47 fold greater pellet densities than stands treated with PCT during the leaf-on season in 2001 and 1.66 fold greater pellet densities during leaf-on season in 2002. There was no effect of thinning class during the leaf-on season ($F = 0.029$, $P = 0.971$), however there was an effect of year ($F = 93.346$, $P < 0.001$) (Figure 2.5). Pellet densities during the leaf-on season were 2.44 times greater during 2001 than 2002. Lastly, all interaction terms including year were significant ($P \leq 0.10$) for the leaf-on season, which suggests inconsistent responses of hare to treatment and thinning classes during the 2 summers of study. Untreated

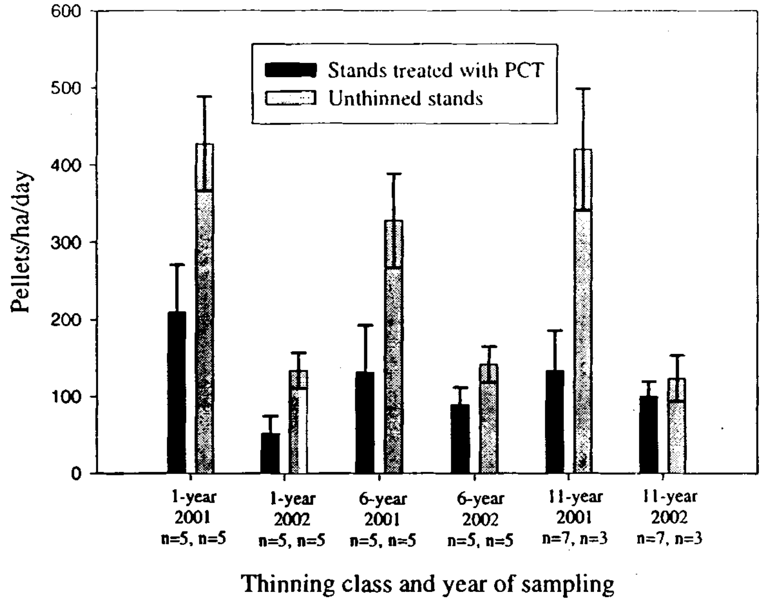


Figure 2.4. A comparison of mean (SE) number of snowshoe hare pellets/ha/day between PCT stands and similar unthinned stands in northern Maine during leaf-on seasons 2001-2002; 1 = treated in 1999, 6 = treated in 1994, 11 = treated in 1989-1990.

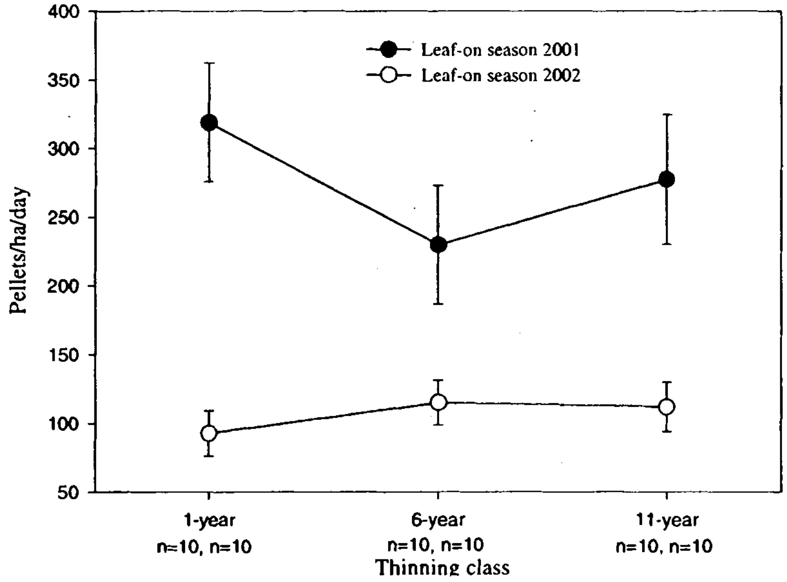


Figure 2.5. Mean (SE) pellets/ha/day averaged across stands treated with PCT and unthinned stands during the leaf-on seasons, from 1-11 years post-treatment. No significant effect of thinning class was observed (P ≥ 0.842, F = 0.173).

Table 2.3. A comparison (Two-way ANOVA) among means (SE) for 6 stand-scale habitat variables selected *a priori* between treatments (17 regenerating clearcut stands treated with PCT and 13 stands untreated) and among 3 thinning classes (1-2, 6-7, 11-12 years post-thinning) in northern Maine. Non-transformed means and standard errors are presented for transformed variables[a] and P-values < 0.10 are depicted in bold.

	Variable					
	#CON≥7.6[b]	TOTUNDER≥7.6[c]	SCU[d]	CANOPY[e]	VEGDIST[f]	LOGS[g]
Treatment						
F-statistic	1.832	32.471	38.445	2.447	12.570	25.196
P	0.188	**< 0.001**	**< 0.001**	0.131	**0.002**	**< 0.001**
PCT (n = 17)	1,199 (98)	3,146 (707)	6,089 (2,037)	78.2 (2.5)	10.0 (0.4)	1.6 (0.3)
No-PCT (n =13)	1,402 (114)	8,997 (821)	12,199 (2,367)	84.1 (2.8)	7.6 (0.5)	3.5 (0.3)
Thinning class						
F-statistic	1.911	3.241	1.849	0.588	1.811	2.389
P	0.170	**0.057**	0.179	0.563	0.185	0.113
1-year (n = 10)	4632 (908)	6210 (910)	15,474 (2,622)	78.8 (3.2)	8.6 (0.6)	2.9 (0.4)
6-year (n = 10)	4778 (908)	7551 (910)	17,107 (2,622)	80.7 (3.2)	8.2 (0.6)	2.8 (0.4)
11-year (n = 10)	3449 (991)	4453 (993)	11,351 (2,861)	83.9 (3.4)	9.7 (0.6)	2.0 (0.4)
Treatment*Thinning class						
F-statistic	0.380	1.301	1.091	1.694	0.032	0.431
P	0.688	0.291	0.352	0.205	0.969	0.655
1-year PCT (n = 5)	1,176 (178)	2,840 (1,287)	6,768 (3,708)	72.1 (4.5)	9.7 (0.8)	1.8 (0.5)
6-year PCT (n = 5)	1,084 (178)	3,892 (1,287)	5,964 (3,708)	76.9 (4.5)	9.5 (0.8)	1.8 (0.5)
11-year PCT (n = 7)	1,337 (151)	2,706 (1,088)	5,534 (3,134)	85.6 (3.8)	10.9 (0.7)	1.1(0.4)
1-year no PCT (n = 5)	1,520 (179)	9,580 (1,287)	24,180 (3,708)	85.6 (4.5)	7.5 (0.8)	4.0 (0.5)
6-year no PCT (n = 5)	1,120 (179)	11,210 (1,287)	28,250 (3,708)	84.6 (4.5)	6.8 (0.8)	3.8 (0.5)
11-year no PCT (n = 3)	1,557 (230)	6,200 (1,661)	17,167 (4,787)	82.1 (5.8)	8.6 (1.0)	2.8 (0.6)

Table 2.3. Continued.

[a] TOTUNDER, SCU, and LOGS were $\log_e$ transformed prior to analysis.

[b] #CON≥7.6 = number of conifer trees/ha (≥ 7.6 cm dbh, >1.0 m ht, alive).

[c] TOTUNDER = number conifer trees (< 7.6 cm dbh >1.0 m ht, alive) + number deciduous trees (< 7.6 cm dbh >1.0 m ht, alive) per ha.

[d] SCU = (3 × number of conifer trees < 7.6 cm dbh >1.0 m ht, alive) + (1 × number of deciduous trees < 7.6 cm dbh per ha >1.0 m ht) per ha.

[e] CANOPY = average overhead canopy cover closure at 1.0 m height during summer, percent.

[f] VEGDIST = average understory lateral foliage density (average distance that an entire 2.0 m pole is obscured), m.

[g] LOGS = number of logs per ha.

stands had greater densities of hare pellets across all thinning classes for both years of the study except for the 11-year thinning class during 2002, which may have accounted for the significant interaction terms.

Live-trapping demographics

I captured 128 adult hares (69 M, 59 F) 308 times in 2001, and 114 adult hares (64 M, 49 F, 1 unknown) 464 times in 2002. Differences in the proportion of lactating female hares between thinned (68%, n = 28, 90% C.I. 46-84%) and unthinned stands (58%, n = 80, 90% C.I. 46-68%) were not significant (Z = 0.97, P = 0.416). Further, the proportion of male and female hares was not significantly different (Z = 0.59, P = 0.360) between stands treated with PCT (58% males, n = 67, 90% C.I. 45-70%) and unthinned stands (54% males, n = 174, 90% C.I. 46-62%).

Habitat sampling

Measures of the density of total understory stems, stem cover units, and logs were lower ($P \leq 0.001$) in thinned stands compared to unthinned stands (Table 2.3). Measures of the density of the total number of understory stems and stem cover units in treated stands were 1/3 and 3/10 the density in untreated stands, respectively. Conversely, the distance to obstruction by horizontal vegetation was greater (P = 0.002) in stands treated with PCT. Of the 6 structural variables examined, only the density of understory stems varied among thinning classes (P = 0.057) of thinned and unthinned stands; the 11-year thinning class had fewer understory stems ($P < 0.10$) than the 1-year or 6-year thinning classes.

DISCUSSION

Effects of PCT

Previous studies of PCT and its effects on wildlife examined relatively short-term changes (4 years or less) in densities of hares after thinning (Sullivan and Sullivan 1988, de Bellefeuille et al. 2001). My results indicate that PCT reduced hare densities from 1–11 years post-thinning (Figure 2.5). Mean differences in hare densities between stands treated with PCT and unthinned stands across 2 years of sampling and 2 seasons ranged from -45 to -54 % for 1-year stands, -39 to -55 % for 6-year stands, and -13 to -61 % for 11-year stands. Despite annual changes in hare densities, PCT reduced densities of snowshoe hare during both leaf-off and leaf-on seasons during both years of my study. Further, hare densities were greatest in stands 17 to 24 years after clearcutting (13-20 years post-herbicide) (1-year thinning class) during the leaf-off season, which was consistent with previous studies that have indicated that hares reach their greatest abundances in mid-successional stands and avoid very young clearcuts and mature stands (Litvaitis et al. 1985a, Monthey 1986, Koehler 1990, Ferron et al. 1998, Hoving 2001, de Bellefeuille et al. 2001).

The consistent effect of PCT on densities of hares from 1 to 11-years post-treatment suggests that forest understories in thinned stands likely did not regain the structural complexity that existed prior to treatment. Regenerating stands without PCT supported the greatest densities of hares for 17-24 years after clearcutting (mean = 2.30 hares/ha, n = 5), whereas PCT-treated stands supported the lowest densities of hares (mean = 1.04 hares/ha, n = 7) 25-32 years after clearcutting. In contrast, radio tracked hares avoided all regeneration treatments on landscapes in Quebec, Canada that included recently thinned stands (de Bellefeuille et al. 2001). Those results were somewhat inconclusive because pellet counts indicated that all sites, which were 7-9 years post-clearcut harvest, were rarely used, regardless of whether they had been treated with PCT. The authors concluded that longer than 9 years were necessary for clearcuts to regenerate to suitable hare habitat in Quebec; my sites were clearcut 17-32 years prior to study, which had allowed stands to develop the structural attributes required by hares (Wolfe 1982, Litvaitis et al. 1985a).

My observations that hare densities were reduced by PCT by 1-year after treatment were inconsistent with results from British Columbia, Canada (Sullivan and Sullivan 1988), where hare density exhibited no short-term (1-2 year) response to thinning. By 3-4 years after treatment, however, densities of hare in thinned stands fell below unthinned stands in British Columbia. These differences in conclusions may have resulted from felled trees losing their needles and value as food and cover more quickly in Maine. During 2001, Maine received the lowest annual precipitation of the last 100 years (National Oceanic and Atmospheric Administration 2002), which could have contributed to the rapid desiccation of felled trees. Additionally, hares could have relocated from thinned stands into nearby unthinned stands soon after treatment (Ferron et al. 1998). I speculate that it may be important to consider responses in hare densities at the scale of the landscape in addition to the scale of the stand to account for confounding affects of individual movements by hares and shifts in home ranges in response to PCT.

Hares are thought to concentrate habitat use in stands with high densities of saplings during winter, presumably to provide protection from predators and weather (O'Donoghue 1983, Litvaitis et al. 1985a, Koehler and Brittell 1990). During summer, hares have a weaker association with understory stem density and canopy closure because food is more widespread and cover is less limiting (Wolff 1980, Litvaitis et al. 1985a). Despite that hares exhibit a more generalist preference for habitat during summer (Wolff 1980, O'Donoghue 1983), I observed greater densities of hares in unthinned regenerating clear-cut stands compared to stands treated with PCT during both leaf-off (late-fall – early spring) and leaf-on (late spring - early fall) seasons. Consequently, regenerating stands with high densities of conifer saplings are likely selected for by snowshoe hares year-round in my study areas. During the leaf-on seasons, there was not a detectable difference in hare densities among stands of various treatment classes; however, hares were more abundant in younger stands than in older stands during the leaf-off season. Winter is the limiting season for snowshoe hares (Pease 1979, Pietz and Tester 1983), and they more strongly prefer the forest structure found in mid-successional stands for thermal and escape cover during that season.

Habitat associations of snowshoe hare have been reported to change with fluctuations of hare densities both in Maine at a landscape scale (Hoving 2001) and in Alaska at a stand scale (Wolff 1980). Even though densities of hares (across all stands) decreased by 33.0 % from the leaf-off season 2000-01 to leaf-off season 2001-02, and by 49.5 % from the leaf-on season 2001 to leaf-on season 2002, a consistent and negative effect of PCT was still detectable ($P \leq 0.10$). This indicates that, within the range of annual changes in hare densities that I observed, the negative effects of PCT occurred despite inter-annual fluctuations in densities of hare.

Hare densities in response to alternative forest practices

From a management perspective, the effects of PCT on reducing densities of hare are only relevant when compared to alternative forest practices. Maine has nearly 17 million acres of commercial timberland that is likely to continue to be harvested, so if stands are not under a harvest plan including PCT, they likely will be managed via alternative silvicultural regimes. Although stands treated with PCT support lower densities of hares than similar unthinned stands, they still retain greater densities of hares than many other forest stand types (Table 2.4). Of 7 forest-stand types studied in northern Maine, regenerating stands and PCT stands had the greatest hare densities. This pattern likely reflects hares' affinity to structure typically found in early seral stages, such as high stem densities and horizontal cover. Regenerating and PCT stands are early to mid-successional, whereas most of the other stand types are in later seral stages. Although PCT stands supported lower densities of hares when compared to similar unthinned stands, PCT stands supported more hares than mature conifer, deciduous, or mixed coniferous-deciduous stands, or than mature mixed stands that had been recently partially harvested. Forest practices other than PCT should also be considered with regard to potential indirect effects on carnivores because they may exert a stronger influence on stand-scale and landscape-scale densities of snowshoe hare than thinning. For example, partial harvests, which may support fewer hares than PCT stands, (Table 2.4) composed 221,029 ha of land harvested in Maine during 2001, whereas PCT-treated stands composed 8,860 ha of intensively managed land for 2001 (Maine Forest Service 2002). Further, the acres of land clearcut harvested annually, which regenerate into the

Table 2.4. Average density[a] of snowshoe hares estimated in 7 overstory types[b] (number of stands) in northern Maine during leaf-off seasons (October – May). Densities of hares reported for this study were averaged across 2 leaf-off seasons (2000-2001 and 2001-2002).

Overstory[b] (n)	Years since regenerating event (range)	Hares/ha (SE)[c]	Year of sampling	Study
REG (n = 7)	12 - 20	2.43 (2.04)	1995 - 1996	Lachowski (1997)
REG (n = 13)	18 - 26	1.83 (0.16)	2000 - 2002	This study
REG (n = 2)	15	1.63 (0.93)	1997 - 1998	Fuller (1999)
PCT (n = 17)	18 - 32	0.99 (0.09)	2000 - 2002	This study
BK[d] (n = 2)	12-13	0.59 (0.41)	1995 - 1996	Lachowski (1997)
MIX (n = 7)	n/a	0.29 (0.27)	1995 - 1996	Lachowski (1997)
CON (n = 2)	n/a	0.23 (0.05)	1995 - 1996	Lachowski (1997)
CON (n = 2)	n/a	0.23 (0.04)	1997 - 1998	Fuller (1999)
MIX (n = 7)	n/a	0.21 (0.03)	1997 - 1998	Fuller (1999)
DEC (n = 2)	n/a	0.16 (0.00)	1997 - 1998	Fuller (1999)
DEC (n = 2)	n/a	0.15 (0.01)	1995 - 1996	Lachowski (1997)
PH (n = 7)	3-6	0.15 (0.00)	1997 - 1998	Fuller (1999)

[a] Estimates of hares/ha were derived using the most biologically appropriate model for Maine described in Chapter I: hares/ha = 0.145303 +0.0001(pellets/ha/month). Densities from Fuller (1999) were recalculated based on the modified Litvaitis-Long equation presented in Chapter 1

[b] REG = regenerating forest, including unthinned stands for this study (leaf-off season densities), CON = coniferous, DEC = deciduous, MIX = mixed coniferous-deciduous, BK = killed by eastern budworm, PH = partial harvest, PCT = precommercially thinned (leaf-off season densities).

[c] As hare populations may vary temporally, these differences should be viewed as relative, not absolute values.

[d] Osawa (1986) reported that budworm mortality was complete for balsam fir and nearly complete for spruce by 1980 in Baxter State Park, Maine.

habitat supporting the greatest densities of hares, have declined from about 45,998 ha to 6,102 ha harvested annually since 1986.

PCT may also include several other methods of reducing stand density (e.g., mechanical spacing and herbicide spray thinning) that were not evaluated in my study. Further, my results were for precommercially thinned herbicide-treated clearcuts with crop tree spacing of 1.8 to 2.4 m (6-8 feet); in other geographic areas with different dominant conifers, weather, soils, and silvicultural objectives, forest managers prescribe thinnings with varying spacing between crop trees. In this study, all PCT stands were treated with an aerial herbicide several years prior to being spaced. In Quebec, deciduous understory stem density in non-herbicided stands increased dramatically after PCT (Bujold 2002), and provided cover for hares that was not present on my study sites. Thus, the results from my study should be used with caution when applied to other regions, thinning regimes, or to systems where herbicide application does not precede PCT.

Vegetation changes associated with PCT

The structural attributes that were lower in forest stands treated with PCT explain much of the observed differences in thinned versus unthinned stands on my study sites. Complex understory structure provides thermal and escape cover from predators for snowshoe hares, was correlated to survival of hares in other regions of Maine (Litvaitis et al. 1985a), and influenced length of dispersal movements of translocated hares in Idaho (Wirsing et al. 2002). Woody debris may substitute for horizontal cover in geographic areas where understory stem densities do not approach those required by snowshoe hare (Conroy et al. 1979, Scott and Yahner 1989, Ferron et al. 1998); however, woody debris likely only provides measurable cover during the leaf-on season, when not buried by snow. Measures of understory density, horizontal cover, and abundance of logs were greater in unthinned reference stands than stands treated with PCT, indicating that these structural attributes were associated with higher densities of hares on my study areas; untreated stands with more horizontal structure (i.e. stems, cover, and logs) supported the greatest densities of hare. A minimum of 40-60% understory horizontal cover has been suggested to maximize local densities of snowshoe hare in forest stands during winter (Wolfe et al. 1982, Litvaitis et al. 1985). Stands treated with PCT likely were below the structural threshold associated with higher densities of hares during my study. Thus, stands treated with PCT that also maintain understory complexity may mitigate the negative effects of thinning on densities of hare. To maximize post-treatment densities of snowshoe hare, forest managers could attempt to maintain greater horizontal cover (i.e. greater number of stems/ha) in thinned stands by reducing spacing distances between crop trees; however, silvicultural objectives of the thinning treatment could be compromised (Seymour 1993).

CONCLUSIONS

The stand-scale effects of PCT were incredibly consistent at reducing densities of snowshoe hare by nearly 50% from 1 to 11 years post-treatment during both leaf-off and leaf-on seasons and across 2 years of study. Although thinning appeared to reduce the density of snowshoe hare at the stand-scale, it may have a weaker, negative effect on hare numbers across the landscape than more widespread silvicultural practices that favor retention of overstory trees throughout the rotation, such as some forms of partial harvesting. Maintaining greater horizontal cover by reducing the spacing distance between crop trees in regenerating conifer stands treated with PCT may partially mitigate the negative effects of thinning on densities of snowshoe hare. However, the silvicultural objectives and the cost efficiencies of thinning could be compromised. Caution should be taken when applying these stand-scale results to indirect effects on forest carnivores because landscape-scale responses of hares to PCT may not directly translate into negative effects on foraging efficiency and density of species such as lynx, who likely respond to habitat at larger spatial scales. At the scale of the forested landscape, the effects of distribution and extent of intensive forest management, including PCT, on snowshoe hare are also poorly understood and might differ from the stand-scale effects studied here.

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CHAPTER 3

TEMPORAL EFFECTS OF PRECOMMERCIAL THINNING ON SMALL MAMMALS IN NORTHERN MAINE

ABSTRACT

Precommercial thinning (PCT) is being practiced increasingly throughout the Acadian forests of eastern North America to meet silvicultural objectives; however, the effects of this practice on wildlife, both immediately after treatment and several years later, are not well understood. Forest dependent small mammals have ecological roles as prey for numerous avian and mammalian predators, dispersers of seeds, fruit, and spores, and contribute to nutrient cycling. Researchers in the northwestern USA have suggested that thinning of young regenerating clearcuts may increase the abundance and diversity of some taxa of forest-dependent small mammals by increasing rates of forest development and by enhancing the ecological representation of mid-successional stands across managed landscapes. I examined the effects of PCT, from 1 to 16 years post-treatment, on abundances of mice, voles, shrews, and on within-stand structure in the commercial forests of northern Maine. I live-trapped small mammals on 24 herbicided clearcuts treated with PCT and 13 similar, unthinned stands during summers of 2000 and 2001. Thinning of mid-successional conifer stands resulted in increased abundances (red-backed voles, *Clethrionomys gapperi*, $P = 0.008$; masked shrews, *Sorex cinereus*, $P < 0.001$) or had no detectable effect on (deer mice, *Peromyscus maniculatus*, $P = 0.544$; short-tailed shrews, *Blarina brevicauda*, $P = 0.517$) the 4 most common species of small mammals in northern Maine. Several within-stand habitat characteristics associated with stand maturity, such as larger stem diameters and a partially open canopy, occurred

in thinned stands. Thus, PCT may accelerate development of habitat attributes typical of mid-successional conifer stands. At the scale of the forest stand, PCT produced within-stand habitat conditions favorable to small mammals, and may be an appropriate management tool to increase the abundances of red-backed voles and masked shrews, and may accelerate stand succession in intensively managed stands within the Acadian Forest. However, PCT will involve tradeoffs for early successional wildlife species associated with high stem densities, such as snowshoe hare (*Lepus americanus*) (Chapter 2).

INTRODUCTION

The Acadian forest, ranging from northern New England east through the maritime Canadian provinces, includes the ecological transition zone of eastern deciduous forest to the south and boreal forest to the north (Seymour and Hunter 1992). Commercial timberland is a primary economic use of this region and accounts for 86% of the land area of Maine (Maine Forest Service 1998), 82% of New Brunswick, 68% of Nova Scotia, and 35% of Quebec (Canadian Council of Forest Ministers 2002). Over the past 2 decades, commercial forestry in this region has evolved from extensive management towards more intensive silviculture. Currently, about 4% of Maine's commercial timberland is in high production silviculture, including precommercial thinning (PCT), herbicide release, and plantations (Maine Forest Service 1998). Similarly, the eastern Maritime Provinces in Canada have experienced increases in the land area under intensive management, with 1.2 to 1.5-fold increases from 1990-2000. One form of intensive forest management, PCT, increased from 4,352 ha to 9,950 ha in Maine (Maine Forest Service unpublished data, 2001), from 14,930 ha to 40,354 ha in New Brunswick, from 22,791 ha to 98,158 ha in Quebec, and from 3,228 ha to 8,113 ha in Nova Scotia (Canadian Council of Forest Ministers 2002), 1990-2000. Thus, thinning has affected an increasing percentage of regenerating forest habitat across the Acadian forest and this practice has been questioned in relation to its effects on early successional wildlife species such as snowshoe hare (*Lepus americanus*), the primary prey of the U.S. Federally threatened Canada lynx (*Lynx candadensis*) (Hickenbottom et al. 1999).

Precommercial thinning reduces the density of overstocked stands to minimize mortality from competition and to accelerate growth of residual trees (Ker 1987, Seymour 1984, Brissette and Frank 1999, Brissette et al. 1999). Characteristics of forest overstory (Ker 1987, McCormack and Lemin 1998, Brissette and Frank 1999, Chapter 4), understory (Doerr and Sandburg 1986, Newton et al. 1989, Wilson and Watts 1999, Lindgren and Sullivan 2001, Chapter 4), and microclimate (Reynolds et al. 1997) change dramatically after PCT and with stand succession. By reducing competition from crop trees via thinning, stem diameters (Harrington and Reukema 1983, Ker 1987, McCormack and Lemin 1998, Brissette and Frank 1999, Brissette et al. 1999, Pothier 2002) and crowns (McCormack and Lemin 1998, Brissette and Frank 1999, Brissette et al. 1999, Lindgren and Sullivan 2001, Sullivan et al. 2001) of residual crop trees increase rapidly, causing stands to bypass the stem exclusion stage of forest succession characterized by self-thinning (Smith et al. 1997). The reduction of competition among crop trees for nutrients, space, and light results in reduced mortality of residual stems (Ker 1987, Brissette and Frank 1999, Brissette et al. 1999); without mortality of large diameter trees, recruitment of CWD may be reduced (Carey and Johnson 1995, Hayes et al. 1997, Harrison 1999). These changes within stands could potentially influence, either positively or negatively, a variety of forest wildlife species (early to late seral) dependent on overstory, understory, structure, or coarse woody debris (CWD). Application of PCT to regenerating conifer stands reduces densities of snowshoe hare (Sullivan and Sullivan 1988, Chapter 2); however, studies in the Pacific Northwest have indicated that thinning of second growth forests may diversify the landscape and increase richness of wildlife species by accelerating stand succession (Carey and Johnson 1995, Hayes et al. 1997, Sullivan et al. 2001).

Forest dwelling voles (*Clethrionomys* spp.), mice (*Peromyscus spp.*, *Napeozapus spp.*), and shrews (Soricidae) are relevant taxa for examining responses to PCT because they are consumers of invertebrates, fungi, and vegetation (Hamilton 1941) and are prey for many avian (Mendall 1944) and mammalian carnivores (Soutiere 1979, Dibello et al. 1990, Cumberland et al. 2001). Additionally, small mammals may assist the revegetation of nonforested areas by dispersing spores of hypogeous fungi present in their feces (Maser et al. 1978, Kirkland 1990) and contribute to nutrient cycling (Brooks and Healy 1988). Small mammal abundances have been reported to be positively associated with some attributes of forest structure, including downed and decaying dead wood (Richens 1974, Hayes and Cross 1987, Carey and Johnson and 1995), microclimatic conditions associated with closed overhead cover and diverse ground structure (Miller and Getz 1977, Yahner 1986), and with characteristics of understory vegetation (Yahner 1986, Bowman et al. 2001). Habitat variables describing the structural attributes of mature forest at both the stand scale and microhabitat scale have been positively associated with densities of small mammals (Martell 1983b, Lachowski 1997). Thus, silvicultural practices that accelerate forest succession and reduce stand rotation, such as PCT, could accelerate the development of favorable habitat conditions for small mammals that prefer the overstory and understory characteristics of mature forest.

Stand thinning is designed to minimize natural mortality resulting from intra- and inter-specific competition among crop trees. This could reduce recruitment of CWD below levels required by small mammals, and might reduce abundance, age structure, or reproductive performance in affected populations. However, previous studies of the habitat relationships of red-backed voles (*Clethrionomys gapperi*), deer mice (*Peromyscus maniculatus*), short-tailed shrews (*Blarina brevicauda*), and masked shrews (*Sorex cinereus*) in commercial forests of Maine have uncovered few unequivocal relationships between population abundance and CWD (Lachowski 1997, Fuller 1999, Billig *in prep.*). These findings suggest that woody debris usually occurs above levels required by small mammals across a wide range of extensively managed and unmanaged stands in commercial forests of Maine. Alternatively, structures (e.g. slash) created from logging activities might serve as functional surrogates to CWD immediately after harvest. These inter-relationships among intensive silviculture (e.g. PCT), CWD, and forest dwelling small mammals require further study in eastern North America.

Understanding the response of small mammals to silvicultural prescriptions for longer than 2-3 years after treatment is necessary to evaluate the ecological effects of forest practices that influence long-term stand development. For example, initial changes in microclimate of stands directly after thinning could cause a decrease in small mammal populations, but populations could rebound as the growth of crop trees accelerates following treatment. Few studies have explored the temporal effects of PCT on small mammals longer than 4 years post-treatment (exception: Sullivan et al. 2001) and statistical replications have been limited (n ≤ 4) (Lautenschlager et al. 1997, Sullivan et al. 2001).

Published effects of PCT on forest dwelling small mammals have involved stands that were clearcut and thinned, but not treated with an herbicide (Lautenschlager et al. 1997, Sullivan et al. 2001); in the Acadian forest, PCT often occurs on stands that were previously herbicided (typically 3-10 years after clearcutting). Sullivan et al. (2001) presented results of effects of thinning on small mammals in British Columbia immediately after treatment and 10 years later; however, their study design did not allow for treatment effects to be distinguished from temporal variations in abundances of small mammals. Temporal effects potentially confound studies of small mammal responses to forest practices because densities of small mammals often exhibit significant inter-annual variation (Richens 1974, Krebs and Wingate 1976, Lachowski 1997, Bayne and Hobson 1998, Fuller 1999).

Stands previously treated with PCT in Maine have grown at a sufficient rate to allow for the first economically viable commercial entry as soon as 16 years after thinning (ages 30-35 years). Thus, I evaluated effects of PCT on small mammals at intervals of 1-2, 5-7, 9-12, and 14-17 years post-thinning in stands that were clearcut 17-33 years previously and treated with herbicides 2-19 years after harvest. My objectives were to retrospectively compare the relative abundances of small mammals and associated overstory and within-stand habitat attributes in herbicide treated clearcuts, with and without PCT. Generalizing the responses of wildlife to forest management across species of small mammals may be inappropriate because large changes in the densities of one or more dominant species may obscure changes in community composition or densities of individual species (Martell and Radvanyi 1977, Martell 1983b). I compared species-level abundance of red-backed voles, deer mice, short-tailed shrews, and masked shrews among regenerating, unthinned stands and similarly aged, thinned stands 1-16 years post-treatment. Overstory and within-stand habitat variables were also compared between thinned and unthinned stands and successional patterns in habitat and structural (e.g. CWD) characteristics of stands were documented from 1-16 years post-thinning.

Densities of animal populations are not always greatest in habitat types with the greatest habitat quality (Van Horne 1983). The proportion of individuals in a reproductive condition is frequently used as an indirect index of habitat quality for small mammals (Hobbs and Hanley 1990); therefore, I also compared lactation rates of female red-backed voles and deer mice between thinned and unthinned stands to evaluate effects of PCT on reproductive performance of these 2 dominant small mammals in the Acadian forest.

STUDY AREA

Seven townships in northern Maine (Days Academy Grant, Spencer Bay, T1 R13 WELS, T4 R 12, T4 R11, T5 R11, and Hersey) composed the study area (Figure 3.1). Hersey Township is in Aroostook County and the other 6 townships are in Piscataquis County. Most of the land in these towns is managed for pulpwood and sawtimber production by Plum Creek Timber, Fairfield, Maine; Great Northern Paper, Millinocket, Maine; and International Paper Company, Costigan, Maine. The study area spans 110 km east to west and 49 km north to south. Stands were chosen so that topography was relatively flat (< 15° slope).

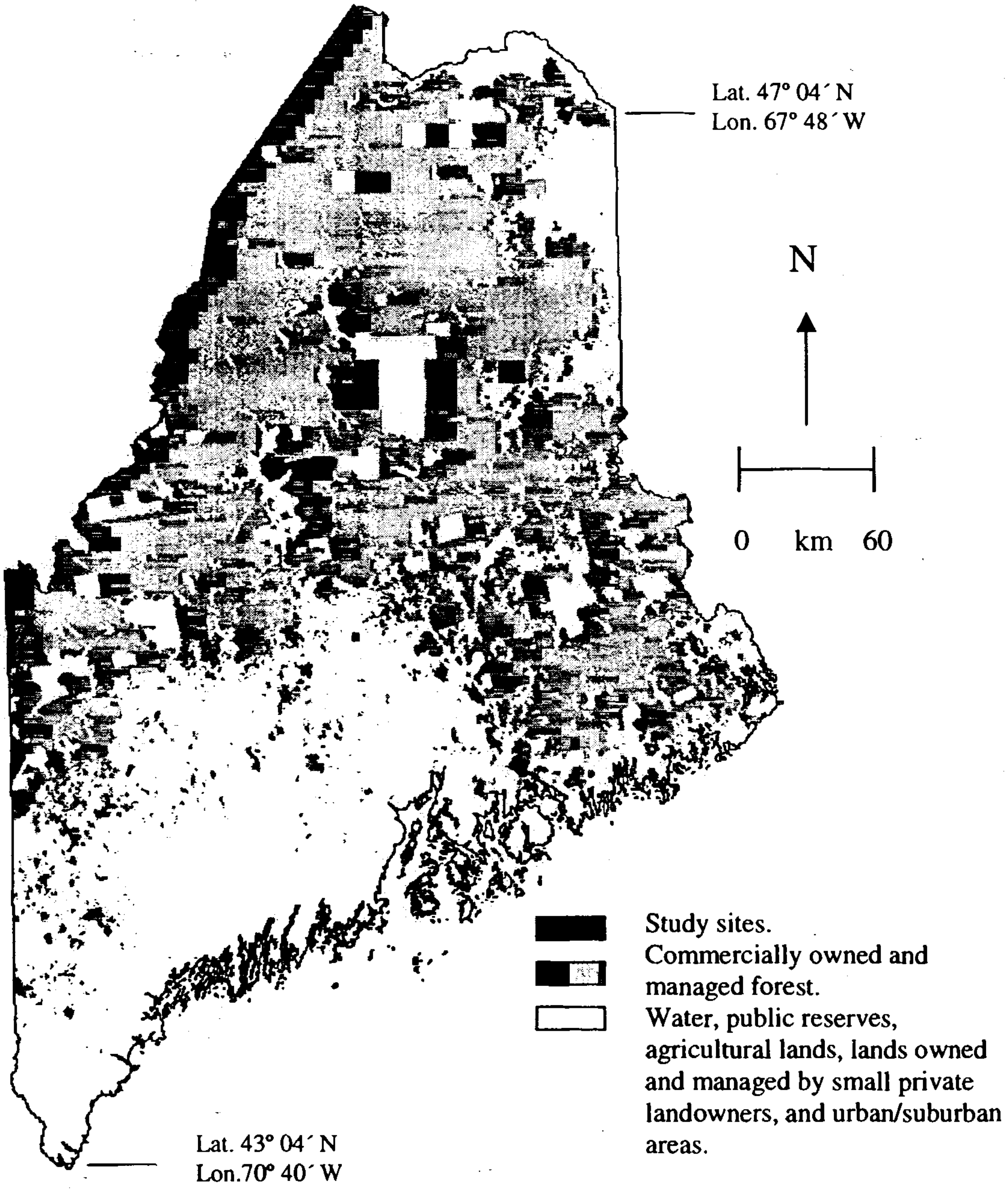

Figure 3.1. Location of study sites containing 37 stands where abundances of small mammals were investigated within 7 townships in the commercially owned and managed forests of northern Maine, 2000-2001.

Northern Maine is part of the Acadian forest, known also as the sub-boreal spruce-fir ecosystem (Seymour and Hunter 1992). Study sites were dominated by balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), and black spruce (*Picea nigra*), but also had minor components of white pine (*Pinus strobus*), larch (*Larix spp.*), white cedar (*Thuja occidentalis*), paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), and red maple (*Acer rubra*). The climate was generally cool and moist, with an annual mean temperature for the region of 3.3° C and 101 cm of average annual precipitation (Garoogian 2000). The area received an average of 2.75 m of snowfall yearly (averaged from 1970 to 2000) and the ground was usually snow-covered from December through April.

METHODS

I evaluated the site quality, tree density, diameter at breast height (dbh) of dominant trees, size, and spatial independence of stands before selecting study sites. Sites were considered spatially independent when separated by > 0.40 km or a body of water to minimize population exchange of small mammals (Bowman et al. 2000a). Site quality, which can strongly influence the rate of succession of conifer stands (Briggs and Lemin 1994), was estimated based on 4 to 6 soil cores sampled at 50-100 m intervals within the stand with a soil auger. According to Brigg's (1994) scale of forest productivity, site-quality ranged from 1 (highly productive) to 5 (unproductive). I attempted to minimize among-stand variation within a treatment × thinning class block by pairing treated and untreated stands based on year of initial clearcut, year of herbicide, time since PCT, site quality, topography and pre-thinning species composition (based on live trees and stumps in stands treated with PCT). Stands were paired retrospectively so were not treated as statistical pairs during analyses.

Treatment stands were clearcut (timber harvesting resulting in residual basal area of acceptable growing stock trees > 4.5 in. dbh of < 30 ft^2/acre) 1967-1983, aerially herbicided with Glyphosate (applied at a rate of ≈ 1.68 kg/ha acid equivalent) 1977-1988, and precommercially thinned with motor-manual brush-saws from 1984-1999. Unthinned reference stands were clearcut 1974-1982 and herbicided with Glyphosate (≈ 1.68 kg/ha acid equivalent) 1982-1988 (Table 3.1). The study design included 24 treatment stands that were surveyed for small mammal abundances at 5-year intervals since thinning (1-2 year post-thinning, n = 6; 5-7 years, n = 6; 9-12 years, n = 6; 14-17 years, n = 6) and 13 similar, unthinned stands (1 year, n = 5; 6 year, n =5; 11 year, n = 3), whose histories were comparable with treatment stands. I allowed some latitude (1-2 years) in separating stands into thinning classes so that I could maximize the number of stands studied. The study design was unbalanced; a greater number of stands were treated with PCT (n = 24) compared to unthinned stands (n = 13). I was unable to locate comparable, unthinned stands for the 16-year thinning class and located only 3 unthinned replicates for the 11-year thinning class. Nearly all stands that had been clearcut and herbicided prior to 1985 in my study areas had already been treated with PCT.

Small mammal trapping

I surveyed the relative abundances of red-backed voles, deer mice, short-tailed shrews, and masked shrews by live-trapping within 37 stands (Table 3.1) during June-August 2000 and 2001. I established 70 m by 70 m trapping grids with 64 trap stations at 10 m intervals (Figure 3.2). Grids were positioned > 50 m from edges of forest stands to

Table 3.1. Stand history, location, and site quality for 24 precommercially thinned stands and 13 unthinned stands located in 7 townships, northern Maine. (T = treated with PCT, C = unthinned stand). Site quality ranged from 1 (well drained, productive) to 5 (poorly drained, unproductive) according to Briggs (1994) classification guidelines.

Site number	Year of Clearcut	Year of Herbicide	Year of PCT	Township	Site Quality
1-1-T	1982	1988	1999	T 4 R 11	4+
1-2-T	1980	1983	1999	T4 R 12	3-
1-3-T	1977	1983	1999	T4 R 11	4+
1-4-T	1982	1988	1999	T4 R 11	4
1-5-T	1976	1983	1999	T4 R 12	4
1-6-T	1983	1988	1999	T 4 R 11	3
6-1-T	1979	1988	1994	Hersey	3+
6-2-T	1979	1988	1994	Hersey	2-
6-3-T	1987	1988	1994	Hersey	2
6-4-T	1974	1982	1994	T 5 R 11	3-
6-5-T	1976	1985	1995	T 5 R 11	3-
6-6-T	1979	1982	1994	T 5 R 11	3-
11-1-T	1975	1983	1989	T 1 R 13	3
11-2-T	1968	1987	1990	Spencer Bay	3-
11-3-T	1975	1983	1989	T 1 R 13	2-
11-4-T	1975	1986	1990	T 1 R 13	3
11-5-T	1975	1983	1989	T 1 R 13	2
11-6-T	1975	1984	1991	T 1 R 13	2-
16-1-T	1967	1986	1985	Spencer Bay	2-
16-2-T	1972	1980	1986	Days Acad.	3
16-3-T	1970	1977	1986	Days Acad.	2-
16-4-T	1969	1981	1986	Days Acad.	3+
16-5-T	1970	1981	1985	Days Acad.	3+
16-6-T	1968	1981	1984	Days Acad.	2-
1-1-C	1982	1988	n/a	T 4 R 11	4
1-2-C	1979	1983	n/a	T 4 R 11	3-
1-3-C	1981	1984	n/a	T 4 R 11	4+
1-4-C	1983	1988	n/a	T 5 R 11	4+
1-5-C	1976	1985	n/a	T 4 R 11	3-
6-1-C	1979	1988	n/a	Hersey	3+
6-2-C	1981	1988	n/a	Hersey	3+
6-4-C	1974	1982	n/a	T 5 R 11	4
6-5-C	1974	1985	n/a	T 4 R 12	3
6-6-C	1976	1983	n/a	T 4 R 11	4
11-1-C	1976	1982	n/a	T 5 R 11	3
11-3-C	1976	1982	n/a	T 5 R 11	3+
11-4-C	1974	1985	n/a	T 5 R 11	3

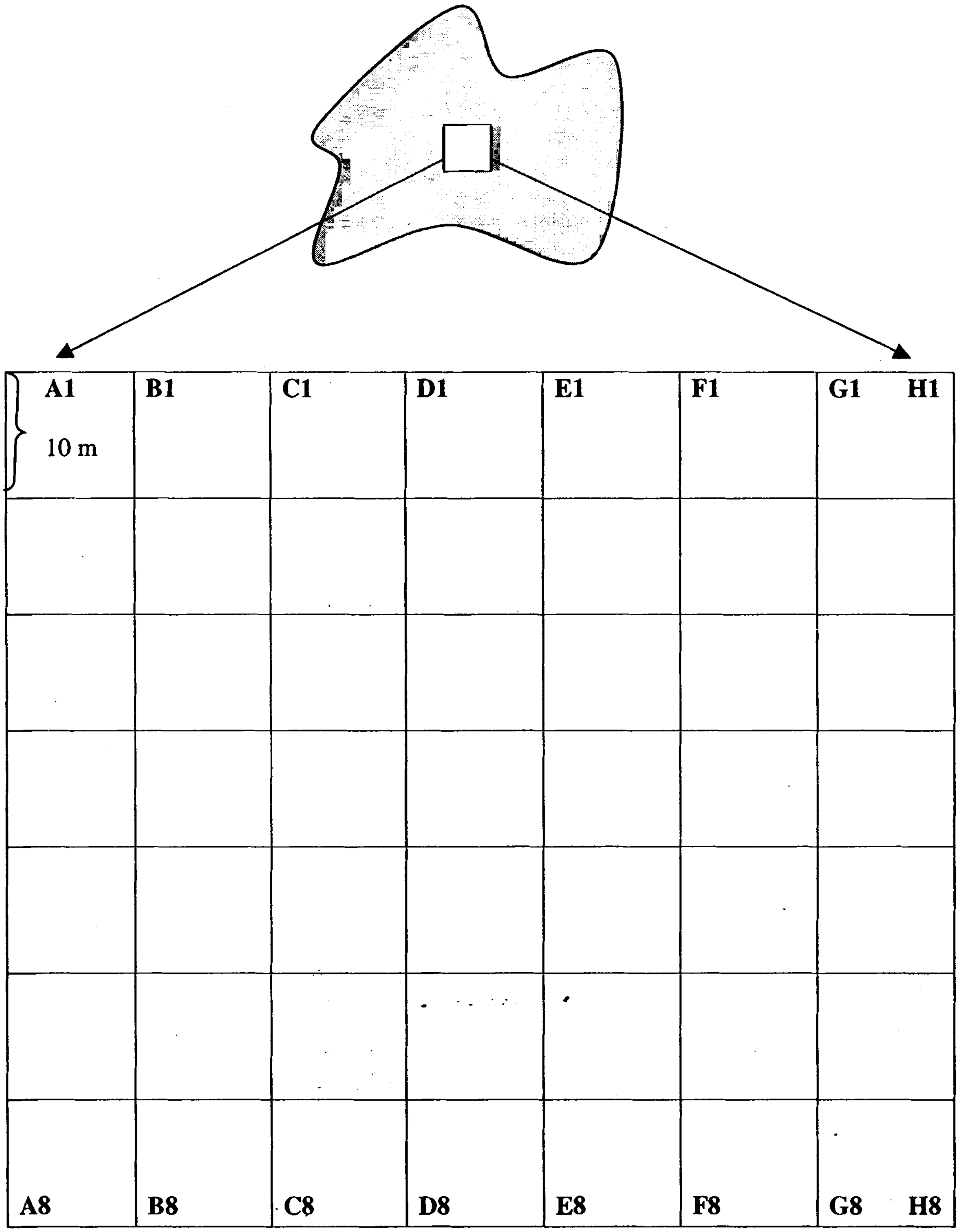

Figure 3.2. Small mammals were live-trapped during June-August 2000 and 2001 on 70 m by 70 m trapping grids established within PCT-treated (n = 24) and unthinned (n = 13) stands within 7 townships of northern Maine.

minimize edge-effects (Harris 1988, Fraver 1994). I placed one live-trap (B. N. Bolton, Inc. Vernon, B. C.; use of commercial names does not imply endorsement) baited with a mixture of rolled oats and peanut butter within 1 m of each trap station. Bolton live traps have an attached nest compartment to provide shelter and protection from predators. I placed 5 cotton balls in the nest compartment as material for nesting and placed the traps with the door facing downslope so that rainfall or condensation would drain. I covered traps with moss, leaves, and bark to provide additional thermal and visual protection.

I trapped each stand for 6 consecutive days and nights and tagged mice and voles with a unique, individually numbered ear-tag (Monel 1005-1; National Band and Tag Co., Newport, Kentucky). Short-tailed and masked shrews were not marked; therefore, only the number of captures was recorded for shrews. I recorded species, sex, age, and reproductive condition of each individual. I categorized small mammals as adult or juvenile by pelage color and relative size. I determined the reproductive condition of adult female mice and voles as lactating (mammaries swollen) or non-lactating (mammaries not swollen). Traps were checked from 0600 to 1300 hours, and after processing, animals were released at the trap site. The Institutional Animal Use and Care Committee, University of Maine, approved trapping and handling procedures. Field technicians took several safety precautions for hantavirus pulmonary syndrome. A baseline blood sample was drawn from technicians prior to handling of small mammals. Further, field technicians wore rubber gloves and full body coveralls when handling study animals, and traps were washed in a diluted bleach solution after each 6-day trapping session. Coveralls, traps, and trapping supplies were transported to and from study sites in an open-bed truck.

Within-stand habitat characteristics

I selected variables *a priori* that previous studies of habitat relationships of small mammals (Hamilton 1941, Miller and Getz 1977, Yahner 1986, Clough 1987, Hayes and Cross 1987, Carey and Johnson 1995, Lachowski 1997, Bowman et al. 2000b) have reported as important correlates or predictors of abundance. These variables included: total basal area, density of trees, total density of coarse woody debris, percent live ground cover, density of understory stems, and canopy density.

Habitat characteristics were measured within the small-mammal grids following the methods of Lachowski (1997) and Fuller (1999). I randomly selected 16 of the 64 trapping stations on the 37 trapping grids and oriented a 10-m by 2-m plot following a randomly selected compass direction at the center of each station. Within each plot I measured the diameter at breast height (dbh) of all coniferous trees and deciduous trees (≥ 7.6 cm dbh, ≥ 2 m height, > 45° from the ground) (DBH), and counted the number of herbaceous ground stems (HGSTEMS) (< 0.5 m height, < 7.6 cm dbh), number of deciduous and coniferous saplings (< 7.6 cm dbh, alive) at 1.5 m height (UNDERSTORY), the number of root masses (≥ 7.6 cm diameter), stumps (< 2 m height, ≥ 7.6 cm diameter), logs (≥ 1 m length, ≥ 7.6 cm diameter, < 45° from ground), and snags (≥ 7.6 cm dbh, ≥ 2 m height, > 45° from the ground) within the plot. I termed the number of logs/ha + stumps/ha + snags/ha as TOTDEBRIS. I measured the basal area of coniferous + deciduous trees (TOTBA) using a 2 m^2 / ha prism held at the center-point of the plot (Avery and Burkhart 2002). I measured percent canopy closure (CANOPY) at the 4 cardinal compass directions using a spherical densiometer held at waist height (Lemmon 1956).

Analysis of small mammal abundances

To determine if species-specific abundances met the parametric assumptions of Analysis of Variance (ANOVA), I examined across treatments and blocks for normality of residual errors using normal probability plots and Lilliefor's tests, and I examined data for constant variance using the modified Levene's test (Neter et al. 1996). I transformed data exhibiting heteroscedasticity (modified Levene's ≤ 0.10) or nonnormal errors (Lilliefor's ≤ 0.10) and then re-evaluated assumptions of normality and constant variance. The minimum number alive (MNA) of red-backed voles and MNA of deer mice were transformed using $\log_e$. Number of captures of short-tailed shrews (from 1-11 years post-treatment) met parametric assumptions following a square root transformation; however, number of captures of masked shrews did not meet assumptions after transformations and were analyzed using nonparametric alternatives to ANOVA.

To test whether the effects of PCT differed from effects of stand development, I conducted 2 separate analyses on the relative abundances (MNA and number of captures) of small mammals. I tested whether abundance of small mammals differed between stands treated with PCT and unthinned stands, from 1-11 years post-treatment, using a repeated-measures two-way ANOVA for each species (Zar 1999). I evaluated effects of treatment (PCT or unthinned), thinning class (1, 6, 11 years), year of sampling (2000 or 2001), and any interactions on the MNA index of abundance of red-backed voles, deer mice, and for the index of total number of captures for short-tailed shrews. I excluded the 16-year thinning class, which did not include any similar untreated stands, to avoid biasing effects and interactions with the 1, 6, and 11-year thinning classes.

Similarly, I used non-parametric alternatives to test whether number of captures of masked shrews differed between PCT and unthinned stands, by thinning class of stand, and between the 2 years of sampling. I examined for an effect of year by conducting a Wilcoxon signed rank test, while ignoring grouping factors (thinning class and treatment) (Zar 1999). Next, I summed the number of captures of masked shrews across 2000 and 2001 and ranked the resulting sum. I then conducted a two-way ANOVA with thinning class and treatment as main effects. I examined interaction terms with year in them by calculating the difference in number of captures between years, ranking the resulting data, and conducting a one-way ANOVA.

To evaluate changes in relative abundances of the 4 small mammal species in the PCT-treated stands through time, I conducted a repeated-measures ANOVA examining the effects of thinning class (1-year, 6-year, 11-year, 16-year post-thinning), year of sampling (2000 or 2001), and thinning class × year interaction with stands treated with PCT. I conducted this analysis on the MNA for both deer mice and red-backed voles. Non-parametric alternatives were necessary to analyze data for short-tailed and masked shrews. For shrews, I conducted a Wilcoxson signed rank test to determine if a year effect was present, and conducted a one-way ANOVA with thinning class as the main effect on the ranked sum of the number of captures in 2000 + 2001. I calculated the difference between years, ranked the resulting data, and conducted a one-way ANOVA to evaluate the presence of a year × thinning class interaction. I examined significant main effects for voles and mice *a posteriori* using pairwise comparisons using Tukey's honestly significant difference test (Zar 1999) and Bonferroni multiple contrasts for *a priori* selected pairwise comparisons for significant interaction terms (Neter et al. 1996).

Reproductive indices

I tested for differences in lactation rates of adult female deer mice and red-backed voles among treatment and control stands using a Chi-square test for proportions (Zar 1999). I captured few adult female small mammals during summer 2000; therefore, I pooled reproductive data for each species across years and stand-ages to maximize statistical power (the total number of adult female captures within each treatment ranged from 40-87).

Within-stand habitat analyses

The size of the trapping grid was approximately 1.0-2.5x the size of the average home range for red-backed voles and 0.3-3.0x for deer mice (Witt and Huntly 2001); therefore, within-stand habitat characteristics were described at the scale of the trapping grid. I averaged 6 overstory, understory, and CWD variables across the 16 sampling locations in each of 37 stands to produce an average value of each variable for each stand. Modified Levene's tests, Lilliefor's tests and normal probability plots were used to examine data for homoscedasticity and normal errors (Neter et al. 1996). DBH and UNDERSTORY were log transformed and CANOPY was arcsine transformed prior to analysis so that variables met parametric assumptions of ANOVA. I conducted a two-way ANOVA on the means of each habitat variable for the 1-year, 6-year and 11-year stands to examine for effects of thinning class (1-year, 6-year, 11-year), treatment (PCT or unthinned), and treatment × thinning class interaction. Significant pairwise differences among stand-ages were examined *a posteriori* with Tukey's honestly significant differences test (Zar 1999).

I tested for differences in habitat and structural variables among PCT stands of different (1-year, 6-year, 11-year, 16-year) ages since thinning by conducting a one-way ANOVA, with age-class as a main effect. Pairwise comparisons were conducted *a posteriori* using Tukey's honestly significant differences test (Zar 1999).

Sample sizes of thinned and unthinned stands ranged from only 3 to 6 within each class since thinning; thus, the probability of type II statistical error was relatively high. I attempted to balance type I and type II error by using $P < 0.10$ as my threshold for statistical inference.

RESULTS

Abundance of small mammals

I captured 600 red-backed voles (1,296 times), 399 short-tailed shrews, 386 masked shrews, 347 deer mice (824 times), 51 eastern chipmunks (*Tamias striatus*), 15 weasels (*Mustela spp.*), 11 red squirrels (*Tamiasciurus hudsonicus*), 10 woodland jumping mice (*Napeozapus insignis*), 5 smoky shrews (*Sorex fumeus*), 2 Southern bog lemmings (*Synaptomys cooperi*), and 1 meadow vole (*Microtus pennsylvanicus*) during 2000 and 2001, combined. Species except for red-backed voles, deer mice, short-tailed and masked shrews were excluded from further analyses of effects of PCT and thinning class on abundance because capture success was too low for a meaningful or statistically powerful analysis. Each of the 4 species of small mammal that were statistically evaluated exhibited different responses to treatment and thinning classes (Figures 3.3, 3.4, 3.5, 3.6, Table 3.2, 3.3), indicating strong effects of PCT and thinning class among red-backed voles, deer mice, short-tailed shrews, and masked shrews.

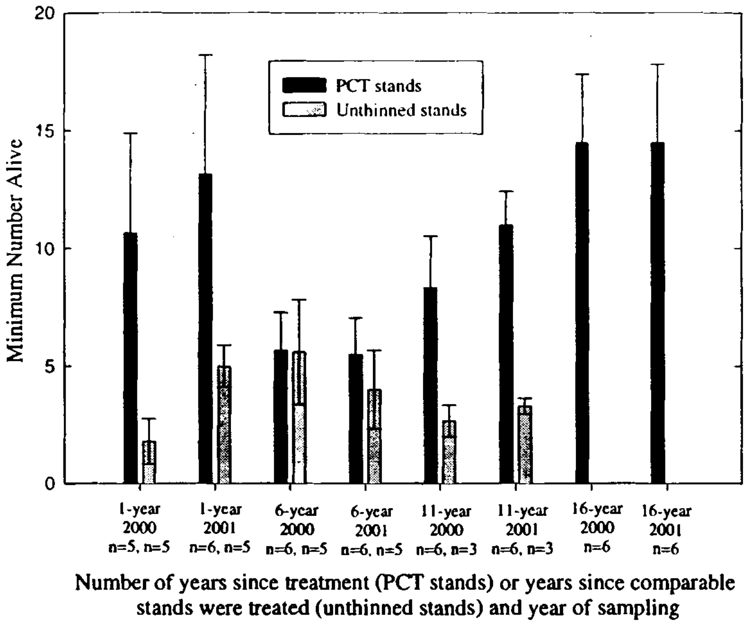

Figure 3.3. Mean minimum number alive (SE) of red-backed voles (*Clethrionomys gapperi*) in 24 stands treated with PCT and 13 unthinned stands during summer 2000 and 2001, northern Maine. Unthinned stands had similar years of clearcut and herbicide, and similar site quality to comparable PCT stands.

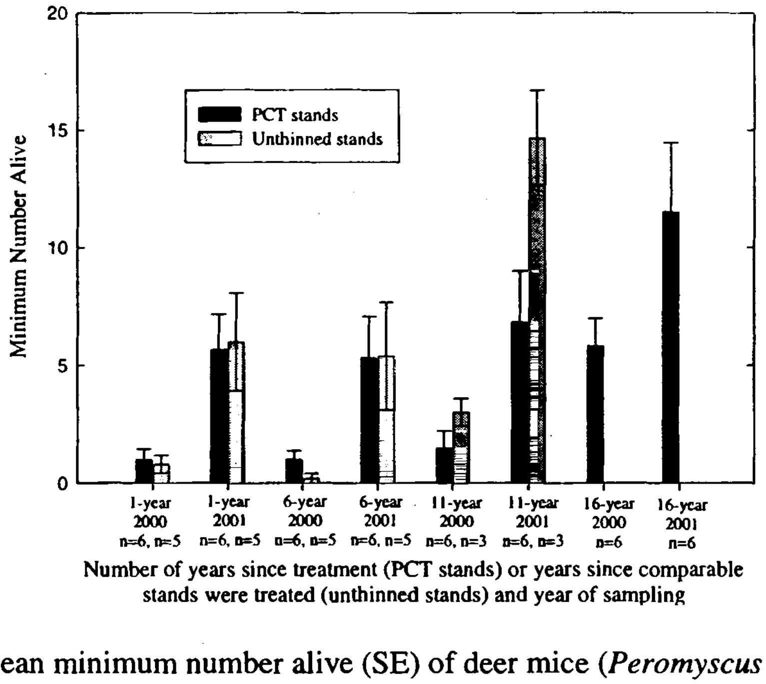

Figure 3.4. Mean minimum number alive (SE) of deer mice (*Peromyscus maniculatus*) in 24 stands treated with PCT and 13 similar unthinned stands during summer 2000 and 2001, northern Maine. Unthinned stands had similar years of clearcut and herbicide, and similar site quality to comparable PCT stands.

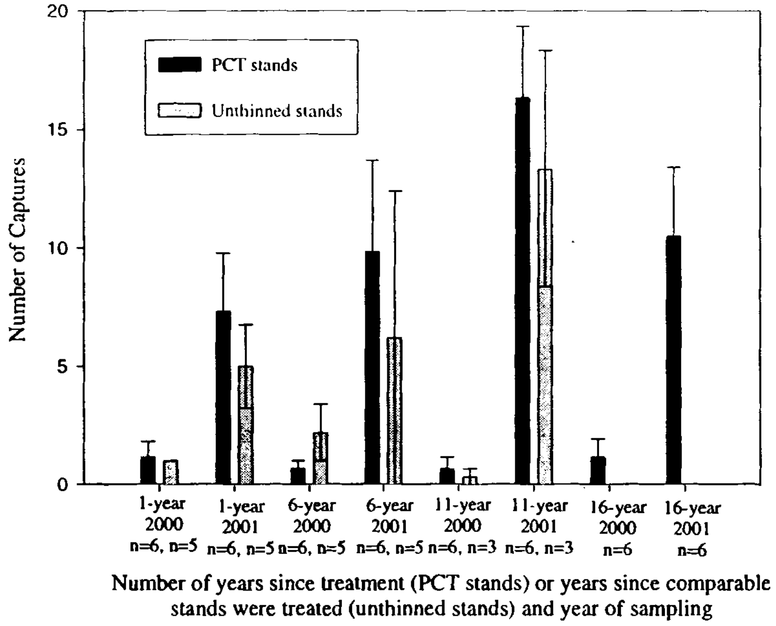

Figure 3.5. Total number of captures of short-tailed shrews (*Blarina brevicauda*) (SE) in 24 stands treated with PCT and 13 unthinned stands during summers 2000 and 2001, northern Maine. Unthinned stands had similar years of clearcut and herbicide, and similar site quality to comparable PCT stands.

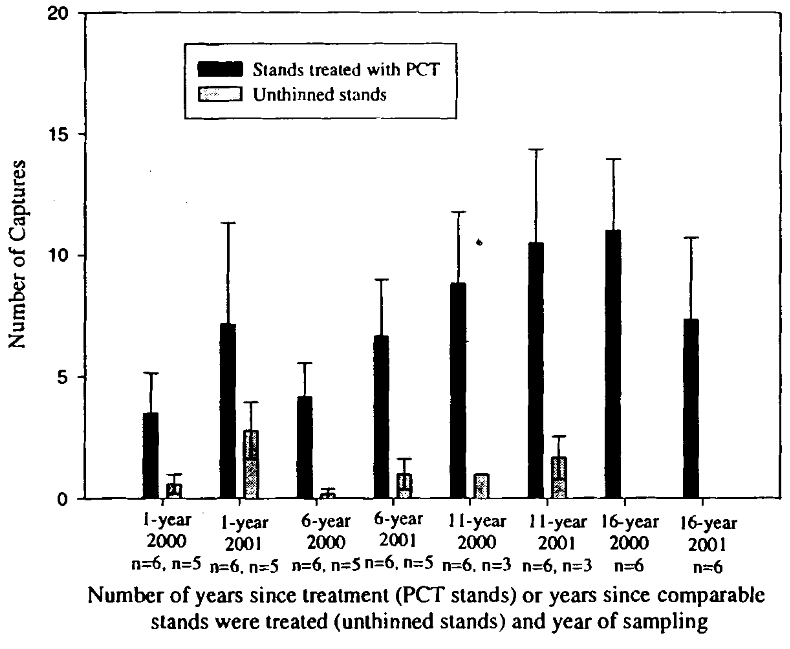

Figure 3.6. Total number of captures of masked shrews (*Sorex cinereus*) (SE) in 24 stands treated with PCT and 13 unthinned stands during summers 2000 and 2001, northern Maine. Unthinned stands had similar years of clearcut and herbicide, and similar site quality to comparable PCT stands.

Table 3.2. Comparisons of mean (SE) abundances (minimum number alive) of red-backed voles and deer mice and relative abundances (total number of captures) of short-tailed and masked shrews[a] on precommercially thinned stands (n = 18) and unthinned reference stands (n = 13) in northern Maine, 2000-2001. Data were analyzed using repeated-measures two-way Analysis of Variance; non-transformed means and standard errors are presented for transformed variables.[b]

	Species of small mammal[c]			
	Red-backed vole	Deer mouse	Short-tailed shrew	Masked shrew
Treatment				
F-Statistic	8.316	0.377	0.431	n/a
P-value	0.008	0.544	0.517	n/a
Abundance in PCT stands	9.06 (1.24)	3.56 (0.66)	6.00 (1.30)	6.81 (1.18)
Abundance in unthinned stands	3.84 (0.61)	4.42 (1.05)	4.35 (1.00)	1.19 (0.31)
Thinning class[d]				
F-Statistic	0.620	3.073	2.380	n/a
P-value	0.546	0.064	0.113	n/a
Abundance in 1-year stands	8.05 (1.96)	3.36 (0.80)	3.68 (0.95)	3.68 (1.28)
Abundance in 6-year stands	5.23 (0.82)	3.00 (0.84)	4.77 (1.32)	3.23 (0.90)
Abundance in 11-year stands	7.44 (1.15)	5.72 (1.35)	7.94 (2.16)	6.89 (1.81)
Year of sampling				
F-Statistic	3.815	29.271	51.175	n/a
P-value	0.062	< 0.001	< 0.001	n/a
Abundance in 2000	6.23 (1.12)	1.13 (0.23)	1.03 (0.26)	3.42 (0.86)
Abundance in 2001	7.52 (1.23)	6.71 (0.89)	9.58 (1.33)	5.48 (1.28)
Treatment × Thinning class				
F-Statistic	2.934	2.337	0.242	n/a
P-value	0.072	0.117	0.787	n/a

Table 3.2. Continued.

	Species of small mammal			
	Red-backed vole	Deer mouse	Short-tailed shrew	Masked shrew
Treatment × Year				
F-Statistic	0.389	0.277	1.175	n/a
P-value	0.539	0.604	0.289	n/a
Thinning class × Year				
F-Statistic	1.389	0.262	4.156	n/a
P-value	0.268	0.771	0.028	n/a
Treatment × Thinning class × Year				
F-Statistic	2.546	1.656	0.055	n/a
P-value	0.099	0.211	0.947	n/a

[a] Number of captures of masked shrews were not distributed normally; therefore a nonparametric analyses was conducted. Results are presented in the text.

[b] MNA of red-backed voles and deer mice were log transformed and number of captures of short-tailed shrews were square root transformed. The non-transformed mean and SE are presented here.

[c] Red-backed vole (*Clethrionomys gapperi*), deer mouse (*Peromyscus maniculatus*), short-tailed shrew (*Blarina brevicauda*), masked shrew (*Sorex cinereus*).

[d] Stands in the 1-year thinning class include stands (n = 6) that were treated with PCT in 1999 and unthinned stands (n=5). Stands in the 6-year thinning class include stands treated with PCT (n = 6) in 1994-1995 and unthinned stands (n = 5). Stands in the 11-year thinning class include stands (n = 6) that were treated with PCT 1989-1991 and unthinned stands (n = 3). Unthinned stands had similar years of clearcut and herbicide, and similar site quality to comparable PCT stands.

Table 3.3. Comparison of mean (SE) abundances (minimum number alive) of red-backed voles and deer mice and median (range) of number of captures of short-tailed shrews and masked shrews across 4 thinning classes of stands treated with PCT (1-year post-treatment, n = 6; 6-years post-treatment, n = 6; 11 years post-treatment, n = 6; 16 years post-treatment, n = 6) in northern Maine, 2000-2001. Means were compared using one-way ANOVA and medians were compared using nonparametric analyses[a]; non-transformed means and standard errors are presented for deer mice.

	Species of small mammal[b]			
	Red-backed vole	Deer mouse	Short-tailed shrew[a]	Masked shrew[a]
Thinning class[c]				
F-statistic	1.837	3.423	1.755	1.567
P-value	0.173	0.037	0.188	0.228
1-year	11.917 (3.156)	3.333 (1.032)	3 (0-18)	1.5 (0-25)
6-years	5.583 (1.062)	3.167 (1.072)	1.5 (0-27)	5 (0-17)
11-years	9.667 (1.305)	4.167 (1.359)	6 (0-28)	9.5 (1-25)
16-years	14.500 (2.091)	8.667 (1.738)	3.5 (0-22)	9.5 (0-20)
Year of sampling				
F-statistic	1.042	14.259	Z = 4.154	Z = 0.383
P-value	0.320	< 0.001	< 0.001	0.702
2000	9.792 (1.507)	2.333 (0.547)	0 (0-4)	4.5 (0-19)
2001	11.042 (1.652)	7.333 (1.135)	9.5(0-28)	5 (0-25)
Thinning class × Year				
F-statistic	0.397	3.502	2.017	0.599
P-value	0.757	0.034	0.144	0.623

[a] Presence of a year-effect for shrews was tested for using a Wilcoxsin signed rank test. An effect of age-class was tested for using a one-way ANOVA on the ranked sum of the number of captures in 2000 + 2001 and an age-class × year interaction term was tested for with the difference in abundances between years.

[b] Red-backed vole (*Clethrionomys gapperi*), deer mouse (*Peromyscus maniculatus*), short-tailed shrew (*Blarina brevicauda*), masked shrew (*Sorex cinereus*).

[c] Stands in the 1-year age-class include stands (n = 6) that were treated with PCT in 1999. Stands in the 6-year age-class include stands treated with PCT (n = 6) in 1994-1995. Stands in the 11-year age-class include stands (n = 6) that were treated with PCT 1989-1991.

I did not detect an effect of thinning class of stands on voles (P = 0.546), but there was a significant treatment × thinning class interaction (P = 0.072) (Table 3.2). Although red-backed voles were 2.5× more abundant in stands treated with PCT than unthinned stands (P = 0.008), the effect of PCT was not consistent across thinning-classes. Thinned stands had greater numbers of voles in the 1-year (P < 0.001) and 11-year age-class (P < 0.005), but treatments had similar abundances in the 6-year thinning class (P > 0.600). There was significant inter-annual variation in abundances of voles; a greater number were captured during 2001 (n = 233) than 2000 (n = 193) (P = 0.062). A significant year × thinning class × treatment interaction (P = 0.099) was observed indicating that the effects of PCT on voles were inconsistent across thinning classes of stands and years of sampling. Within solely PCT stands, from 1 to 16 years post-treatment, I did not detect an effect of year since thinning (thinning class, P = 0.173), year of sampling (P = 0.320), or a thinning class × year interaction term (P = 0.757) on the abundance of red-backed voles (Table 3.3).

Differences between the MNA of deer mice in thinned and unthinned stands was not significant (P = 0.544) from 1 to 11 years post-treatment (Table 3.2). Abundances of deer mice were different among thinning classes (P = 0.064); however interpretations were confounded by a significant (P = 0.034) thinning class × year interaction. The 16-year thinning class had 2.1-2.7× greater abundance of deer mice than each of the 3 younger thinning classes (Table 3.3). Across all thinning classes, abundance of deer mice was nearly 4× greater in 2001 (n = 277) than in 2000 (n = 70) (P < 0.001) (Table 3.3).

Treatment and thinning class of stands did not have a detectable effect on the number of captures of short-tailed shrews from 1 to 11 years post-treatment (P > 0.100).

There was, however, a marked change (9.2×) in shrew abundance between 2000 and 2001 ($P < 0.001$). Additionally, there was an inconsistent effect of thinning class on abundance of short-tailed shrews across the 2 years sampled (thinning class × year interaction, $P = 0.028$). During 2000, the 3 thinning classes had similar abundances ($P > 0.10$), but during 2001 the 11-year age-class had greater numbers of shrews than the 1-year age-class ($P < 0.01$).

Masked shrews responded strongly and positively to thinning ($P < 0.001$) and abundances were 5.7× greater in thinned stands than in similar reference stands, from 1 to 11 years post-treatment. I did not detect a significant effect of year of sampling or thinning class on masked shrews ($P > 0.10$); however, the treatment × thinning class interaction was significant ($P = 0.092$), indicating that there was an inconsistent effect of PCT across the 3 thinning classes. Pairwise comparisons indicated that stands treated with PCT had greater numbers of masked shrews than in unthinned stands in the 6-year ($P < 0.001$) and 11-year ($P < 0.001$) thinning classes, but not within the 1-year stands ($P = 0.82$).

Reproductive indices

No significant difference ($\chi^2 = 0.93$, $P = 0.34$) in the proportion of lactating adult female red-backed voles was observed between stands treated with PCT (41%, n = 187, 90 % C.I. 33 – 48 %) and unthinned reference stands (30%, n = 40, 90 % C.I. 16 –46 %). A greater proportion of adult female deer mice were lactating ($\chi^2 = 9.18$, $P < 0.001$) on unthinned stands (58 %, n = 43, 90 % C.I. 42 –72 %) than in thinned stands (31 %, n = 108, 90 % C.I. 23-41 %).

Habitat in PCT versus unthinned stands

Of the 6 *a priori* selected microhabitat variables, average diameter at breast height of trees was 1.15× greater (P = 0.003), total basal area was 1.38× greater (P = 0.002), and understory density was 1.40× greater (P = 0.022) within small mammal grids that had been treated with PCT, compared to grids within unthinned stands with a similar history of clearcutting and herbiciding (Table 3.4). Canopy closure was greater in unthinned stands than in stands treated with PCT up to 11-years post-treatment (P = 0.009). Canopy closure differed among thinning classes (P = 0.040); pairwise comparisons indicated that the 11-year thinning class had greater canopy closure than the 1-year thinning class (P = 0.070). Total understory density differed by thinning class, and the 6-year thinning class had a greater density of understory stems/ha than the 1-year (P = 0.008) or 11-year (P = 0.023) thinning classes.

Temporal effects of PCT on within-stand habitat characteristics

Average dbh, canopy closure, and total basal area generally increased with thinning class (Table 3.5). The 1-year thinning class had a lower dbh than the 6, 11, or 16-year thinning class (P = 0.080). Canopy closure (P = 0.011) and total basal area (P = 0.076) were greater in the 16-year thinning class than the 1-year thinning class. The 16-year thinning class also had greater total basal area than the 6-year thinning class (P = 0.018). Abundance of coarse woody debris was greater 11 years after treatment compared to 16 years post-thinning in PCT-treated stands (P = 0.005), but there were not differences in total amount of CWD between treatments (P = 0.180) or among thinning classes (1-year, 6-year, 11-year; pooled across treatments) (P = 0.231). Density of understory stems was greater 6-years post thinning than 1-year post-thinning (P = 0.001).

Table 3.4. Comparison of means (SE) for 6 habitat variables selected *a priori* between precommercially thinned stands (n = 18) and unthinned reference stands (n = 13) in northern Maine, 2000-2001. Differences in means by treatment for each variable were tested using two-way Analysis of Variance; non-transformed means and standard errors are presented for transformed variables[a].

	DBH[b]	CANOPY[c]	HGSTEM[d]	TOTDEBRIS[e]	TOTBA[f]	UNDERSTORY[g]
Treatment						
F-Statistic	11.171	8.417	1.321	1.900	12.351	5.928
P-value	0.003	0.009	0.261	0.180	0.002	0.022
PCT (n = 18)	12.7 (0.4)	74.68 (2.85)	400,398 (47,545)	1,531 (132)	20.19 (0.99)	3,376 (507)
No PCT (n = 13)	10.5 (0.2)	81.35 (2.17)	279,865 (56,379)	2,038 (172)	26.11 (2.09)	2,397 (676)
Thinning-class[h]						
F-Statistic	2.521	3.672	0.070	1.553	1.623	9.248
P-value	0.101	0.040	0.933	0.231	0.217	0.001
1-year (n = 11)	10.6 (0.3)	69.87 (5.07)	323,563 (74,625)	1,946 (257)	20.49 (1.81)	1,642 (271)
6-year (n = 11)	11.9 (0.7)	75.1 (2.4)	301,463 (42,658)	1,602 (121)	21.4 (2.7)	5,028 (990)
11-year (n = 9)	12.0 (0.5)	82.13 (3.18)	376,191 (89,445)	2,063 (157)	24.32 (1.45)	2,125 (429)
Treatment × thinning class						
F-Statistic	6.256	0.767	0.639	1.611	0.587	3.619
P-value	0.006	0.439	0.566	0.220	0.563	0.042

[a] DBH and UNDERSTORY were log transformed prior to analysis.

[b] DBH = average diameter breast height (cm) of closest tree ($\geq$ 7.6 cm dbh, $\geq$ 2 m height, > 45° from horizontal, alive) in each quarter.

[c] CANOPY = average overhead percent canopy closure during summer.

[d] HGSTEMS = number of herbaceous ground stems (< 0.5 m height, < 7.6 cm dbh, alive) per ha.

[e] TOTDEBRIS = number of (snags + logs + stumps + root masses) per ha.

[f] TOTBA = Basal area of hardwood trees + softwood trees + snags (m^2/ha).

[g] UNDERSTORY = total number of understory stems (number of saplings ($\leq$ 7.6 cm dbh, alive) at 1.5 m height per ha.

[h] Stands in the 1-year thinning class include stands (n = 6) that were treated with PCT in 1999 and similar unthinned stands (n=5). Stands in the 6-year thinning class include stands treated with PCT (n = 6) in 1994-1995 and similar unthinned stands (n = 5). Stands in the 11-year thinning class include stands (n = 6) that were treated with PCT 1989-1991 and similar unthinned stands (n = 3). Unthinned stands had similar years of clearcut and herbicide, and similar site quality to comparable PCT stands.

Table 3.5. Comparisons (one-way ANOVA) of mean (SE) values for 6 habitat variables across 4 thinning classes[a] based on years since precommercial thinning within 24 herbicided, regenerating clearcut stands treated with PCT in northern Maine. Non-transformed means and standard errors are presented for transformed variables[b].

Factor	DBH[c]	CANOPY[d]	HGSTEM[e]	TOTDEBRIS[f]	TOTBA[g]	UNDERSTORY[h]
Thinning class						
F-statistic	8.120	4.336	0.861	5.079	4.462	6.569
P-value	0.001	0.017	0.478	0.009	0.015	0.030
1-year	10.5 (0.3)	62.33 (8.05)	325,927 (84,972)	1,578 (303)	18.15 (2.43)	1,630 (494)
6-year	13.4 (0.8)	72.68 (3.52)	323,792 (72,761)	1,490 (147)	16.56 (1.28)	5,848 (1,330)
11-year	12.5 (0.6)	77.66 (3.28)	454,073 (18,424)	2,115 (239)	21.92 (0.93)	2,745 (400)
16-year	14.5 (0.7)	86.04 (1.76)	497,802 (101,478)	943 (101)	24.15 (1.53)	3,281 (796)

[a] Stands in the 1-year thinning class include stands (n = 6) treated with PCT. Stands in the 6-year thinning class include stands treated with PCT (n = 6) in 1994-1995. Stands in the 11-year thinning class include stands (n = 6) treated with PCT 1989-1991. Stands in the 16-year thinning class include stands (n = 6) treated with PCT in 1984-1986.

[b] DBH and UNDERSTORY were log transformed and CANOPY was arcsine transformed prior to analysis.

[c] DBH = average diameter breast height (cm) of closest tree (≥ 7.6 cm dbh, ≥ 2 m height, > 45° from horizontal, alive) in each quarter.

[d] CANOPY = average overhead percent canopy closure during summer.

[e] HGSTEMS = number of herbaceous ground stems (< 0.5 m height, < 7.6 cm dbh, alive) per ha.

[f] TOTDEBRIS = number of (snags + logs + stumps + root masses) per ha.

[g] TOTBA = Basal area of hardwood trees + softwood trees + snags (m^2/ha).

[h] UNDERSTORY = total number of understory stems (number of saplings (≤ 7.6 cm dbh, alive) at 1.5 m height per/ha.

DISCUSSION

PCT positively affected or produced no detectable effect on abundances of the 4 most common species of voles, mice, and shrews on my study areas. From 1-11 years post-thinning, the abundances of red-backed voles and masked shrews were greater in stands treated with PCT and abundances of deer mice were not significantly affected by thinning. A trend of greater abundances of short-tailed shrews in stands treated with PCT was evident; however, high variation between stands and low abundances likely prevented statistical differences for that species. Short-tailed shrews, red-backed voles, and deer mice exhibited large inter-annual variation. Despite substantial annual variation in densities within treatments, abundances of deer mice increased with thinning class within regenerating conifer stands in northern Maine.

Reducing competition among crop trees via precommercial thinning accelerated stand development in regenerating clearcut stands with a prior history of gylphosate application. Stands treated with PCT acquired some attributes of more mature forest (without PCT) such as greater stem diameters, diverse understories, and a more broken canopy layer. The silvicultural response of forest stands treated with PCT was consistent with previous reports (Brissette et al. 1999, Brissette and Frank 1999, Lindgren and Sullivan 2001, Sullivan et al. 2001, Pothier 2002); significant increases in dbh of trees, canopy density, and basal area were observed from 1 to 16 years post-treatment.

The acceleration of stand development that occurs within PCT-treated stands was favorable or neutral for common species of small mammals in the Acadian forest. By producing stands containing some characteristics of more mature forest (broken canopy, larger stem diameters), PCT has the potential to increase heterogeneity of forest stand conditions across the mid-successional dominated landscapes that presently occur throughout much of the Acadian forest (Maine Forest Service 1998). As forest rotations associated with intensive management become increasingly shorter, the acceleration of mature stand conditions via PCT across significant portions of the forest landscape could help mitigate some effects of intensive silviculture on small mammals.

Within-stand habitat structure

I observed larger trees, a more open canopy, and more understory stems in stands treated with PCT. The growth of overstory trees and temporary opening of the overstory layer that occurred from 1-6 years post-thinning produced within-stand habitat characteristics more typical of conifer stands in later seral stages, when compared to unthinned stands. Penetration of sunlight allowed understory stems to flourish temporarily from 1-6 years post-treatment, but by 11-years post-PCT understory stem density had declined. Advanced regeneration was released initially from competition and shading in thinned stands; however, a delayed self-thinning response occurred from 6-11 years post-thinning.

Coarse woody debris has often been touted as an element of forested stands that is necessary to maintain small mammal communities. Downed and dead woody material has been suggested to provide subnivian access in winter, habitat for invertebrates, escape cover from predators, growing surface for fungi, and to mediate microclimate by retaining moisture (Hamilton 1941, Hayes and Cross 1987, Hagan and Grove 1999, Fraver et al. 2002). The total density of logs, snags, stumps, and root masses did not differ between thinned and unthinned stands, or among thinning classes of stands; however, 16-year post-PCT stands had less CWD than 11-year post-PCT stands, suggesting that CWD may be lost to decay but not recruited in PCT stands after 11-years post-thinning. Many of the highest small mammal numbers were observed in thinned stands, and especially in the 16-year stands, indicating that CWD may not be limiting from the perspective of forest-dwelling voles, mice, and shrews in regenerating clearcuts or in intensively managed stands. This finding is consistent with other studies in Maine, which have detected few strong relationships among abundances of small mammals and CWD throughout a range of forest types, thinning classes, and harvesting regimes (Lachowski 1997, Fuller 1999, S. Billig, *In prep.*).

Red-backed voles

Red-backed voles have been reported to have ecological relevance as indicators of late successional forest, because their greatest densities often occur in mature or over-mature stands (Martell 1983b, Nordyke and Buskirk 1991). Contrary to those results, voles were abundant across three thinning classes of mid-successional stands in the Acadian forest and I observed no significant effect of thinning class on abundances. Greater abundances of voles were observed in stands treated with PCT; additionally, the proportion of female voles lactating on thinned stands was not detectably different than the proportion lactating on unthinned stands, indicating that habitat quality for voles may have been comparable between treatments. Red-backed voles were the most common species of small mammal within stands 14-33 years post clearcutting (13-24 years post-herbicide treatment). Therefore, the mesic conifer-dominated Acadian forest may accumulate habitat characteristics typical of mature forest more rapidly than in conifer stands of Ontario (Martell 1983b) and the central Rocky Mountains (Nordyke and Buskirk 1991). Abundance of red-backed voles in PCT stands temporarily declined at 6-

years post-treatment, which coincided with the greatest density of understory stems (Table 3.4, 3.5). These results are inconsistent with findings from Wyoming, where understory cover was positively associated with abundance of red-backed voles in conifer stands of various successional stages (Nordyke and Buskirk 1991).

Deer mice

Deer mice are widely considered a habitat generalist and have been reported to respond positively to reduction of the forest overstory following clearcut harvesting (Martell and Radvanyi 1977, Martell 1983a, Martell 1983b, Morrison and Anthony 1988, Kirkland 1990, Sullivan et al. 1999). However, previous studies have indicated that deer mice exhibit little response to PCT of conifer stands (Lautenschlager et al. 1997, Sullivan et al. 2001). Consistent with previous research, I observed that abundances of deer mice were similar among PCT-treated and unthinned stands on my study areas. The greatest abundance of deer mice was observed in the 11 year thinning class, which, pooled across years, was 1.56x greater than the 6-year and 1.40x greater than the 1-year thinning classes. Further, across the 4 classes of stands treated with PCT, the 16-year post-PCT stands had the greatest numbers of deer mice in both 2000 and 2001. The positive effects of thinning class on numbers of deer mice were consistent between years of sampling despite a nearly 4-fold increase in total number of individuals from 2000 to 2001. These observations that populations of deer mice on my study area reached their greatest densities in older stands indicate that attributes of stand maturity may have had a greater influence on densities of deer mice than PCT. Previous investigations of forest-dwelling small mammals have also detected greater abundances of deer mice in older stands than in regenerating stands in the commercial forests of Maine (Lachowski 1997, Fuller 1999).

Although densities of adult female deer mice were similar between thinned (averaged 2.3/grid) and unthinned conifer (averaged 1.7/grid) stands, a greater proportion of adult female deer mice were lactating in unthinned stands compared to similar PCT-treated stands. Reproductive output of deer mice may have been affected by treatment; deer mice often have aggressive intra-specific interactions (Martell 1983a), which may lead to subordinate, non-reproductive individuals occupying areas with lower habitat quality (Van Horne 1983). The observed difference in lactation rates of adult female deer mice between thinned and unthinned stands suggest that habitat quality could be greater in stands without PCT; however, additional information on survival and reproductive success is necessary to evaluate this hypothesis.

Short-tailed shrews

Short-tailed shrews did not significantly respond to thinning from 1-11 years post-treatment or to thinning class, either pooled across treatments or within only the PCT-treated stands from 1-16 years after thinning. However, small numbers of individuals captured/grid in addition to large variation of abundances of short-tailed shrews between grids, may have precluded my detection of a positive effect of PCT. *B. brevicauda* are reported to reach their greatest densities in stands with complex understories with abundant herbaceous vegetation (Miller and Getz 1977, Brooks and Healy 1988, Healy and Brooks 1988, Kirkland 1990), which may be related to positive associations between insects and diversity of plant species and structure (Murdoch et al. 1972). Although 6-year stands had the greatest density of herbaceous vegetation, I did not detect greater abundances of shrews in those stands, which suggests that prey was distributed evenly among treatment and thinning classes, or was not limiting across all sites. Abundance of short-tailed shrews in my study areas was likely related to sub-stand scale attributes other than those that are associated with thinning. The changes in forest structure that occur after thinning and with stand maturation apparently do not exert a strong influence on relative abundance of *B. brevicauda.*

Masked shrews

PCT produced positive and long-lasting effects on the relative abundance of masked shrews in regenerating conifer stands in northern Maine. Number of captures were 4.38 and 10.21× greater in stands treated with PCT than similar unthinned stands up to 11-years post-treatment when data were pooled across thinning classes. In contrast to the greater numbers of masked shrews that I observed in thinned versus unthinned stands, combined densities of masked shrews and pygmy shrews (*Sorex hoyi*) were similar among herbicided stands and stands thinned with brush-saws (but not herbicided) 1-2 years post-treatment in Ontario (Lautenschlager et al. 1997). Application of herbicide has substantial and long-lasting effects on composition and abundance of tree species within stands (Newton et al. 1989, Daggett and Wagner, *In prep.*); therefore, inconsistencies reported between this study and results reported from Ontario likely resulted from the application of either herbicide or PCT, but not both treatments on study sites in Canada.

The positive effects of PCT on masked shrews that I observed suggests that microhabitat structure associated with thinning enhances abundance of masked shrews across a range of thinning classes, from 1 to 11-years post-thinning. Herbaceous vegetation often flourishes after PCT (Hurst et al. 1982, Bell et al. 1997, Thomas et al. 1999, Lindgren and Sullivan 2002), because opening of the canopy allows sunlight to reach the forest floor. Dense herbaceous vegetation may have provided cover to shrews, supported greater densities of foliar-insect prey (Murdoch et al. 1972), or been associated with moister microclimate (Miller and Getz 1977).

CONCLUSIONS

Small mammals had species-specific responses to both PCT and stand development, which complicates prescriptions of forest management activities to increase densities and diversity within small mammal communities. These results indicate that PCT, across an 11-year range since treatment, positively or neutrally affects the abundance of the 4 most common species of small mammals (red-backed voles, deer mice, short-tailed shrews, masked shrews) in the commercial forests of northern Maine. Greater abundances of red-backed voles and masked shrews occurred in stands treated with PCT than in unthinned stands, from 1 to 11-years post-treatment, whereas deer mice and short-tailed shrews did not appear to be affected by PCT. Thinning increased or maintained overall abundances of forest-dwelling small mammals across a range of years since treatment, suggesting that PCT produces positive and long-term responses within the small mammal community. However, lactation rates for deer mice were lower in thinned stands. Additionally, several habitat attributes (e.g. basal area, dbh, canopy closure) that are positively associated with degree of stand maturity were greater in stands treated with PCT than in unthinned stands.

Additional to attaining silvicultural and economic objectives, forest managers may be able to increase the abundance of small mammals across commercial forest landscape via PCT. An increase in the number of small mammals could also have positive effects on other trophic levels, including forest-dependent predators, such as

American Marten (*Martes americana*) (Lachowski 1997) if other structural requirements for denning, rest sites, escape cover (Buskirk 1984, Payer and Harrison 2000), and subnivian access (Sherburne and Bissonette 1994) are present. Increased rates of stand development associated with PCT may help compensate for the short rotations (< 60 years) commonly applied to intensively managed stands in the Acadian forest (Seymour and Hunter 1992). Maintaining significant portion of the landscape in PCT, however, may involve trade-offs for early-successional dependent forest mammals such as snowshoe hare (Sullivan and Sullivan 1988, Chapter 2) and their predators (e.g. Canada lynx (*Lynx canadensis*)). Although this study evaluated stand-scale effects of PCT, broader landscape-scale evaluations of PCT are needed to reconcile silvicultural objectives with desired balances between conflicting habitat needs of early (e.g. snowshoe hare) and mid-successional (e.g. red-backed voles, masked shrews) wildlife species.

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CHAPTER 4

HABITAT AND STRUCTURAL DIFFERENCES BETWEEN PRECOMMMERCIALLY THINNED AND UNTHINNED CONIFER STANDS: IMPLICATIONS FOR WILDLIFE

ABSTRACT

Effects of precommercial thinning (PCT) in young, high-density forest stands on the growth and yield of crop trees has been well-studied, but effects on habitat characteristics, structural attributes, and wildlife populations is lacking. I examined the dominant changes in habitat characteristics and forest structure that occur with PCT and stand development in commercial spruce-fir stands within the Acadian forest of northern Maine. I selected 30 regenerating, herbicide-treated conifer stands (17 treated with PCT) of 3 thinning classes (1, 6, or 11-years) in 6 townships and measured 27 variables that described the characteristics and structure of the understory, overstory, woody debris, or ground cover on 20 circular plots per stand. I conducted a two-way Analysis of Variance (ANOVA) on the stand-scale means of each habitat variable to examine for the effect of treatment (treated with PCT or unthinned) or thinning class (1, 6, or 11-years). Variables with a F-statistic > 2.0 for either main effect were retained for inclusion into a principal components analysis (PCA). Two separate PCAs were conducted; 1 included variables that differed by treatment, and 1 included variables that differed among thinning classes. Changes in vegetation structure that occur with PCT were described by 3 principal components, which accounted for > 80% of the variation: near-ground cover, overstory cover, and understory structure. Horizontal cover, an overstory to understory contrast, and a gradient of herbaceous vegetation described differences in habitat and forest

structure among thinning classes; these components described > 75% of the variation that occurred with development of forest stands. The application of PCT accelerated some characteristics of stand development, resulting in a reduction of understory structure and complexity. However, PCT and the shorter rotations associated with intensively managed stands may reduce recruitment of logs and coarse woody debris (CWD). Species-specific responses of wildlife will likely be associated with the changes in forest structure that occur with PCT and stand development; species that are associated with early successional habitat, including snowshoe hare (*Lepus americanus*) and shrub-nesting songbirds, have been documented to respond negatively to thinning. Other forest-wildlife associated with more mature forest, however, such as red-backed voles (*Clethrionomys gapperi*), and perhaps spruce grouse (*Falcipennis candadensis*), may increase their densities following PCT.

INTRODUCTION

Precommercial thinning (PCT) of overstocked, regenerating conifer stands has been practiced increasingly in Maine and other jurisdictions within the Acadian forest of eastern North America (Maine Forest Service 1994-2001, Canadian Council of Forest Ministers 2002) to reduce competition, increase growth rates, and to shorten rotation length. In the late 1980's, forest landowners thinned about 2,400 hectares of densely stocked, regenerating clearcuts each year in Maine; by 2000 the total acres of land treated with PCT each year had risen to > 8,100 hectares a year, or 3.5% of the total silvicultural activity for the state (Maine Forest Service 2000-2002). The eastern Maritime Provinces of Canada have also experienced large increases in the land area treated with PCT; from 1990 to 2000 the acreage treated with PCT each year increased by 2.5-fold in Nova

Scotia, 2.7-fold in New Brunswick, and 4.3-fold in Quebec (Canadian Council of Forest Ministers 2002). Although the application of PCT to regenerating clearcuts has increased across the commercial forest landscape of the Acadian forest, the ecological effects of PCT on structural attributes of forest stands and the potential influences of structural changes on forest-dependent wildlife have been studied little.

The silvicultural response of crop trees to PCT have been well-documented; thinning increases stem diameters (Harrington and Reukema 1983, Ker 1987, McCormack and Lemin 1998, Brissette and Frank 1999, Brissette et al. 1999, Pothier 2002), increases crown size (McCormack and Lemin 1998, Brissette and Frank 1999, Brissette et al. 1999, Lindgren and Sullivan 2001, Sullivan et al. 2001), decreases mortality of crop trees (Ker 1987, Brissette and Frank 1999, Brissette et al. 1999), increases merchantable volume (Ker 1987), and may reduce rotation length (Sullivan et al. 2001). In contrast, the immediate and long-term ecological changes in habitat characteristics and forest structure that are associated with PCT of overstocked conifer stands are poorly understood. Most studies of structural and habitat changes associated with PCT have focused on short-term (1-3 years post-treatment) changes in understory and overstory characteristics and have been conducted on stands that were thinned, but not previously treated with herbicide (Bell et al. 1997, Sullivan and Lindgren 2001), which is a general practice throughout much of the Acadian forest. The application of herbicide several years before thinning likely has strong effects on overstory and understory responses to subsequent PCT (Dagget and Wagner *In prep.*). Understanding the long-term changes in forest overstory and understory structural attributes and habitat characteristics that occur after PCT of conifer stands is a prerequisite to evaluating biological consequences, to making informed forest management decisions, and to establishing ecological policies.

Manipulation of stem densities in regenerating clearcut stands may have negative consequences for species associated with early successional habitat (Hayes et al. 1997). In contrast, PCT of regenerating stands may diversify second and third growth forests by more rapidly producing stands with characteristics of forest in later seral stages (Carey and Johnson 1995, Hayes et al. 1997, Sullivan et al. 2001). The objectives of this study were to describe the biological changes across a range of intervals since treatment, in habitat characteristics and structural attributes between PCT and non-PCT treated clearcuts with a previous history of herbicide treatment in northern Maine. Instead of focusing on diversity of plant species after thinning (Thomas et al. 1999, Lindgren and Sullivan 2001), the goal of this effort was to describe structural attributes relevant to predicting responses of forest-dependent wildlife to PCT and to stand development in herbicide-treated clearcuts.

STUDY AREA

The study area was located within the matrix of commercial, mixed northern hardwoods-spruce-fir forest of northern Maine. I sampled 30 stands distributed across 6 townships in northern Maine, which spanned 102 km east to west and 49 km north to south. Stands were located in the town of Hersey, T4 R 11 WELS, T 5 R 11 WELS, T4 R 12 WELS, T1 R 13 WELS, and Spencer Bay. These townships were extensively clearcut-harvested during and following the spruce-budworm outbreak of the 1980's and many clearcuts were treated with an aerial herbicide to promote softwood regeneration. Great Northern Paper Company, Millinocket, Maine; Plum Creek Timber, Fairfield, Maine; and International Paper Company, Costigan, Maine managed those townships for pulpwood and timber production. The study area receives abundant precipitation (101 cm annually), with an average of 276 cm falling annually as snowfall, and seasons include mild summers (July mean maximum = 25° C) and cold winters (January mean minimum = -19° C) (Garoogian 2000).

I sampled stands that had been clearcut (timber harvesting resulting in residual basal area of acceptable growing stock trees > 4.5 in. dbh of < 30 ft^2/acre) 1968-1982, treated with an aerial herbicide (e.g. Glyphosate at ≈ 1.68 kg/ha acid equivalent) 1982-1988, and either precommercially thinned with brush-saws 1989-1999 (n = 17) or unthinned (n = 13) (Table 4.1). Balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), and black spruce (*Picea nigra*) were the dominant tree species, but stands also had small components of white pine (*Pinus strobus*), larch (*Larix spp.*), white cedar (*Thuja occidentalis*), paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*) and red maple (*Acer rubra*). Chapter 2 contains a more detailed description of the study sites.

METHODS

Stands were selected based on stand history, size, spatial independence, and site quality. I selected stands that were > 8 ha in size (median = 22.2 ha, range 8.5-74.3 ha) and were separated from each other by > 0.40 km. Site quality was estimated based on 4 to 6 soil cores sampled at 50-100 m intervals within each stands with a soil auger to avoid confounding effects of site quality affecting the rate of development (Briggs and Lemin 1994). I assigned a site quality value to each stand ranging from 1 (highly productive) to 5 (unproductive) based on Brigg's (1994) scale of forest productivity.

Table 4.1. Stand history, location, and site quality for 17 precommercially thinned (PCT) stands and 13 unthinned stands in northern Maine that were sampled for structural attributes and habitat characteristics. (T = stand treated with PCT, C = untreated stand). Site quality ranged from 1 (well drained, productive) to 5 (poorly drained, unproductive) according to Briggs (1994) classification guidelines.

Site number	Year of Clearcut	Year of Herbicide	Year of PCT	Township	Site Quality
1-1-T	1982	1988	1999	T 4 R 11	4+
1-2-T	1980	1983	1999	T4 R 12	3-
1-3-T	1977	1983	1999	T4 R 11	4+
1-4-T	1982	1988	1999	T4 R 11	4
1-5-T	1976	1983	1999	T4 R 12	4
6-1-T	1979	1988	1994	Hersey	3+
6-2-T	1979	1988	1994	Hersey	2-
6-4-T	1974	1982	1994	T 5 R 11	3-
6-5-T	1976	1985	1995	T 5 R 11	3-
6-6-T	1979	1982	1994	T 5 R 11	3-
11-1-T	1975	1983	1989	T 1 R 13	3
11-2-T	1968	1987	1990	Spencer Bay	3-
11-3-T	1975	1983	1989	T 1 R 13	2-
11-4-T	1975	1986	1990	T 1 R 13	3
11-5-T	1975	1983	1989	T 1 R 13	2
11-6-T	1975	1984	1991	T 1 R 13	2-
11-7-T	1975	1986	1989	Spencer Bay	2-
1-1-C	1982	1988	n/a	T 4 R 11	4
1-2-C	1979	1983	n/a	T 4 R 11	3-
1-3-C	1981	1984	n/a	T 4 R 11	4+
1-4-C	1983	1988	n/a	T 5 R 11	4+
1-5-C	1976	1985	n/a	T 4 R 11	3-
6-1-C	1979	1988	n/a	Hersey	3+
6-2-C	1981	1988	n/a	Hersey	3+
6-4-C	1974	1982	n/a	T 5 R 11	4
6-5-C	1974	1985	n/a	T 4 R 12	3
6-6-C	1976	1983	n/a	T 4 R 11	4
11-1-C	1976	1982	n/a	T 5 R 11	3
11-3-C	1976	1982	n/a	T 5 R 11	3+
11-4-C	1974	1985	n/a	T 5 R 11	3

The study design included 17 PCT-treated stands that were sampled for habitat characteristics and structural attributes at 5 year intervals (1-2 year post thinning, n = 5; 5-7 years, n = 5; 9-12 years, n = 7) and 13 similar unthinned stands (1 year, n = 5; 6 year, n = 5; 11 year, n = 3) whose year of clearcut and herbicide treatment were comparable to treatment stands. I allowed 1-2 years of latitude in separating stands into thinning classes to maximize the number of stands studied. The ratio of PCT-treated to unthinned stands in the 11-year thinning class was unbalanced because I was unable to locate more than 3 unthinned stands that met my criteria of similar site quality, year of clearcut, and year of herbicide-treatment. Treatment stands were paired with an unthinned stands with similar site quality, year of clearcut and year of herbicide to avoid gross biases arising from temporal variation in years of treatment. Stands were not statistically paired and were not treated as paired during analyses.

Habitat sampling

Vegetation structure was measured on 20 fixed-area nested plots centered on 4, 400 m transects separated by 65 m and located > 50 m from stand edges (Chapter 2). I centered 5 plots per 400 m of transect at random locations along the transects and distributed plots in a stratified-random design. I used 25 m^2 circular plots within thinned stands and 10 m^2 circular plots within unthinned stands to sample approximately the same number of crop trees, and to maximize number of sample plots across varying stand densities. Within each plot I measured 27 habitat variables to describe the structure of the overstory, understory, woody debris, or ground-level herbaceous vegetation.

Within each plot, I counted the number of coniferous and deciduous overstory trees (≥ 7.6 cm dbh, > 1.0 m height, alive) and measured the diameter breast height (dbh), total height, and the height from the ground to the lowest living branch. Heights were measured using a telescoping height pole. I calculated the live crown ratio of overstory trees as the [(total height – height to crown) / total height]. I also measured the number, type (coniferous or deciduous), dbh, total height, and height to crown for all understory stems (< 7.6 cm dbh, >1 m height, alive) within the plot and calculated the average live crown ratio of the understory. The number of stem cover units (SCU) was computed by summing the number of coniferous understory stems × 3.0 plus the number of deciduous understory stems (Litvaitis et al. 1985).

I counted the number and type (coniferous or deciduous) of woody, regenerating stems (≥ 0.2 m, < 1.0 m, alive) on a 1.0-m diameter nested subplot that was centered within each of the 20 plots/stand. The density of stems/ha in each stands was calculated by summing the total number of regenerating stems, understory stems, and overstory stems and dividing by the number of ha sampled within each stand. The percent of ground covered by grass and forbs, moss, rock, vegetative litter, and other vegetation was also visually estimated in the 1.0-m subplot.

Horizontal vegetation cover was quantified with a 2.0 m cover pole with alternating 0.1 m red and white bands. Following a random compass bearing separated by 180°, the distance to horizontal cover was measured from the center point as the distance where ≥ 25 % of all red and white bands were visually obstructed. I estimated the number and volume of downed logs with a modified version of the planar intersection method used by Payer and Harrison (2000). I established a 20-m randomly oriented transect with the midpoint at the center of each sampling station. I quantified the number of logs that crossed the transect and were ≥ 1.0 m length, ≥ 7.6 cm diameter (at the point of intersection), and ≤ 45° from the ground. Only sound to moderately decayed logs were considered, so that extremely decayed logs were excluded from sampling. Overhead canopy cover was measured with a spherical densiometer; 4 readings in the 4 cardinal compass directions at 1.0 m height (estimated height of mid-winter snowpack) were taken at the center of each plot and averaged to a single value for each plot (Lemon 1956).

Statistical analyses

Analysis of variance

I calculated an average value for each habitat variable within each stand and treated the stand as the unit of replication. Residual errors of each variable were examined for normality and homoscedasticity across stands and I transformed all non-normal data (modified Levene's test < 0.10 and/or Lilliefor's test < 0.10) with $\log_e$, square root, or cube root transformations to meet the parametric assumptions of analysis of variance (ANOVA) (Neter et al. 1996). Next, I conducted a two-way ANOVA on the means of each habitat variable with treatment (PCT or unthinned) and thinning class (1, 6, or 11-years post-treatment) as the main effects. Post hoc, Tukey's honestly significant difference tests were used to examine pairwise differences among thinning classes of habitat variables with significant thinning class effects (Zar 1999).

Principal components analysis

I eliminated all habitat variables with a F-statistic < 2.0 for treatment (PCT or unthinned) or for thinning class (1, 6, or 11-years) from further analyses; however a large number of variables had significant treatment or thinning class effects based on this initial screening procedure. High dimensionality of large and complex multivariate data sets causes interpretation of results to be difficult (McGarigal et al. 2000). To reduce the dimensionality of the habitat variables, I conducted 2 separate principal component analyses (PCA) to describe the variation in habitat structure between treatments and thinning classes: 1) habitat variables that differed between thinned and unthinned stands, and; 2) habitat variables that differed among the 3 thinning classes of stands, regardless of thinning history. PCA is an ordination technique that creates new components that are linear combinations of original variables. These linear combinations of variables, or components, maximize variation among observations in ordination space to more simplistically explain the data with a smaller number of variables.

I included normally distributed (e.g. transformed when necessary) habitat variables for each stand that were standardized by subtracting the mean and dividing by the standard deviation of that variable to the PCA. Standardization of variables was required because the scales of measurement differed among structural variables and this prevents dominance by variables with large variation (Pielou 1984). After computing the principal components, I used scree plots, relative variance criterion, and the latent root criterion to determine how many components to retain (McGarigal et al. 2000). For both analyses, I used a varimax rotation to aid in interpretation of loadings and components. I examined rotated factor loadings to interpret and provide biologically relevant names for the principal components. Variables with loadings (after rotation) of > 0.60 or < -0.60 were considered to have strong effects on that component; these thresholds roughly correspond to variables that account for about 40% of the variance in the component (Tabachnik and Fidell 1983, McGarigal et al. 2000). Ordination diagrams using the first

3 components from each analysis were constructed with Gaussian confidence ellipses for the sample ($P = 0.70$) (SPSS 1997).

RESULTS

Analysis of variance

Fourteen of 27 habitat variables that I measured differed between thinned and unthinned stands ($F > 2.0$); however, those showing the greatest differences in magnitude were stem cover units, total number of understory stems, total number of stems, and the number of logs, which were 3.8, 2.9, 2.2, and 2.2 times greater in unthinned stands, respectively. Other variables that differed between treatment types were the understory height, understory height to crown, understory live crown ratio, average dbh of the understory, number of understory conifer stems, total number of overstory stems, log volume, average dbh of the overstory, canopy density, and the horizontal vegetation distance (Table 4.2).

Twelve of 27 habitat variables differed among the thinning classes ($F > 2.0$). These included the average dbh of understory stems, the height of understory stems, the number of deciduous understory stems, the total number of understory stems, the average dbh of overstory stems, the height of overstory stems, the total number of overstory stems, the total stem density, the percent ground cover of grass and forbs, the percent ground cover of other herbaceous vegetation, the number of logs, and the log volume (Table 4.3). In general, the dbh and height of understory trees and overstory trees were greatest in the 11-year stands ($P < 0.10$). The greatest number of deciduous understory stems and total stem density occurred in the 6-year thinning class ($P < 0.10$). I observed

Table 4.2. The effect of treatment (PCT vs. unthinned) on mean (SE) values of 27 habitat variables sampled within 17 precommercially thinned stands and 13 unthinned reference stands with a previous history of clearcutting followed by herbicide (Glyphosate) application in northern Maine. Non-transformed means and standard errors are presented for transformed variables. Comparisons yielding a calculated F-statistic ≥ 2.0 are depicted in bold.

				Overstory Type	
Variable	Transformation	F	P	PCT	Unthinned
Average dbh of understory stems (cm)		**11.545**	**0.002**	3.2 (0.1)	3.8 (0.1)
Height of understory stems (m)		**49.801**	**< 0.001**	3.1 (0.1)	4.2 (0.1)
Height to crown of understory stems (m)		**19.567**	**< 0.001**	0.9 (0.1)	1.5 (0.1)
Live crown ration of understory stems (value from 0-1.0)	Ln	**5.280**	**0.031**	0.68 (0.02)	0.62 (0.02)
Number of understory conifer stems (#/ha)	Ln	**34.528**	**< 0.001**	1,471 (705)	7,101 (820)
Number of understory deciduous stems (#/ha)	Ln	0.053	0.485	1,675 (409)	1,896 (475)
Total number of understory stems (#/ha)	Ln	**32.471**	**< 0.001**	3,146(707)	8,997 (821)
Stem cover units (#/ha)	Ln	**38.445**	**< 0.001**	6,089 (2,037)	21,199 (2,367)
Average dbh of overstory stems (cm)		**7.897**	**0.010**	12.1 (0.3)	10.8 (0.4)
Height of overstory stems (m)		0.000	0.983	8.1 (0.2)	8.1 (0.2)
Height to crown of overstory stems (m)		0.700	0.412	1.4 (0.1)	1.6 (0.2)
Live crown ratio of overstory (value from 0-1.0)		1.870	0.184	0.84 (0.02)	0.80 (0.02)
Number of overstory conifer stems (#/ha)		1.832	0.188	1,199 (98)	1,402 (114)
Number of overstory deciduous stems (#/ha)	Ln	1.645	0.212	75 (37)	151 (43)
Total number of overstory stems (#/ha)		**3.064**	**0.093**	1,274 (104)	1,553 (121)
Number of coniferous regenerating stems (#/ha)		0.334	0.569	299 (70)	361 (81)
Number of deciduous regenerating stems (#/ha)		0.710	0.408	571 (92)	690 (107)
Total number of regenerating stems (#/ha)		1.344	0.258	870 (102)	1,051 (119)
Total number of stems (#/ha)	Ln	**36.422**	**< 0.001**	5,289 (730)	11,601 (849)
Percent ground cover of grass and forbs (%)	Square root	1.510	0.231	5 (1)	3 (1)
Percent ground cover of rock (%)	Ln	0.137	0.714	1 (0)	1 (0)
Percent ground cover of litter (%)		1.249	0.275	64 (3)	69 (4)
Percent ground cover of other herbaceous vegetation (%)		0.675	0.419	13 (2)	11 (1)
Horizontal vegetation distance (m)		**12.570**	**0.002**	10.0 (0.4)	7.6 (0.5)
Number of logs (#/transect)	Ln	**25.196**	**< 0.001**	1.6 (0.3)	3.5 (0.3)
Log volume (m^3/transect)	Cube root	**14.793**	**0.001**	0.24 (0.12)	0.79 (0.14)
Canopy density (%)		**2.447**	**0.131**	78.2 (2.5)	84.1 (2.8)

Table 4.3. The effect of thinning class (1-year, 6-year, or 11-year) on mean (SE) values of 27 habitat variables sampled within 17 precommercially thinned stands and 13 unthinned reference stands with a previous history of clearcutting followed by herbicide (Glyphosate) application in northern Maine. Non-transformed means and standard errors are presented for transformed variables. Comparisons yielding a calculated F-statistic ≥ 2.0 are depicted in bold.

Variable	Transformation	F	P	Thinning Class		
				1-year (n = 10)	6-year (n = 10)	11-year (n =10)
Average dbh of understory stems (cm)		**11.678**	**< 0.001**	3.9 (0.1)	3.0 (.1)	3.6 (0.15)
Height of understory stems (m)		**8.956**	**0.001**	3.9 (0.1)	3.2 (0.1)	3.8 (0.1)
Height to crown of understory stems (m)		1.135	0.338	1.3 (0.1)	1.1 (0.1)	1.3 (0.1)
Live crown ration of understory stems (value from 0-1.0)	Ln	0.155	0.857	0.66 (0.02)	0.65 (0.02)	0.65 (0.02)
Number of understory conifer stems (#/ha)	Ln	0.772	0.473	4632 (908)	4778 (908)	3448.8 (991)
Number of understory deciduous stems (#/ha)	Ln	**2.855**	**0.077**	1578 (526)	2773 (526)	1004 (574)
Total number of understory stems (#/ha)	Ln	**3.241**	**0.057**	6210 (910)	7551 (910)	4453 (993)
Stem cover units (#/ha)	Ln	1.849	0.179	15474 (2622)	17107 (2622)	11351 (2861)
Average dbh of overstory stems (cm)		**5.425**	**0.011**	10.5 (0.4)	11.4 (0.4)	12.4 (0.4)
Height of overstory stems (m)		**13.314**	**< 0.001**	7.4 (0.2)	7.9 (0.2)	9.0 (0.2)
Height to crown of overstory stems (m)		1.423	0.261	1.4 (0.2)	1.3 (0.2)	1.7 (0.2)
Live crown ratio of overstory (value from 0-1.0)		0.978	0.391	0.81 (0.02)	0.84 (0.02)	0.80 (0.02)
Number of overstory conifer stems (#/ha)		1.911	0.17	1348 (126)	1102 (126)	1452 (138)
Number of overstory deciduous stems (#/ha)	Ln	1.854	0.178	129 (47.5)	72 (48)	137 (52)
Total number of overstory stems (#/ha)		**2.416**	**0.111**	1477 (134.2)	1174 (134)	1589 (147)
Number of coniferous regenerating stems (#/ha)		0.699	0.507	332 (90)	408 (90)	250 (98)
Number of deciduous regenerating stems (#/ha)		0.517	0.603	722 (119)	625 (119)	544 (130)
Total number of regenerating stems (#/ha)		1.07	0.359	1054 (131)	1033 (131)	795 (143)
Total number of stems (#/ha)	Ln	**2.642**	**0.092**	8741 (940)	9758 (940)	6837 (1026)
Percent ground cover of grass and forbs (%)	Square root	**2.317**	**0.12**	2 (1)	5 (1)	3 (2)
Percent ground cover of rock (%)	Ln	0.055	0.947	1 (1)	0 (1)	1 (1)
Percent ground cover of litter (%)		1.971	0.161	65 (4)	61 (4)	72 (4)
Percent ground cover of other herbaceous vegetation (%)		**3.076**	**0.065**	13 (2)	16 (2)	8 (2)
Horizontal vegetation distance (m)		1.811	0.185	8.6 (0.6)	8.2 (0.6)	9.7 (0.6)
Number of logs (#/transect)	Ln	**2.389**	**0.113**	2.9 (0.4)	2.8 (0.4)	2.0 (0.4)
Log volume (m^3/transect)	Cube Root	**2.362**	**0.116**	0.79 (0.15)	0.48 (0.15)	0.27 (0.16)
Canopy density (%)		0.588	0.563	78.8 (3.2)	80.7 (3.2)	83.9 (3.4)

the greatest total number of overstory stems in the 11-year stands. Measures of logs were greater in the 1-year thinning class than the 11-year thinning class ($P < 0.10$) and herbaceous vegetation other than grass and forbs was greatest in 6-year stands.

Four variables, the average dbh of understory stems, the number of deciduous understory stems, the live crown ration of understory stems, and the number of coniferous regenerating stems had significant (F-statistics > 2.0) treatment × stand-thinning interactions. This study was not designed with adequate sample sizes to describe the complex interactions between treatment and thinning class; therefore, variables with significant interaction terms were excluded from PCA models.

Principal components analysis

Three principal components described 83.2 % of the variability of the habitat data between thinned and unthinned stands (Table 4.4). The first Principal component (PC1) in this analysis included positively loaded variables that described the density of the understory and downed woody structure and negatively loaded variables that were associated with sparse understory cover (labeled "near-ground cover"). PC2 included positively loaded variables (> 0.60) that described overstory structure and cover (labeled "overhead cover"). The third principal component (labeled "understory structure") was positively associated with understory height and the dbh of the understory. Principal components 4 – 14 had eigenvalues < 1.0 and contributed little (< 18 % of variation Ordination diagrams for this analysis portrayed that the greatest differences in forest structure between thinned and unthinned stands occurred with near-ground cover, and greater similarity between treatments was evident with overhead cover and understory structure (Figure 4.1).

Table. 4.4. Loadings of stand-scale habitat variables that separated thinned and unthinned regenerating conifer stands (n = 30) into 3 principal components after varimax rotation. Habitat variables were sampled within 30 forest stands (17 precommercially thinned, 13 unthinned) in northern Maine, June – August, 2001-2002.

Habitat variable	Principal Components		
	PC1 – Near-ground cover	PC2 – Overhead cover	PC3 – Understory structure
Stem cover units	0.9501	0.1601	0.1341
Understory stem density	0.9365	0.2437	-0.0484
Total stem density	0.9038	0.3738	0.0047
Understory conifer density	0.8590	0.1012	0.3369
Vegetation distance	-0.7927	-0.0662	-0.0240
Log volume/transect	0.7609	0.0421	0.1676
Logs/transect	0.7275	-0.0308	0.4158
Dbh of overstory	-0.6259	0.1790	-0.5515
Canopy density	0.0484	0.9409	-0.0022
LCR of understory	-0.3191	-0.8782	0.2001
Understory height to crown	0.3384	0.7741	0.4537
Overstory stem density	-0.1519	0.6624	0.5371
Dbh of understory	0.1007	-0.0584	0.9573
Height of understory	0.2932	0.3010	0.8360
Eigenvalue	6.9916	2.5319	2.1292
% Variance explained	41.4344	21.8761	19.9227

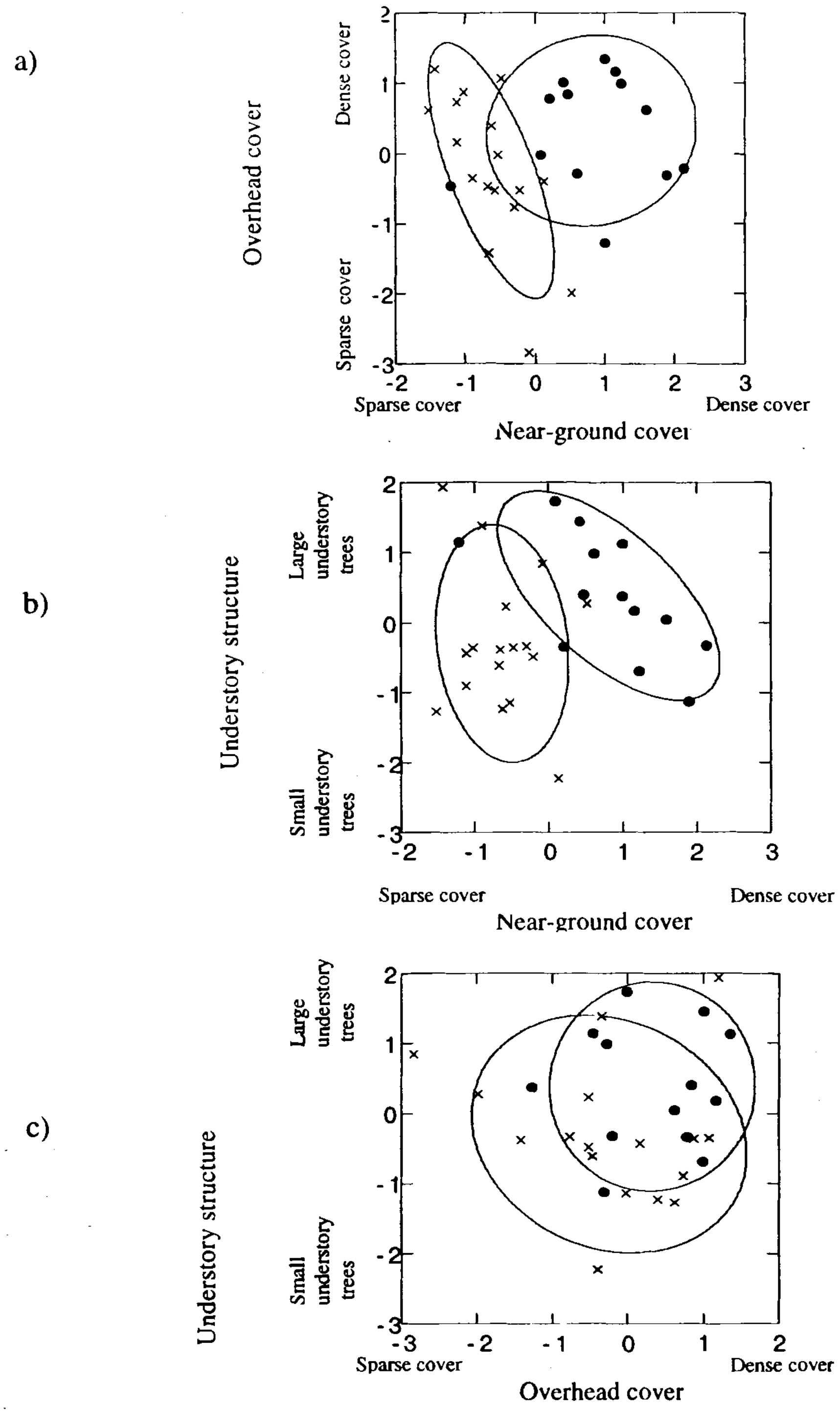

Figure 4.1. Ordination diagrams for 3 dominant (eigenvalue > 1.0) principal components describing the heterogeneity of stand-scale forest structure between 17 stands treated with PCT (x symbol) and 13 unthinned stands (• symbol). Gaussian confidence ellipses (P = 0.70) are shown centered around the sample means.

Three principal components also described the variation in habitat variables across the 3 thinning class intervals. The remaining 9 components cumulatively added 25% to the total explained variance and were not included in further discussion. Highly loaded variables onto the first principal component described vegetation characteristics associated with low-level horizontal structure (Table 4.5). PC1 (labeled "horizontal cover") included strong positive loadings from total stem density, the density of understory stems, and 2 measures of coarse woody debris (logs and log volume). The principal component with the second largest eigenvalue included large positive loadings for the average dbh of overstory trees, the density of deciduous trees in the understory, and overstory height (Table 4.5). Further, PC2 had strong negative loadings with the average dbh and height of the understory. This component described the relationship of forest structure between the overstory and understory (labeled "overstory to understory contrast"). Lastly, the component with the third largest eigenvalue described the presence of ground-level herbaceous vegetation (labeled "herbaceous vegetation gradient"). PC3 included positive associations with the density of overstory trees and strong negative loadings of the percent cover of other vegetation and grass and forbs. Ordination diagrams of the 3 principal components suggest that stands in the 1-year thinning class interval had more variable horizontal cover, overstory trees, and herbaceous vegetation than stands in the 6 or 11-year thinning class intervals (Figure 4.2). In each of the 3 diagrams, the 1-year stands overlapped older thinning classes, but the 6 and 11-years stands separated more distinctly from each other based on confidence ellipses of ordination scores.

Table. 4.5. Loadings of stand-scale habitat variables that separated regenerating conifer stands (n = 30) of 3 thinning classes (1-year, n = 10; 6-year, n = 10; 11-year, n = 10) into 3 principal components after varimax rotation. Habitat variables were sampled within 30 forest stands (17 precommercially thinned, 13 unthinned) in northern Maine, June – August, 2001-2002.

Habitat variable	Principal Components		
	PC1 – Horizontal cover	PC2 – Overstory to understory contrast	PC3 – Herbaceous vegetation gradient
Total stem density	0.9533	0.0440	0.1557
Understory stem density	0.9504	0.0557	0.0263
Log volume/transect	0.7645	-0.2318	-0.0142
Logs/transect	0.7580	-0.4352	0.0130
Dbh of overstory	-0.5306	0.7284	0.1173
Dbh of understory	0.0687	-0.8743	0.3173
Deciduous understory density	0.4824	0.6947	-0.0152
Height of overstory	-0.2810	0.6792	0.5253
Height of understory	0.3524	-0.6023	0.4960
Overstory stem density	0.0428	-0.1986	0.8335
% Other herbaceous vegetation	0.1541	-0.2207	-0.7193
% Grass and forbs	-0.2926	0.1843	-0.6023
Eigenvalue	4.5468	2.3199	2.1465
% Variance explained	31.7032	24.7673	18.6393

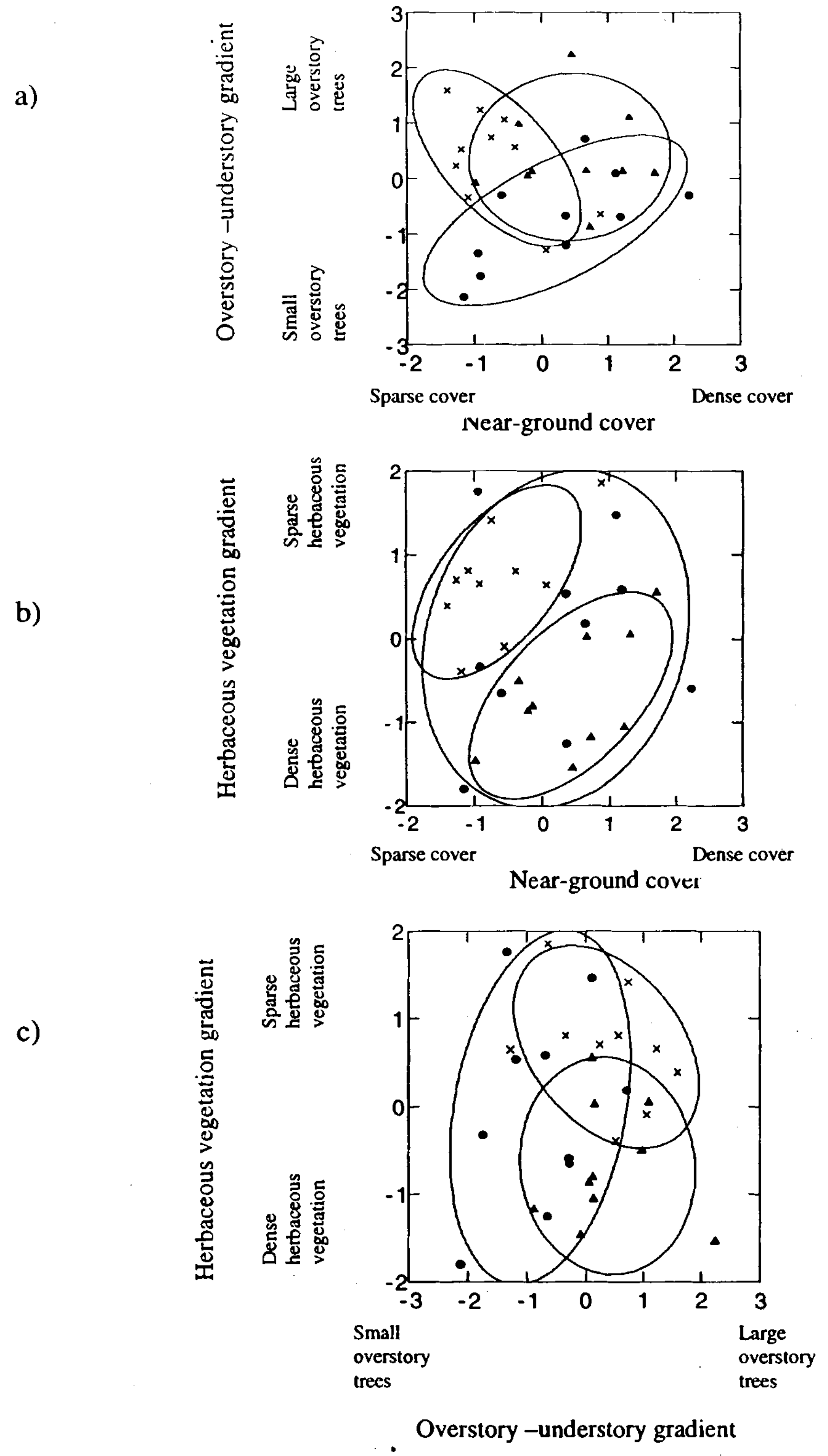

Figure 4.2. Ordination diagrams for 3 dominant (eigenvalue > 1.0) principal components describing the heterogeneity of stand-scale forest structure between stands of 3 thinning classes, including 1-year stands, n = 10 (• symbol); 6-year stands, n = 10 (▲ symbol); and 11-year stands, n = 10 (x symbol). Gaussian confidences ellipses are shown (P = 0.70) centered around sample means.

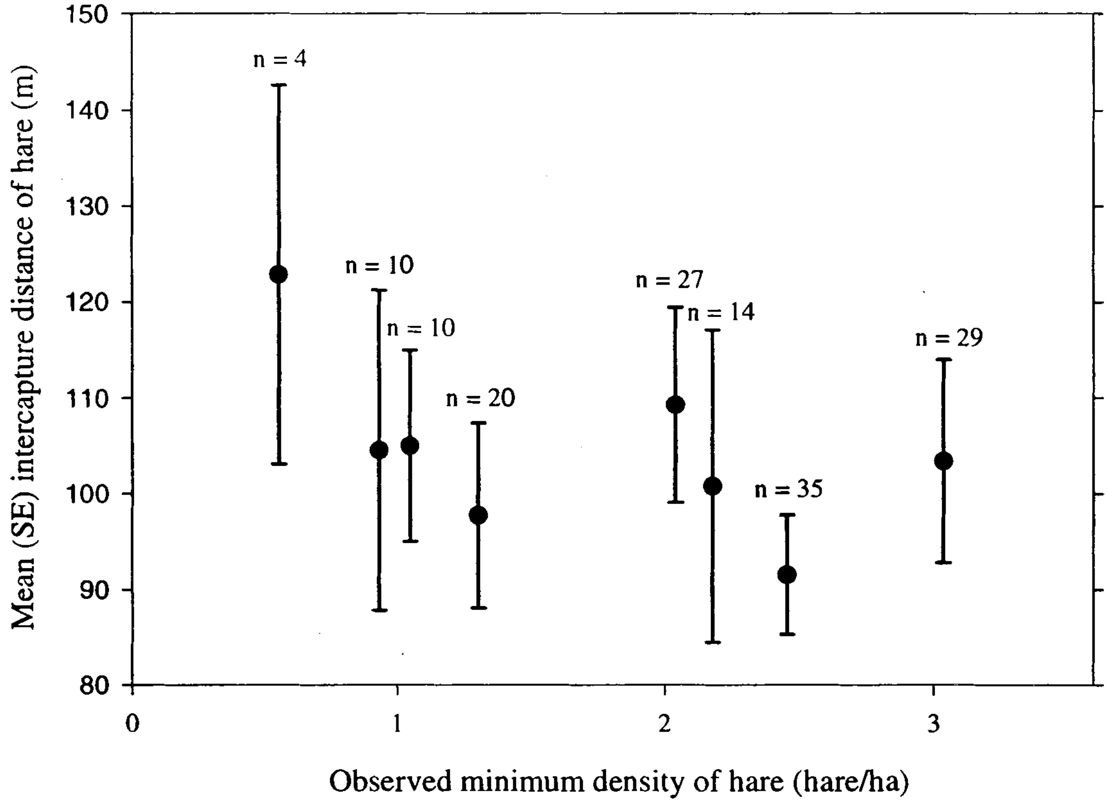

Figure 1.3. Relationship between mean inter-capture distance (SE) and density of snowshoe hare within 8 forest stands in north-central Maine, 2001-2002 (n = number of hares with > 1 capture). Inter-capture distance was defined as the average distance that hares (per stand) traveled between successive captures.

There was a positive relationship between pellets/ha/month and hares/ha ($r^2 = 0.89$, $n = 8$, $P < 0.001$) on my study sites in northern Maine (Figure 1.4). Errors were normally distributed (Lilliefors, $P = 0.225$) and variance was constant (Modified Levene's, $P = 0.718$). The relationship between hare densities appeared to be linear for densities ranging from 0.555 to 3.037 hares/ha in Maine. The slope of the line was 0.00008 with a standard error of 0.000011. The regression equation describing this relationship is:

$$\text{Hares/ha} = 0.281 + 0.00008\ (\text{pellets/ha/month}).$$

Recalculating the Long-Litvaitis relationship caused a small reduction of the slope, from 0.000116 (95% CI 0.000093, 0.000139) to 0.00010 (95% CI 0.000061, 0.000140); however, this relationship was still highly significant ($r^2 = 0.87$, $N = 8$, $P < 0.001$). The equation for this relationship is:

$$\text{Hares/ha} = 0.145 + 0.00010\ (\text{pellets/ha/month}).$$

Similar to previous studies conducted in northwestern Canada (Krebs et al. 2001b), western U.S.A. (Murray et al. 2002), and elsewhere in eastern and western Maine (Litvaitis et al. 1985, Long 1995), densities of hares were strongly correlated ($r = 0.94$) across a range (1,935-31,315 pellets/ha/month) of pellet densities in north-central Maine (Table 1.1). The model developed for northern Maine on my 8 study sites had the lowest AIC_c value ($\Delta AIC_c = 0.00$) and the Litvaitis-Long model also received support ($\Delta AIC_c = 2.77$), but these data did not support models developed outside of Maine ($\Delta AIC_c > 25.00$) (Table 1.1). Based on the Akaike weights, there was > 99% probability that the 2

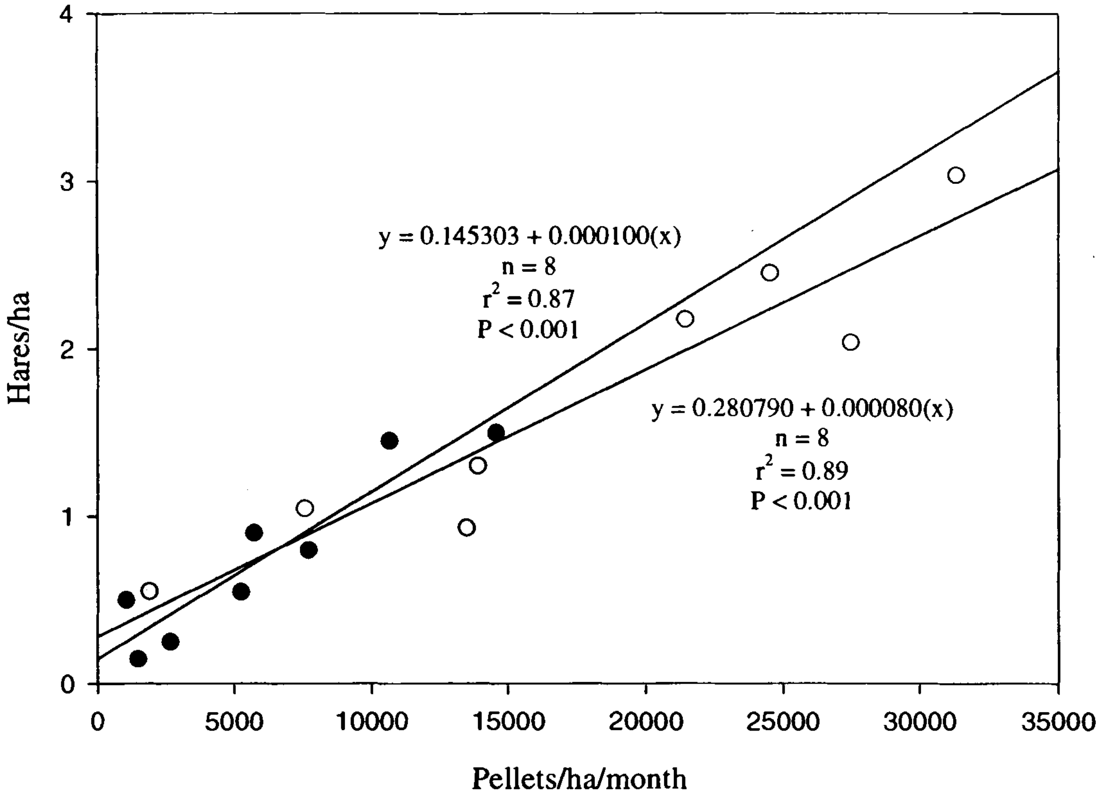

Figure 1.4. Relationships between density (hares/ha) of snowshoe hares and pellet density (pellets/ha/month) using mark-recapture estimates of hare densities as reported by Long 1995 (adapted and recalculated from Litvaitis et al. 1985) (closed circles) and minimum densities based on minimum number alive (open circles) in Maine. The model reported by Long (1995) was recalculated to avoid forcing the relationship through the origin.

Table 1.1. Reported correlation coefficients (r) and relative strength of evidence (Δ AIC$_c$, w_i) to support 4 area-specific predictive relationships of snowshoe hare densities from pellet densities based on pellet counts conducted in northern Maine, 2000-2002. The 4 predictive relationships are from northern Maine (this study), eastern and western Maine (Litvaitis et al. 1985, Long 1995), the Yukon Territory, Canada (Krebs et al. 2001), and Idaho (Murray et al. 2002).

Model	Region of study	Reported correlation coefficient (r)	K	AIC$_c$	Δ AIC$_c$	Akaike weights (w_i)
Homyack[a]	Northern Maine, USA	0.94	3	2.781	0.000	0.800
Litvaitis-Long[b]	Eastern & Western Maine, USA	0.93	3	5.551	2.770	0.200
Krebs et al. 2001a[c]	Yukon Territory, Canada	0.76	3	31.811	29.030	0.000
Murray et al. 2002[d]	Northern Idaho, USA	0.87	3	35.570	32.789	0.000

[a] Model given by: hares/ha = 0.281 + 0.000080(pellets/ha/month).

[b] Model given by: hares/ha = 0.145 + 0.00010(pellets/ha/month).

[c] Model given by: $\log_e$(hares/ha) = -1.203 + 0.899 $\log_e$(mean number of pellets/plot).

[d] Model give by: $\log_e$(mean number of hares) = 1.569 + 1.133 $\log_e$(mean number of pellets/plot).

models developed in Maine fit the data better than either of the models from the Yukon or Idaho.

DISCUSSION

Not surprisingly, the linear regression developed with the 8 data points from northern Maine was the strongest ($\Delta AIC_c = 0.00$) of the candidate model set, but the Litvaitis-Long model developed in Maine also described the data well. Models with a ΔAIC_c of ≤ 2 have substantial support, a $\Delta AIC_c > 3$ and < 7 have less support, and models with a $\Delta AIC_c > 10$ have virtually no support (Burnham and Anderson 2002). The Akaike weights (w_i) are conditional on both the data and *a priori* models and describe the approximate probability that a model is the "best" model (Anderson et al. 2000). If all models were similar and explained the hare density × pellet density relationship for northern Maine similarly, then all models would have had small Δ_i values and the Akaike weights would have been nearly equal. However, the regression model developed from this study received 0.80 of the model weight, and the remaining weight (0.20) was attributable to the Long-Litvaitis regression. Thus, predictive relationships of hare densities developed outside of Maine were not appropriate to explain the observed variation in these data.

The information-theoretic framework strongly advises towards biological significance trumping statistical significance. This approach does not rely heavily on arbitrary cutoffs to determine whether a model is "significant." Instead, the approach favors biological interpretation of results and only presents rough guidelines to gauge the appropriateness of a model (Burnham and Anderson 2002). Although these guidelines based on the relative strength of evidence and model weights (w_i) suggested that the site-specific regression developed for these data was the strongest model, I believe that the modified Litvaitis-Long model developed from data in eastern and western Maine should be considered the most biologically meaningful model. My goal was not to find the best fit for my data, but to determine a predictive relationship for future researchers to translate pellet densities into hare densities. Because of insufficient numbers of captures and recaptures of hares per sampling grids during my study, I was unable to obtain actual density estimates from multiple mark-recapture population models. Therefore, I used the minimum number of hares known alive within each stand (MNA) to derive my regression model for predicting hare densities. In contrast, Litvaitis (1990) captured a greater number of hares (496 hares 1,060 times) on larger trapping grids (49 ha) and was able to produce closed-capture population estimates for his grids; thus the Litvaitis-Long regression equation was based on estimates of actual densities. Therefore, I believe that equations that predict estimated densities of hares are superior to my conservative estimates of densities based on MNA.

Mark-recapture models take into account behavioral and temporal factors such as trap-happiness, trap shyness, and time dependent recapture rates to estimate the number of animals present in the population that were never captured (White et al. 1982). Thus, it is not surprising that a regression equation derived from mark-recapture population estimates did not receive most of the model weight when fit to observed MNA densities × pellet densities. However, the densities of hares estimated based on the modified Litvaitis-Long (1995) equation differed little from the MNA-based densities computed from live trapping data obtained from my 8 sites. Average hare densities predicted based on my regression equation averaged 2.5% lower than densities estimated based on the

Litvaitis-Long equation. The recalculated Long-Litvaitis equation predicted densities 0.22 (range –0.22 to 0.85) hares/ha greater than observed densities calculated based on MNA across my 8 stands in north-central Maine. The apparent repeatability of the separate experiments at different times, places, using different methods, and by different researchers suggests that there were not great differences between the 2 functional relationships (Johnson 1999). Further, Long and Litvaitis developed their linear regression using observed pellet densities that ranged from only 1,000–15,000 pellets/ha/month (0.15-1.50 hares/ha). Despite the limited range of data used to develop the model, it reasonably predicted hare densities from 1,000 to 31,000 pellets/ha/month during my study (0.15-3.04 hares/ha). Therefore, I considered the modified Litvaitis-Long equation have greater biological relevance than the other 3 models.

Although regression models developed outside of Maine were inferior for predicting hare densities on the 8 stands that I sampled, I also wished to estimate the effect size, or how poorly these models predicted hare densities in Maine. I used the 8 pellet densities from stands sampled during this study and the 8 pellet densities recorded for stands sampled in eastern and western Maine (Litvaitis et al.1985a) to predict hare densities using regression coefficients from the Yukon Territory, Canada (Krebs et al. 2001b) and Idaho (Murray et al. 2002). I then compared these estimates with hare densities predicted using the most biologically relevant model developed for Maine (i.e., modified Litvaitis-Long equation). Hare densities for the 16 sites from eastern, western, and northern Maine calculated using the regression model from the Yukon (Krebs et al. 2001b) were substantially lower than densities predicted by the regression model

Table 1.2. Comparison of predicted densities of snowshoe hares calculated from an equation developed in Maine with those predicted using reported relationships from the Yukon Territory, Canada (Krebs et al. 2001) and northern Idaho (Murray et al. 2002).

Predicted densities (hares/ha)[a]	Densities estimated with Krebs et al. 2001b equation (hares/ha)[b]	% Difference between predicted and Krebs et al. 2001	Densities estimated with Murray et al. 2002 (hares/ha)[c]	% Difference between predicted and Murray et al. 2002	Source of pellet densities
0.30	0.15	-49.29	0.08	-71.47	Litvaitis et al. 1985[c]
0.41	0.25	-39.06	0.16	-60.76	Litvaitis et al. 1985
0.25	0.11	-56.33	0.57	-77.34	Litvaitis et al. 1985
0.67	0.46	-31.29	0.35	-48.25	Litvaitis et al. 1985
0.92	0.65	-28.99	0.54	-41.50	Litvaitis et al. 1985
0.72	0.50	-30.62	0.38	-46.65	Litvaitis et al. 1985
1.21	0.87	-28.12	0.77	-36.10	Litvaitis et al. 1985
1.60	1.15	-28.04	1.10	-31.18	Litvaitis et al. 1985
2.29	1.63	-28.72	1.71	-25.38	This study
1.49	1.08	-27.98	1.01	-32.39	This study
0.90	0.64	-29.06	0.53	-41.80	This study
3.28	2.29	-30.00	2.62	-19.93	This study
0.34	0.19	-44.62	0.11	-66.96	This study
1.53	1.10	-28.01	1.05	-31.92	This study
2.89	2.04	-29.50	2.26	-21.79	This study
2.60	1.84	-29.12	1.99	-23.43	This study

[a] Hare densities were predicted with recalculated Long-Litvaitis equation, given by: hares/ha = 0.145303 + 0.0001 (pellets/ha/month)

[b] Relationship reported in Krebs et al. (2001) is given by: $\log_e$(hares/ha) = -1.203 + 0.899 $\log_e$(mean number of pellets/plot). Multiply final estimates by 1.567, a correction factor for the log-log relationship.

[c] Relationship reported in Murray et al. (2002) is given by: $\log_e$(mean number of hares) = 1.569 + 1.133 $\log_e$(mean number of pellets/plot). Multiply estimates by 1.41, a correction factor for the log-log relationship. Divide final estimates by 19 ha for a conservative density estimate. I did not add (1/6) to data as reported in Murray et al. (2002) because I found few zero pellets/plot.

[d] Litvaitis et al. (1985) estimated hares densities that were reported in Long (1995).

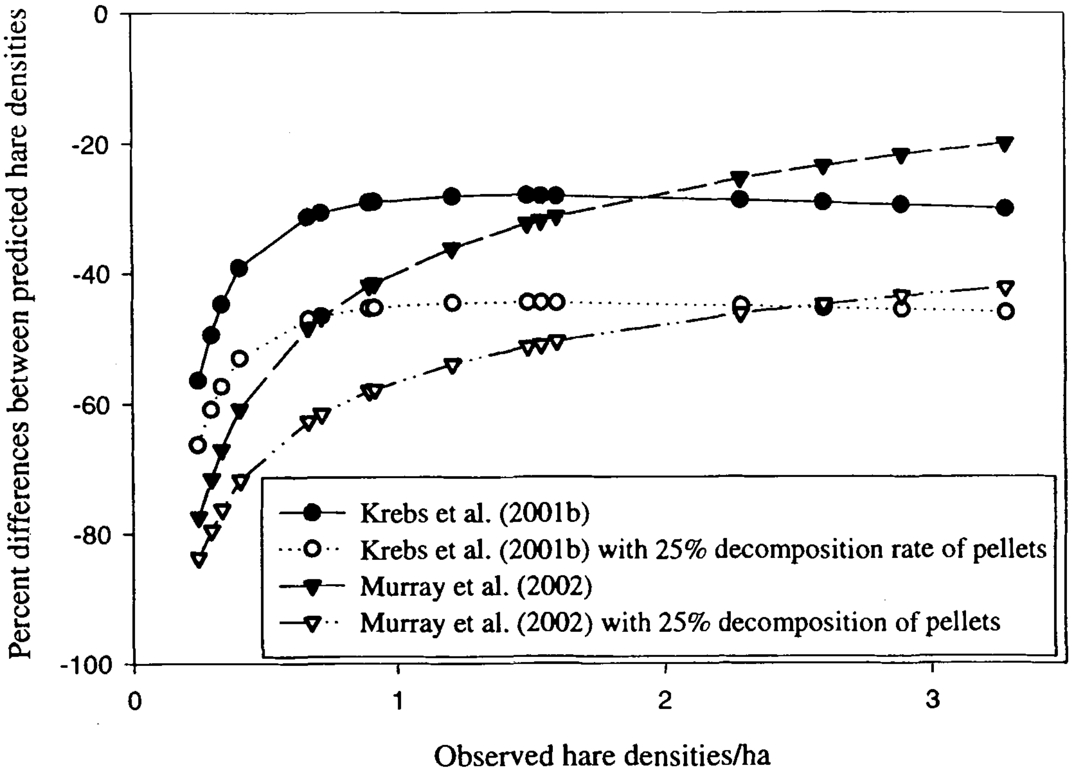

Figure 1.5. Percent difference between observed densities of snowshoe hares predicted using the best model from Maine (modified Litvaitis-Long equation) and densities predicted with models developed by Krebs et al (2001b) and Murray et al. (2002), with and without reducing pellet densities for decomposition. Pellet densities were based on 16 stands surveyed in Maine during 1981-83 (n = 8) and 2000-02 (n = 8). For open symbols, pellet densities were reduced by a decomposition rate of 25% to account for field observations of Murray et al. (2002).

developed for Maine (i.e., modified Long-Litvaitis equation, Table 1.2, Figure 1.5). The mean difference between densities estimated from the Maine versus the Yukon model was -0.40 hares/ha (95% CI -0.26 to -0.55). Similarly, densities predicted from regression coefficients for Idaho (Murray et al. 2002) were also less than predicted densities of hares for the 16 sites in Maine based on the modified Litvaitis-Long model (Table 1.2, Figure 1.5). The estimates for the Idaho model were lower by an average of -0.42 hares/ha (95% CI -0.34 to -0.50).

Geographic variation in relationships between densities of hares and pellets may result from variation in the number of pellets produced by snowshoe hares over time (Hodges 1999), and from differences in digestibility and chemical composition of primary foods (Sinclair et al. 1988). Thus, regional differences in diet quality of hares and species composition of available browse may impair estimates of density based on pellet x density relationships developed in other ecoregions. For example, wild-caught snowshoe hares from the Yukon Territory produced a greater number of pellets/day than captive hares in Vancouver, British Columbia fed similar diets (Hodges 1999). Further, cottontail rabbits (*Sylvilagus floridanus*) fed similar diets had large variation in daily numbers of pellets produced among individuals that was not explained by sex or size of rabbits (Cochran and Stains 1961). Pellet production rate is inversely related to the quality of food eaten, so that lagomorphs eating higher quality forage produce fewer pellets (Arnold and Reynolds 1943, Sinclair et al. 1988, Cochran and Stains 1961). Available forage for hares in Maine may have higher average digestibility than that of northwestern Canada and northern Idaho, which might account for a smaller number of pellets produced per hare per unit of time.

Diets of hares during the leaf-off season are dominated by low-quality woody browse and conifer needles, while in the summer, diets change dramatically to consist of herbaceous vegetation of with low fiber content (Wolff 1978, Larter 1999). Murray et al. (2002) suggested that pellets produced from higher-quality foods deposited during the leaf-on season may degrade more quickly than the larger and more fibrous pellets deposited during winter. Cochran and Stains (1961) reported that cottontail rabbit pellets produced from a high-quality commercial food decayed faster than pellets produced from low-quality diet of sumac (*Rhus spp.*). I noticed obvious differences in pellet size and color between seasons, with leaf-on pellets being smaller in size and darker in color. Both Krebs et al. (2001b) and Murray et al. (2002) only counted pellets once yearly during late spring (i.e. annual estimate of density), whereas I cleared pellets from plots in fall and counted pellets in spring (i.e. winter estimate of density). Persistence of pellets may have been greater for the larger, lighter-colored and more fibrous pellets deposited by hares during the leaf-off season, and annual estimates of density conducted in spring may have occurred after pellets from the leaf-on season had weathered and decayed. Failure to count some pellets deposited by hares during leaf-on season because of decomposition may explain discrepancies among relationships of densities of pellets and hares.

Others have raised concerns about potentially large biases arising from variations in pellet deposition rates caused by seasonal variation in forage quality and losses of pellets to decomposition (Orr and Dodds 1982, Angerbjorn 1983, Murray 2002). Murray et al. (2002) was unable to detect a difference in persistence of snowshoe hare pellets between recent clearcuts and mature forest, but Angerbjorn (1983) reported that pellets deposited by mountain hares (*Lepus timidus*) decayed more quickly in grass than other cover types and Cochran and Stains (1961) suggested that decomposition of pellets varies with cover type, food quality and weather. I avoided confounding seasonal effects of deposition and decomposition rates by calculating the relationship of snowshoe hare pellets deposited during the leaf-off season (Oct.–May) to densities of adult hares surviving the following May-June. Average monthly temperatures in northern Maine during this period ranged from only -10.17 to 13.33° C (National Oceanic and Atmospheric Administration 2000, 2001, 2002), which would slow decomposition of pellets.

It is unlikely that pellets would decompose during 8-9 months of cool and subfreezing temperatures during the leaf-off season throughout most of the geographic range of hares. Pellets from cottontail rabbits decomposed quickly during the summer months, but most persisted through winter in Illinois (Cochran and Stains 1961). Thus, if decomposition did occur, weathering would most likely affect pellets deposited by hares during leaf-on seasons (June–September). Murray et al. (2002) reported that only 75% of fresh pellets ($n = 540$ pellets) placed on plots survived an entire year in Idaho, suggesting that decomposition may reduce pellet densities in a year or less. To examine this hypothesis further, I compared predicted hare densities in Maine to those predicted by Krebs et al. (2001b) and Murray et al. (2002) after pellet densities were reduced by the 25% decomposition rate. Accounting for decomposition of hare pellets in Maine did not explain the underestimation of hare numbers by regressions outside of Maine ($P < 0.001$); in fact, a 75% persistence rate widened the gap between observed and predicted densities, but still in a nonlinear fashion (Figure 1. 5). These results indicate that decomposition of hare pellets does not explain the discrepancy between observed hare densities in Maine and densities predicted using regressions from the western United States and Canada.

Although decomposition of pellets may not explain geographic variation in predicted hare densities, there are still biologically important reasons to survey seasonal pellet densities rather than annual counts. Association of leaf-off season pellet densities with densities of hares during early spring should be conservative because spring corresponds with the fewest hares. I excluded leverets in density estimates so that all marked individuals were > 8 months in age. Snowshoe hares select cover types based on understory cover in winter, but in summer occupy open habitats with more herbaceous vegetation (Wolff 1980, O'Donoghue 1983). Seasonal changes in habitat use by hares coupled with variation in pellet deposition rates caused by forage of different quality, may confound estimates of pellet densities based on annual counts. Further, winter is thought to be the limiting season for snowshoe hares (Pease et a. 1979, Pietz and Tester 1983) and estimates of densities of adult hares surviving at the end of the critical limiting season may more accurately depict differences in habitat quality by incorporating aspects of population performance such as over-winter survival (Van Horne 1983).

Whereas MNA densities of snowshoe hare from northern Maine were strongly correlated ($r = 0.94$) to pellet densities from the previous leaf-off season, leaf-on season pellet densities explained considerably less ($r = 0.65$) variation in numbers of hares. The weaker relationship between leaf-on season (June-September) pellet densities and number of hares residing in stands in early spring (May-June) suggests that counts of pellets that include the summer months, when hares are more like habitat generalists (Wolff 1980, O'Donoghue 1983) and forage primarily on herbaceous vegetation (Wolff

1978, Larter 1999), produce more variable predictions of hare densities than leaf-off season counts. Therefore, I suggest that counts of pellets during leaf-off seasons be used to predict densities of hares to avoid these potential biases and produce more biologically meaningful estimates of hare numbers.

Krebs et al. (2001b) and Murray et al. (2002) reported that a $\log_e$-$\log_e$ relationship best fit their data because variances increased with the observed mean number of both pellets and hares. I hypothesized several explanations for why a log-log relationship was needed to describe pellet densities as a function of hare density for data from northern Canada and the western United States, but not Maine. First, variances may have increased with the mean in northern Canada when densities changed significantly within a year. It is well documented that hares undergo dramatic population cycles in northern Canada and densities can widely fluctuate, even within a year (Hodges 2000). Krebs et al. (2001b) only counted pellets once yearly and related those pellet densities to hare densities estimated from live trapping that began the previous year. Or, perhaps data sets for my model and the modified Litvaitis-Long model were too small and had little power to detect heteroscedasticity (Krebs et al. 2001b, $n = 85$; Murray et al. 2002, $n = 24$; Long 1995, $n = 8$; this study, $n = 8$). To ensure that a $\log_e$-$\log_e$ relationship was not a better fit to my data than the 4 *a priori* models, I computed the AIC_c for a model with my 8 MNA hare density × pellet density points from northern Maine with the predictor and response variables $\log_e$ transformed. This model was added after my *a priori* models were developed; therefore interpretation of this model can only be considered exploratory (Burnham and Anderson 2002). The $\log_e - \log_e$ model developed for northern Maine ($\Delta AIC_c = 4.704$) received less support than the other models from Maine (Table 1.1).

Further, the recalculated Akaike model weights (w_i) from greatest to smallest were as follows: the linear model from northern Maine ($w_i = 0.743$), the Litvaitis-Long model from eastern and western Maine ($w_i = 0.186$), the $\log_e - \log_e$ model developed for northern Maine ($w_i = 0.071$), the Krebs et al. (2001b) model from western Canada ($w_i < 0.001$), and the Murray et al. (2002) model from Idaho ($w_i < 0.001$). The approximately 2.6× more weight given to the linear model from eastern and western Maine than the post hoc $\log_e - \log_e$ model developed for northern Maine indicate that the hare density × pellet density relationship for northern Maine was better fit by a linear function than a log-normal function.

CONCLUSIONS

Although a functional relationship between pellet densities and densities of hares was established in the Yukon Territory, Canada, the relationship may differ for hares near the southern periphery of their range. Observed relationships of pellet × hare density during 2000-2002 in northern Maine were similar to relationships observed in 1981-1983 for eastern and western Maine. Thus, the linear relationship between densities of pellets and hares may be stable through time and across a range of habitat types in the eastern spruce-fir, northern hardwood forests, and within a range of 0-3 hares/ha. My estimated relationship between MNA density and pellet density was consistent with a previously derived relationship for Maine; however hare densities estimated using regression equations developed for the Yukon Territory, Canada (Krebs et al. 2001b) and northern Idaho (Murray et al. 2002) underestimated predicted densities for north-central, eastern, and western Maine.

I suggest that densities of snowshoe hares in northeastern North America be estimated from pellet counts using the modified linear regression (i.e. not forced through the origin) model derived by Long (1995) which was adapted from data collected by Litvaitis et al. (1985) for eastern and western Maine. Previous investigators conducted yearly pellets counts (Krebs et al. 2001b, Murray et al. 2002); however, densities of hares estimated based on pellets deposited during the leaf-off season may be more biologically meaningful and might avoid potential biases arising from the dynamic summer-winter diets of hares, differential losses of pellets to decomposition during summer and winter months, and to seasonal shifts in habitat use by hares.

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CHAPTER 2

TEMPORAL EFFECTS OF PRECOMMERCIAL THINNING ON SNOWSHOE HARES IN MAINE

ABSTRACT

Snowshoe hares (*Lepus americanus*) are an important prey species and dominant herbivore across much of their North American range, and forestry practices that degrade habitat for hare may have community-wide effects. Further, the effects of precommercial thinning (PCT) on hares have been questioned in relation to indirect effects on recovery of the Federally threatened Canada lynx (*Lynx canadensis*). I examined the effects of PCT on snowshoe hares, from 1-11 years post-treatment in the commercial forests of northern Maine. I established > 46 km of pellet transect across 13 unthinned, regenerating conifer stands, and 17 regenerating conifer stands treated with PCT. Hare pellets were counted and cleared along transects twice a year during 2001 and 2002, and stand-level vegetation characteristics previously documented as correlates with hare density were measured in all stands. Densities of snowshoe hares were consistently lower in stands treated with PCT than in similar unthinned stands across all thinning classes and seasons during both years of the study ($P < 0.10$). Stands treated with PCT supported hare densities approximately ½ those observed in untreated stands when averaged across seasons and 2 years of sampling. In general, hare density was greatest in stands in the 1-year thinning class when compared to 6 and 11-year thinning classes, but a statistical difference ($P < 0.10$) among thinning classes was evident only during leaf-off seasons. Several habitat characteristics previously reported to be important positive correlates of hare densities, such as understory stem densities and horizontal cover, were

lower in thinned versus unthinned stands. PCT was associated with densities of snowshoe hare that were lower than those in similar unthinned stands; however, thinned stands may retain densities of hares greater than stands managed using other forest harvesting regimes (e.g., some types of partial harvests).

INTRODUCTION

In March 2000, the U.S. Fish and Wildlife Service (USFWS) listed Canada lynx as threatened under the Endangered Species Act (ESA) (United States Department of the Interior 2000). Lynx are specialized predators (O'Donoghue et al. 1998) of snowshoe hares and density of hares is positively and exponentially associated with stands with high densities of conifer saplings (Litvaitis et al. 1985a). Maine has the only verified population of resident lynx in the northeastern USA and the relationships among lynx, habitat, and forestry practices are not thoroughly understood (Aubry et al. 2000). At a statewide scale, large areas of regenerating conifer stands are a habitat variable that is positively associated with both occurrence of lynx and relative abundance of snowshoe hares in Maine (Hoving 2001). Thus, extensive areas of regenerating forest may promote persistence of the only verified population of lynx in the northeastern USA. However, little is known about the temporal effects of stand succession on densities of snowshoe hare at the southern periphery of their range, particularly after intensive management of vegetation.

Thirteen environmental organizations, including Defenders of Wildlife and the Biodiversity Legal Foundation, legally challenged the ESA listing of lynx as threatened in the contiguous United States. They alleged that the listing of lynx as endangered and designation of critical habitat was necessary to ensure survival and recovery. If USFWS designates critical habitat, it is likely, because lynx are strongly tied to high densities of hares (O'Donoghue et al. 1998, Mowat et al. 2000), that foraging habitat will be designated as "critical." Because large areas of regenerating conifers are known to support high densities of snowshoe hares, forestry practices that degrade habitat for hares may be questioned under ESA.

Precommercial thinning (PCT) is a silvicultural technique that decreases stem density and may reduce densities of hares relative to unthinned, regenerating stands (Sullivan and Sullivan 1988). Further, the biological assessment of the effects of U.S. National Forest land and resource management plans on Canada lynx suggested that forest thinning might reduce foraging habitat of lynx in the northeastern USA (Hickenbottom et al. 1999). During 1993 to 2001, greater than 67,000 ha (167,000 acres) of forest were precommercially thinned in Maine (Maine Forest Service 1994-2002). Because total acreage of PCT is projected to increase, forest managers will be asked to justify this practice based on maintaining wildlife habitat and biodiversity.

Limited information about the effects of precommercial thinning on snowshoe hares has indicated that thinning reduces density of hare for 3-4 years after treatment (Sullivan and Sullivan 1988), but how long after treatment abundances of snowshoe hares continue to be lower relative to unthinned stands is unknown. It is also unknown how the acceleration of stand development associated with PCT affects snowshoe hares compared to untreated stands. Further, previous studies of hares and thinning included non-herbicided stands that were released with brushsaws (Sullivan and Sullivan 1988, de Bellefeuille et al. 2001). In Maine, stands treated with PCT are first aerially sprayed with herbicides (e.g., Glyphosate or Triclopyr) and later manually thinned; the combination of these treatments may have different effects on densities of hares than in stands treated solely with brushsaws.

Investigators have consistently related high densities and relative abundances of snowshoe hares to mid-successional habitats with high stem densities of saplings (Wolff 1980, O'Donoghue 1983, Pietz and Tester 1983, Litvaitis et al. 1985a, Litvaitis et al. 1990, Koehler 1990, Fuller 1999, Hoving 2001). Thus, it would be expected that a forest practice that decreases the stem density of regenerating forest stands and promotes rapid growth of crop trees would decrease densities of snowshoe hare. Therefore, I hypothesized that PCT would reduce snowshoe hare densities relative to similar untreated stands, and that these changes would be related to reduced densities of coniferous and deciduous stems.

The objectives of this study were to: 1) determine if precommercial thinning with brush-saws decreases abundances of snowshoe hare on herbicide treated clearcuts, from 1-11 years post-treatment; 2) determine the magnitude of differences in hare densities between unthinned and PCT stands; and 3) describe the differences in vegetation characteristics preferred by hares between thinned and unthinned clearcut stands from 1–11 years after treatment.

STUDY AREA

I selected 6 townships (Hersey, T4 R 11 WELS, T 5 R 11 WELS, T4 R 12 WELS, T1 R 13 WELS, and Spencer Bay) in the commercial forests of northern Maine that fall within the historical distribution of Canada lynx (Hoving 2001) as my study area (Figure 2.1). Hersey Township is located in Aroostook County, Maine whereas the other

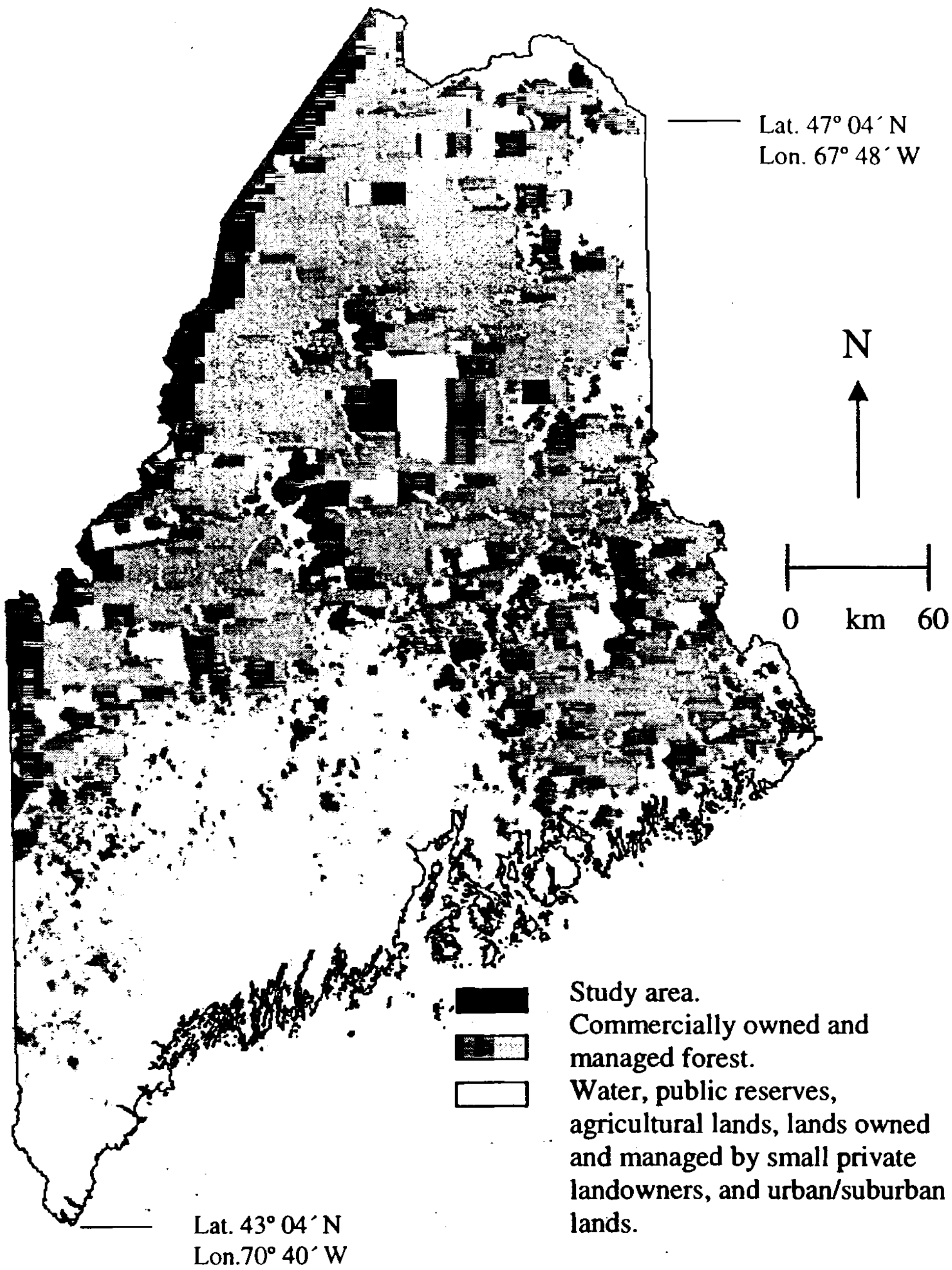

Figure 2.1. Location of study areas within 6 townships in the commercially owned and managed forests of north-central Maine.

5 townships are located in Piscataquis County, Maine. These towns range from 102 km east to west and from 49 km north to south. Great Northern Paper Company, Millinocket, Maine; Plum Creek Timber Company, Fairfield, Maine; and International Paper Company, Costigan, Maine managed the study areas for pulp and sawtimber production.

The study areas occur within the ecotone between the northern boreal forest and the eastern deciduous forest that is referred to as the sub-boreal Acadian forest (Seymour and Hunter 1992). Balsam fir (*Abies balsamea*) and spruce (*Picea spp.*) dominate the study sites, but stands also have minor components of white pine (*Pinus strobes*), northern white cedar (*Thuja occidentalis*), larch (*Larix laricina*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), paper birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*). The annual mean temperature in this region was 3.78 °C and the area received an average of 101 cm of precipitation annually, with 276 cm of snowfall (Garoogian 2000). Stands (n = 30) surveyed on the study areas were chosen based on flat to gently sloping topography, and ranged from 8.5 to 74.3 ha in size (Median = 22.2 ha).

METHODS

I examined site quality, tree density, diameter breast height (dbh) of dominant trees, and size and spatial independence of stands before selecting them as study sites. I estimated site quality of stands with 4 to 6 soil cores taken throughout the stand with a soil auger. Stands were assigned a drainage value from 1 (highly productive) to 5 (unproductive) according to Brigg's (1994) scale of forest tree productivity.

Treatment stands were clearcut (timber harvesting resulting in residual basal area of acceptable growing stock trees > 11.43 cm dbh of < 20.66 m^2/ ha) 1968-1982, aerially herbicided (e.g. Glyphosate at ≈ 1.68 kg/ha acid equivalent) 1982-1988, and precommercially thinned with motor-manual brush-saws from 1989-1999. Unthinned stands were clearcut 1974-1982 and herbicided (e.g. Glyphosate at ≈ 1.68 kg/ha acid equivalent) 1982-1988 (Table 2.1). Stands were divided into blocks based on date of precommercial thinning. The study design included 17 treatment stands at 5-year intervals since thinning (1-2 year post-thinning, n = 5; 6-7 years, n = 5; 11-12 years, n = 7) and 13 stands with management histories and site quality similar to treated stands, but that were not thinned (1-2 year, n = 5; 6-7 years, n =5; 11-12 years, n = 3). I allowed some latitude (1-2 years) in separating stands into thinning class categories based on the date of silvicultural treatments. When selecting study sites, I paired a treatment stand with an unthinned stand with a similar year of clearcut, year of herbicide, and site quality to avoid any large differences between treatment and unthinned stands within a thinning class. This was a retrospective study; therefore stands were not paired in a statistical sense and were analyzed as unpaired replicates.

Pellet counts

Fecal pellet counts can be a reliable estimate of snowshoe hare abundance (Krebs et al. 1987, Long 1995, Krebs et al. 2001, Murray et al. 2002, Chapter 1) and are more practical than live-trapping over large areas because indirect estimates of abundance are more economical and less labor intensive than typical mark-recapture techniques (Litvaitis et al. 1985b). I established 46.68 km of pellet transect across the 30 stands. The stand was considered the unit of replication because the median stands size was 3.6 ×

Table 2.1. Stand history, location, and site quality of 17 PCT and 13 unthinned stands in northern Maine. (T = stand treated with PCT, C = unthinned stand). Site quality ranged from 1 (well drained, productive) to 5 (poorly drained, unproductive) according to Briggs (1994) classification guidelines.

Site number	Year of Clearcut	Year of Herbicide	Year of PCT	Township	Site Quality
1-1-T	1982	1988	1999	T 4 R 11	4+
1-2-T	1980	1983	1999	T4 R 12	3-
1-3-T	1977	1983	1999	T4 R 11	4+
1-4-T	1982	1988	1999	T4 R 11	4
1-5-T	1976	1983	1999	T4 R 12	4
6-1-T	1979	1988	1994	Hersey	3+
6-2-T	1979	1988	1994	Hersey	2-
6-4-T	1974	1982	1994	T 5 R 11	3-
6-5-T	1976	1985	1995	T 5 R 11	3-
6-6-T	1979	1982	1994	T 5 R 11	3-
11-1-T	1975	1983	1989	T 1 R 13	3
11-2-T	1968	1987	1990	Spencer Bay	3-
11-3-T	1975	1983	1989	T 1 R 13	2-
11-4-T	1975	1986	1990	T 1 R 13	3
11-5-T	1975	1983	1989	T 1 R 13	2
11-6-T	1975	1984	1991	T 1 R 13	2-
11-7-T	1975	1986	1989	Spencer Bay	2-
1-1-C	1982	1988	n/a	T 4 R 11	4
1-2-C	1979	1983	n/a	T 4 R 11	3-
1-3-C	1981	1984	n/a	T 4 R 11	4+
1-4-C	1983	1988	n/a	T 5 R 11	4+
1-5-C	1976	1985	n/a	T 4 R 11	3-
6-1-C	1979	1988	n/a	Hersey	3+
6-2-C	1981	1988	n/a	Hersey	3+
6-4-C	1974	1982	n/a	T 5 R 11	4
6-5-C	1974	1985	n/a	T 4 R 12	3
6-6-C	1976	1983	n/a	T 4 R 11	4
11-1-C	1976	1982	n/a	T 5 R 11	3
11-3-C	1976	1982	n/a	T 5 R 11	3+
11-4-C	1974	1985	n/a	T 5 R 11	3

greater than the average home range size of hares in Maine (Litvaitis 1984). I established 1.6 km of transect in 28 stands and the remaining two stands had 1.18 km and 1.34 km of transect resulting from their size and irregular shape. I placed transects greater than 50 m from stand boundaries to minimize edge-effects (Harris 1988, Fraver 1994). When possible, I established 4 parallel, 400 m transects in a stand and separated transects by 65 m. I marked 5m by 30 cm pellet plots at 20 m intervals along transects for a total of 84 plots per stand and a total of 2,480 pellet plots for the study. I randomly oriented pellet plots along transects and marked them with orange wooden stakes at either end of the plot.

I cleared all plots of hare pellets during October 18-25, 2000 so that only pellets deposited after leaf-off were counted during spring 2001. Subsequently, I counted and cleared pellets 4 times during the remainder of the study: May 17-June 14, 2001, September 13-29, 2001, and May 10-June 17, 2002, and September, 13-October 13, 2002. I averaged the number of pellets/plot for each stand and converted it to a value of pellets/ha/day. I divided the year into 2 seasons, leaf-off season and leaf-on season. Thus, spring pellet counts (May-June) were used to estimate abundance during the previous winter (defined as leaf-off season, October-May) whereas fall pellet counts (September-October) were used to estimate abundance during the previous summer (defined as leaf-on season, June-September).

Live-trapping

I live-trapped hares within the core portions of 2 thinned stands and 2 untreated stands during May-June, 2001 and in 2 different thinned and 2 different untreated stands during May-June 2002 to evaluate the relationship between pellet densities and estimated densities of snowshoe hares. I also evaluated whether there were any differences in sex ratios or lactation rates among stands treated with PCT and unthinned stands. Greater densities of animals in a particular cover type may not necessarily indicate higher habitat quality (Lidicker 1975, Van Horne 1983); thus, I examined the sex ratios and lactation rates as additional indicators of the habitat quality for hares in thinned and unthinned stands. Chapter 1 provides a detailed description of methods used to trap, mark, sex, and determine lactation status of hares.

Habitat sampling

Across their geographical range, snowshoe hares respond numerically to stand structure and densities of hares are consistently related to a few key stand-level habitat characteristics, including positive associations with understory stem density (O'Donoghue 1983, Sullivan and Sullivan 1988, Litvaitis et al.1985a, Monthey 1986, Koehler and Brittell 1990, Long 1995, Fuller 1999), woody debris (Conroy et al. 1979, Scott and Yanhner 1989, Ferron et al. 1998), and horizontal vegetation density (Wolfe et al. 1982, Pietz and Tester 1983, de Bellefeuille et al. 2001, Wirsing et al. 2002). Therefore, differences among stand structure between PCT and untreated stands (low hare-density and high hare-density stands) may explain some variation in hare numbers among my study sites in northern Maine.

I selected 6 forest structural variables *a priori* based on previous studies of habitat relationships of snowshoe hares, including measures of overstory, understory, woody debris, and horizontal cover. I measured those stand-scale habitat characteristics on fixed area nested plots placed along the pellet transects. Five plots per 400 m of transect were established at random distances on the pellet transects for a total of 20 plots per stand. I measured vegetation within 25 m^2 plots in thinned stands and within 10 m^2 plots in unthinned stands. Larger plots were established on thinned stands because stem density was reduced in these stands, and I wished to sample approximately 100 crop trees per stand.

I quantified the number of coniferous trees (≥ 7.6 cm dbh, >1 m height, alive) within the plot and measured the number and type (coniferous or deciduous) of all understory stems (< 7.6 cm dbh, >1 m height, alive) within the plot. I quantified the number of stem cover units ((3 × number of understory conifer stems) + number of understory deciduous stems) (Litvaitis et al. 1985a) per/ha. Horizontal vegetation structure was measured as a continuous variable using a 2.0 m cover pole with alternating 0.1 m red and white bands (Griffith and Youtie 1988). Visual obstruction was measured in opposite directions from the center point following a random compass bearing. The distance from the center point where ≥ 25% of all bands were visually obstructed was recorded. I estimated the volume of downed logs with a modified version of the planar intersection method used by Payer and Harrison (2000). I established a 20-m randomly oriented transect with the midpoint at each sampling station and quantified the number of logs that crossed the transect and were ≥ 1.0 m length, ≥ 7.6 cm diameter (at the point of intersection), and ≤ 45° from the ground. I considered only sound to moderately decayed logs, so that extremely decayed logs were excluded from sampling. I also measured overhead canopy cover with a spherical densiometer (Lemmon 1956) to simulate the cover perceived by hares during the winter on top of snowpack. Four readings in the 4 cardinal compass directions at 1.0 m height were taken at the center of each plot and averaged to a single value for each plot.

Statistical analyses

I examined pellet densities separately during leaf-off and leaf-on seasons to avoid confounding effects of seasonal change in diets and shifts in habitat use that might contribute to variation in pellet deposition rates by hares. I conducted a repeated measures two-way Analysis of Variance (ANOVA) for the observed densities of pellets during the leaf-off season to determine if there were any differences among thinning classes (1, 6, 11 years since treatment), treatment (stands treated with PCT, unthinned stands), year of sampling (2000-2001 leaf-off season, 2001-2002 leaf-off season) and any interactions (Zar 1999). Similarly, I conducted a repeated measures two-way ANOVA for the observed pellet densities during the leaf-on season to determine if there was any differences among thinning classes, treatments, or years of sampling. I examined normality of error terms with normal probability plots and Lilliefor's test. I examined the data for constant variance with the modified Levene's test and plots of the residuals. I examined any significant differences among thinning classes *a posteriori* with Tukey's Honest Significant Difference Tests (Zar 1999).

Densities of snowshoe hare pellets were highly correlated with and linearly related to densities of hares on my northern Maine study sites (Chapter 1). Thus, observed differences in pellet densities directly correspond with differences in absolute densities of hares. All statistical comparisons were conducted using pellet densities; however, estimated densities of hares are also presented to enhance biological interpretations from statistical conclusions. I used the modified Litvaitis-Long model (hares/ha = 0.145303 + 0.0001 (pellets/ha/month)) to predict hare densities from pellet densities (Chapter 1).

Differences in proportions of males versus females and number of lactating females versus non-lactating females in PCT and unthinned stands were tested using a Z-test (Zar 1999). I pooled the data across years of sampling and stands within a treatment to maximize statistical power.

I used the mean of each habitat variable for each stand to descriptively analyze differences in stand structure among thinning classes and treatments by conducting a Two-way ANOVA on the means of each habitat variable (averaged across 20 plots within each stand) with thinning class (1, 6, 11 years since treatment) and treatment (stands treated with PCT and unthinned stands) as factors. I examined error terms for normality with a Lilliefor's test and probability plots and conducted a Modified Levene's test to examine the data for constant variance. Non-normal habitat variables were transformed using $\log_e$ transformations (Neter et al. 1996).

RESULTS

Pellet densities

Residual errors of pellet densities for the leaf-off seasons were normally distributed ($P > 0.10$) and variance was constant ($P > 0.10$), suggesting that the effects of treatment, thinning class, and year of sampling could be appropriately evaluated using parametric ANOVA. Previously herbicided clearcuts treated with PCT had lower pellet densities relative to similar unthinned stands during the leaf-off seasons ($F = 17.881$, $P < 0.001$) (Figure 2.2, Table 2.2). Unthinned stands had 1.97- and 2.01-fold greater densities of pellets than stands that were treated with PCT during both the 2000-2001 and 2001-2002 leaf-off seasons, respectively. Further, there was an effect of thinning class on pellet densities during the leaf-off season ($F = 3.451$, $P = 0.048$). In 2000-2001

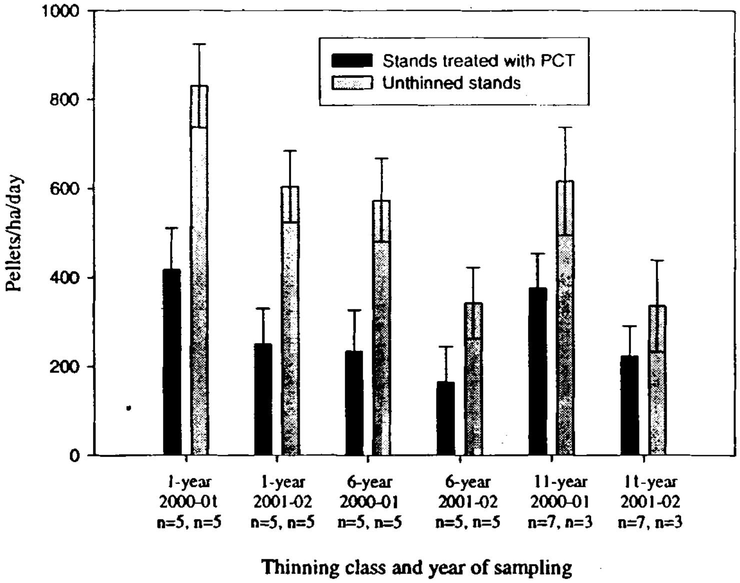

Figure 2.2. A comparison of mean (SE) number of snowshoe hare pellets/ha/day between PCT stands and similar unthinned stands in northern Maine during leaf-off seasons, 2000-2002.

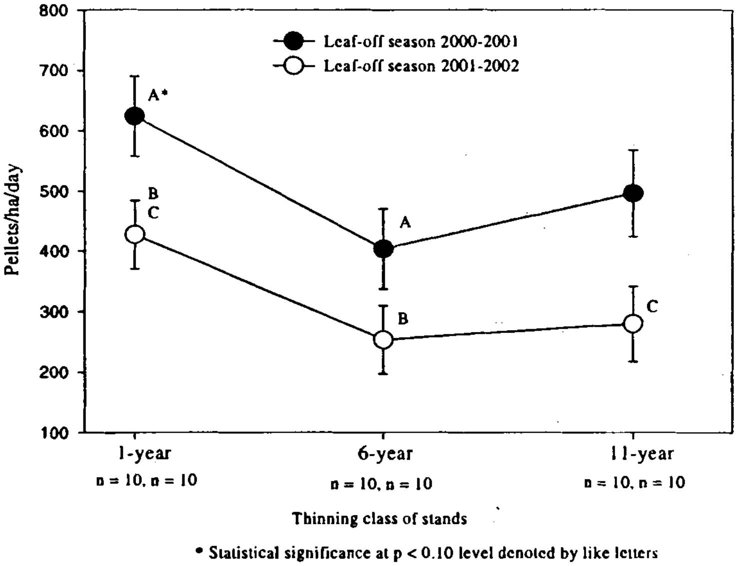

Figure 2.3. Mean (SE) pellets/ha/day averaged across stands treated with PCT and unthinned stands during the leaf-off seasons, from 1-11 years post-treatment in northern Maine; 1 = treated in 1999, 6 = treated in 1994, 11 = treated in 1989-1990. Statistical significance at $P < 0.10$ level is denoted by like letters.

Table. 2.2. Effects of treatment, thinning class, and year of sampling on pellet density and estimated density[a] of snowshoe hares within 30 stands (17 treated with PCT, 13 unthinned) and among leaf-off (October – May) and leaf-on (June-September) seasons in northern Maine, 2000-2002.

Season	Factor	F-Statistic	P-value	Pellets/ha/day (SE)	Hares/ha (SE)
Leaf-off, 2000-02	**Treatment**	**17.881**	**< 0.001**		
	PCT			227.36 (30.41)	0.83 (0.24)
	No-PCT			562.38 (52.83)	1.80 (0.30)
	Thinning class	**3.451**	**0.048**		
	1-year			525.91 (68.92)	1.72 (0.35)
	6-year			328.63 (47.71)	1.13 (0.29)
	11-year			352.46 (48.48)	1.31 (0.29)
	Year	**29.825**	**< 0.001**		
	2000-2001			491.82 (49.87)	1.62 (0.29)
	2001-2002			312.84 (39.86)	1.08 (0.26)
Leaf-on, 2001-02	**Treatment**	**21.231**	**< 0.001**		
	PCT			116.30 (12.07)	0.49 (0.18)
	No-PCT			261.27 (36.70)	0.93 (0.26)
	Thinning class	0.173	0.842		
	1-year			205.92 (38.93)	0.76 (0.26)
	6-year			167.79 (32.23)	0.65 (0.24)
	11-year			163.67 (30.62)	0.73 (0.24)
	Year	**93.346**	**< 0.001**		
	2001			256.30 (32.08)	0.91 (0.24)
	2002			101.94 (10.49)	0.45 (0.18)

[a] Hare densities were estimated from pellet densities using the most appropriate regression model (Chapter 1). The equation used: Hares/ha = 0.145303 + 0.0001 (pellets/ha/month).

the 1-year thinning class had greater numbers of pellets than the 6-year thinning class ($P < 0.005$), but the 1-year and 11-year stands did not differ significantly ($P < 0.10$) (Figure 2.3, Table 2.2). During 2001-2002, however, the 1-year thinning class supported greater ($P < 0.05$) densities of pellets than either the 6-year or 11-year thinning classes. Pooled across both years, the 1-year thinning class had 1.6 times greater pellet densities than the 6-year and 1.4 times greater pellet densities than the 11-year thinning class. The 2000-2001 leaf-off season had 1.57 × greater pellet densities than the 2001-2002 leaf-off season ($F = 28.825$, $P < 0.001$).

Residual errors were not normally distributed ($P = 0.01$) and variance was not constant ($P < 0.10$) for pellet densities during the leaf-on season. Therefore, I $\log_e$ transformed pellet densities to correct for these violations of the parametric assumptions of ANOVA. After transformation, errors were normally distributed ($P > 0.10$) and variance was constant ($P > 0.10$). Stands treated with PCT had lower densities of snowshoe hare pellets than similar unthinned stands during the leaf-on seasons ($F = 19.499$, $P < 0.001$) (Table 2.2, Figure 2.4). Unthinned stands had 2.47 fold greater pellet densities than stands treated with PCT during the leaf-on season in 2001 and 1.66 fold greater pellet densities during leaf-on season in 2002. There was no effect of thinning class during the leaf-on season ($F = 0.029$, $P = 0.971$), however there was an effect of year ($F = 93.346$, $P < 0.001$) (Figure 2.5). Pellet densities during the leaf-on season were 2.44 times greater during 2001 than 2002. Lastly, all interaction terms including year were significant ($P \leq 0.10$) for the leaf-on season, which suggests inconsistent responses of hare to treatment and thinning classes during the 2 summers of study. Untreated

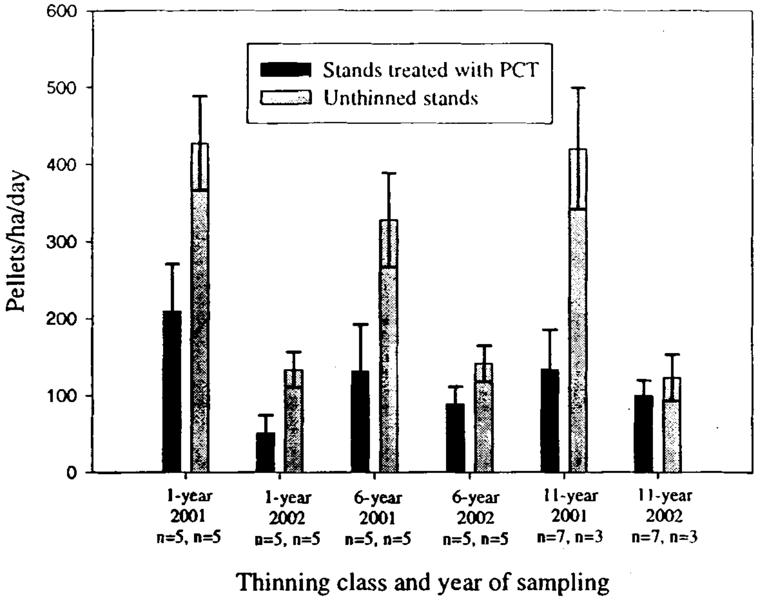

Figure 2.4. A comparison of mean (SE) number of snowshoe hare pellets/ha/day between PCT stands and similar unthinned stands in northern Maine during leaf-on seasons 2001-2002; 1 = treated in 1999, 6 = treated in 1994, 11 = treated in 1989-1990.

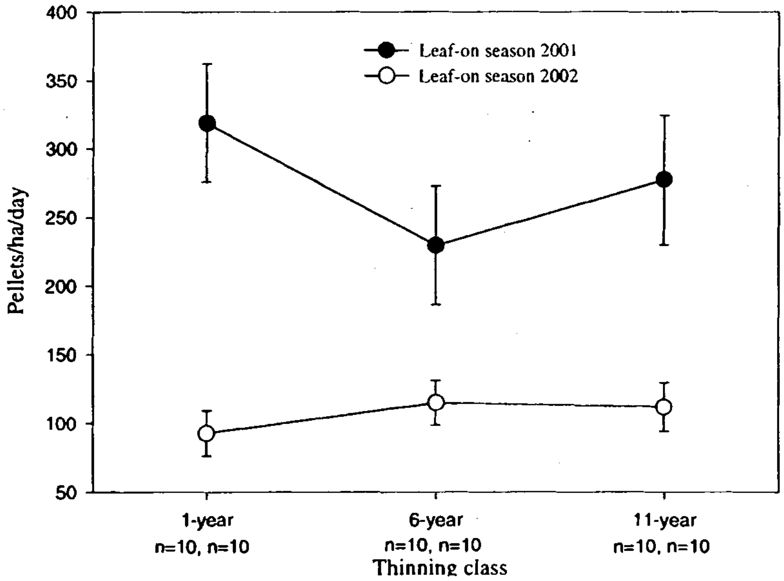

Figure 2.5. Mean (SE) pellets/ha/day averaged across stands treated with PCT and unthinned stands during the leaf-on seasons, from 1-11 years post-treatment. No significant effect of thinning class was observed ($P \geq 0.842$, $F = 0.173$).

Table 2.3. A comparison (Two-way ANOVA) among means (SE) for 6 stand-scale habitat variables selected *a priori* between treatments (17 regenerating clearcut stands treated with PCT and 13 stands untreated) and among 3 thinning classes (1-2, 6-7, 11-12 years post-thinning) in northern Maine. Non-transformed means and standard errors are presented for transformed variables[a] and P-values < 0.10 are depicted in bold.

	Variable					
	#CON≥7.6[b]	TOTUNDER≥7.6[c]	SCU[d]	CANOPY[e]	VEGDIST[f]	LOGS[g]
Treatment						
F-statistic	1.832	32.471	38.445	2.447	12.570	25.196
P	0.188	**< 0.001**	**< 0.001**	0.131	**0.002**	**< 0.001**
PCT (n = 17)	1,199 (98)	3,146 (707)	6,089 (2,037)	78.2 (2.5)	10.0 (0.4)	1.6 (0.3)
No-PCT (n =13)	1,402 (114)	8,997 (821)	12,199 (2,367)	84.1 (2.8)	7.6 (0.5)	3.5 (0.3)
Thinning class						
F-statistic	1.911	3.241	1.849	0.588	1.811	2.389
P	0.170	**0.057**	0.179	0.563	0.185	0.113
1-year (n = 10)	4632 (908)	6210 (910)	15,474 (2,622)	78.8 (3.2)	8.6 (0.6)	2.9 (0.4)
6-year (n = 10)	4778 (908)	7551 (910)	17,107 (2,622)	80.7 (3.2)	8.2 (0.6)	2.8 (0.4)
11-year (n = 10)	3449 (991)	4453 (993)	11,351 (2,861)	83.9 (3.4)	9.7 (0.6)	2.0 (0.4)
Treatment*Thinning class						
F-statistic	0.380	1.301	1.091	1.694	0.032	0.431
P	0.688	0.291	0.352	0.205	0.969	0.655
1-year PCT (n = 5)	1,176 (178)	2,840 (1,287)	6,768 (3,708)	72.1 (4.5)	9.7 (0.8)	1.8 (0.5)
6-year PCT (n = 5)	1,084 (178)	3,892 (1,287)	5,964 (3,708)	76.9 (4.5)	9.5 (0.8)	1.8 (0.5)
11-year PCT (n = 7)	1,337 (151)	2,706 (1,088)	5,534 (3,134)	85.6 (3.8)	10.9 (0.7)	1.1(0.4)
1-year no PCT (n = 5)	1,520 (179)	9,580 (1,287)	24,180 (3,708)	85.6 (4.5)	7.5 (0.8)	4.0 (0.5)
6-year no PCT (n = 5)	1,120 (179)	11,210 (1,287)	28,250 (3,708)	84.6 (4.5)	6.8 (0.8)	3.8 (0.5)
11-year no PCT (n = 3)	1,557 (230)	6,200 (1,661)	17,167 (4,787)	82.1 (5.8)	8.6 (1.0)	2.8 (0.6)

Table 2.3. Continued.

[a] TOTUNDER, SCU, and LOGS were $\log_e$ transformed prior to analysis.
[b] #CON≥7.6 = number of conifer trees/ha (≥ 7.6 cm dbh, >1.0 m ht, alive).
[c] TOTUNDER = number conifer trees (< 7.6 cm dbh >1.0 m ht, alive) + number deciduous trees (< 7.6 cm dbh >1.0 m ht, alive) per ha.
[d] SCU = (3 × number of conifer trees < 7.6 cm dbh >1.0 m ht, alive) + (1 × number of deciduous trees < 7.6 cm dbh per ha >1.0 m ht) per ha.
[e] CANOPY = average overhead canopy cover closure at 1.0 m height during summer, percent.
[f] VEGDIST = average understory lateral foliage density (average distance that an entire 2.0 m pole is obscured), m.
[g] LOGS = number of logs per ha.

stands had greater densities of hare pellets across all thinning classes for both years of the study except for the 11-year thinning class during 2002, which may have accounted for the significant interaction terms.

Live-trapping demographics

I captured 128 adult hares (69 M, 59 F) 308 times in 2001, and 114 adult hares (64 M, 49 F, 1 unknown) 464 times in 2002. Differences in the proportion of lactating female hares between thinned (68%, n = 28, 90% C.I. 46-84%) and unthinned stands (58%, n = 80, 90% C.I. 46-68%) were not significant ($Z = 0.97$, $P = 0.416$). Further, the proportion of male and female hares was not significantly different ($Z = 0.59$, $P = 0.360$) between stands treated with PCT (58% males, n = 67, 90% C.I. 45-70%) and unthinned stands (54% males, n = 174, 90% C.I. 46-62%).

Habitat sampling

Measures of the density of total understory stems, stem cover units, and logs were lower ($P \leq 0.001$) in thinned stands compared to unthinned stands (Table 2.3). Measures of the density of the total number of understory stems and stem cover units in treated stands were 1/3 and 3/10 the density in untreated stands, respectively. Conversely, the distance to obstruction by horizontal vegetation was greater ($P = 0.002$) in stands treated with PCT. Of the 6 structural variables examined, only the density of understory stems varied among thinning classes ($P = 0.057$) of thinned and unthinned stands; the 11-year thinning class had fewer understory stems ($P < 0.10$) than the 1-year or 6-year thinning classes.

DISCUSSION

Effects of PCT

Previous studies of PCT and its effects on wildlife examined relatively short-term changes (4 years or less) in densities of hares after thinning (Sullivan and Sullivan 1988, de Bellefeuille et al. 2001). My results indicate that PCT reduced hare densities from 1–11 years post-thinning (Figure 2.5). Mean differences in hare densities between stands treated with PCT and unthinned stands across 2 years of sampling and 2 seasons ranged from -45 to -54 % for 1-year stands, -39 to -55 % for 6-year stands, and -13 to -61 % for 11-year stands. Despite annual changes in hare densities, PCT reduced densities of snowshoe hare during both leaf-off and leaf-on seasons during both years of my study. Further, hare densities were greatest in stands 17 to 24 years after clearcutting (13-20 years post-herbicide) (1-year thinning class) during the leaf-off season, which was consistent with previous studies that have indicated that hares reach their greatest abundances in mid-successional stands and avoid very young clearcuts and mature stands (Litvaitis et al. 1985a, Monthey 1986, Koehler 1990, Ferron et al. 1998, Hoving 2001, de Bellefeuille et al. 2001).

The consistent effect of PCT on densities of hares from 1 to 11-years post-treatment suggests that forest understories in thinned stands likely did not regain the structural complexity that existed prior to treatment. Regenerating stands without PCT supported the greatest densities of hares for 17-24 years after clearcutting (mean = 2.30 hares/ha, n = 5), whereas PCT-treated stands supported the lowest densities of hares (mean = 1.04 hares/ha, n = 7) 25-32 years after clearcutting. In contrast, radio tracked hares avoided all regeneration treatments on landscapes in Quebec, Canada that included recently thinned stands (de Bellefeuille et al. 2001). Those results were somewhat inconclusive because pellet counts indicated that all sites, which were 7-9 years post-clearcut harvest, were rarely used, regardless of whether they had been treated with PCT. The authors concluded that longer than 9 years were necessary for clearcuts to regenerate to suitable hare habitat in Quebec; my sites were clearcut 17-32 years prior to study, which had allowed stands to develop the structural attributes required by hares (Wolfe 1982, Litvaitis et al. 1985a).

My observations that hare densities were reduced by PCT by 1-year after treatment were inconsistent with results from British Columbia, Canada (Sullivan and Sullivan 1988), where hare density exhibited no short-term (1-2 year) response to thinning. By 3-4 years after treatment, however, densities of hare in thinned stands fell below unthinned stands in British Columbia. These differences in conclusions may have resulted from felled trees losing their needles and value as food and cover more quickly in Maine. During 2001, Maine received the lowest annual precipitation of the last 100 years (National Oceanic and Atmospheric Administration 2002), which could have contributed to the rapid desiccation of felled trees. Additionally, hares could have relocated from thinned stands into nearby unthinned stands soon after treatment (Ferron et al. 1998). I speculate that it may be important to consider responses in hare densities at the scale of the landscape in addition to the scale of the stand to account for confounding affects of individual movements by hares and shifts in home ranges in response to PCT.

Hares are thought to concentrate habitat use in stands with high densities of saplings during winter, presumably to provide protection from predators and weather (O'Donoghue 1983, Litvaitis et al. 1985a, Koehler and Brittell 1990). During summer, hares have a weaker association with understory stem density and canopy closure because food is more widespread and cover is less limiting (Wolff 1980, Litvaitis et al. 1985a). Despite that hares exhibit a more generalist preference for habitat during summer (Wolff 1980, O'Donoghue 1983), I observed greater densities of hares in unthinned regenerating clear-cut stands compared to stands treated with PCT during both leaf-off (late-fall – early spring) and leaf-on (late spring - early fall) seasons. Consequently, regenerating stands with high densities of conifer saplings are likely selected for by snowshoe hares year-round in my study areas. During the leaf-on seasons, there was not a detectable difference in hare densities among stands of various treatment classes; however, hares were more abundant in younger stands than in older stands during the leaf-off season. Winter is the limiting season for snowshoe hares (Pease 1979, Pietz and Tester 1983), and they more strongly prefer the forest structure found in mid-successional stands for thermal and escape cover during that season.

Habitat associations of snowshoe hare have been reported to change with fluctuations of hare densities both in Maine at a landscape scale (Hoving 2001) and in Alaska at a stand scale (Wolff 1980). Even though densities of hares (across all stands) decreased by 33.0 % from the leaf-off season 2000-01 to leaf-off season 2001-02, and by 49.5 % from the leaf-on season 2001 to leaf-on season 2002, a consistent and negative effect of PCT was still detectable ($P \leq 0.10$). This indicates that, within the range of annual changes in hare densities that I observed, the negative effects of PCT occurred despite inter-annual fluctuations in densities of hare.

Hare densities in response to alternative forest practices

From a management perspective, the effects of PCT on reducing densities of hare are only relevant when compared to alternative forest practices. Maine has nearly 17 million acres of commercial timberland that is likely to continue to be harvested, so if stands are not under a harvest plan including PCT, they likely will be managed via alternative silvicultural regimes. Although stands treated with PCT support lower densities of hares than similar unthinned stands, they still retain greater densities of hares than many other forest stand types (Table 2.4). Of 7 forest-stand types studied in northern Maine, regenerating stands and PCT stands had the greatest hare densities. This pattern likely reflects hares' affinity to structure typically found in early seral stages, such as high stem densities and horizontal cover. Regenerating and PCT stands are early to mid-successional, whereas most of the other stand types are in later seral stages. Although PCT stands supported lower densities of hares when compared to similar unthinned stands, PCT stands supported more hares than mature conifer, deciduous, or mixed coniferous-deciduous stands, or than mature mixed stands that had been recently partially harvested. Forest practices other than PCT should also be considered with regard to potential indirect effects on carnivores because they may exert a stronger influence on stand-scale and landscape-scale densities of snowshoe hare than thinning. For example, partial harvests, which may support fewer hares than PCT stands, (Table 2.4) composed 221,029 ha of land harvested in Maine during 2001, whereas PCT-treated stands composed 8,860 ha of intensively managed land for 2001 (Maine Forest Service 2002). Further, the acres of land clearcut harvested annually, which regenerate into the

Table 2.4. Average density[a] of snowshoe hares estimated in 7 overstory types[b] (number of stands) in northern Maine during leaf-off seasons (October – May). Densities of hares reported for this study were averaged across 2 leaf-off seasons (2000-2001 and 2001-2002).

Overstory[b] (n)	Years since regenerating event (range)	Hares/ha (SE)[c]	Year of sampling	Study
REG (n = 7)	12 - 20	2.43 (2.04)	1995 - 1996	Lachowski (1997)
REG (n = 13)	18 - 26	1.83 (0.16)	2000 - 2002	This study
REG (n = 2)	15	1.63 (0.93)	1997 - 1998	Fuller (1999)
PCT (n = 17)	18 - 32	0.99 (0.09)	2000 - 2002	This study
BK[d] (n = 2)	12-13	0.59 (0.41)	1995 - 1996	Lachowski (1997)
MIX (n = 7)	n/a	0.29 (0.27)	1995 - 1996	Lachowski (1997)
CON (n = 2)	n/a	0.23 (0.05)	1995 - 1996	Lachowski (1997)
CON (n = 2)	n/a	0.23 (0.04)	1997 - 1998	Fuller (1999)
MIX (n = 7)	n/a	0.21 (0.03)	1997 - 1998	Fuller (1999)
DEC (n = 2)	n/a	0.16 (0.00)	1997 - 1998	Fuller (1999)
DEC (n = 2)	n/a	0.15 (0.01)	1995 - 1996	Lachowski (1997)
PH (n = 7)	3-6	0.15 (0.00)	1997 - 1998	Fuller (1999)

[a] Estimates of hares/ha were derived using the most biologically appropriate model for Maine described in Chapter I: hares/ha = 0.145303 +0.0001(pellets/ha/month). Densities from Fuller (1999) were recalculated based on the modified Litvaitis-Long equation presented in Chapter I

[b] REG = regenerating forest, including unthinned stands for this study (leaf-off season densities), CON = coniferous, DEC = deciduous, MIX = mixed coniferous-deciduous, BK = killed by eastern budworm, PH = partial harvest, PCT = precommercially thinned (leaf-off season densities).

[c] As hare populations may vary temporally, these differences should be viewed as relative, not absolute values.

[d] Osawa (1986) reported that budworm mortality was complete for balsam fir and nearly complete for spruce by 1980 in Baxter State Park, Maine.

habitat supporting the greatest densities of hares, have declined from about 45,998 ha to 6,102 ha harvested annually since 1986.

PCT may also include several other methods of reducing stand density (e.g., mechanical spacing and herbicide spray thinning) that were not evaluated in my study. Further, my results were for precommercially thinned herbicide-treated clearcuts with crop tree spacing of 1.8 to 2.4 m (6-8 feet); in other geographic areas with different dominant conifers, weather, soils, and silvicultural objectives, forest managers prescribe thinnings with varying spacing between crop trees. In this study, all PCT stands were treated with an aerial herbicide several years prior to being spaced. In Quebec, deciduous understory stem density in non-herbicided stands increased dramatically after PCT (Bujold 2002), and provided cover for hares that was not present on my study sites. Thus, the results from my study should be used with caution when applied to other regions, thinning regimes, or to systems where herbicide application does not precede PCT.

Vegetation changes associated with PCT

The structural attributes that were lower in forest stands treated with PCT explain much of the observed differences in thinned versus unthinned stands on my study sites. Complex understory structure provides thermal and escape cover from predators for snowshoe hares, was correlated to survival of hares in other regions of Maine (Litvaitis et al. 1985a), and influenced length of dispersal movements of translocated hares in Idaho (Wirsing et al. 2002). Woody debris may substitute for horizontal cover in geographic areas where understory stem densities do not approach those required by snowshoe hare (Conroy et al. 1979, Scott and Yahner 1989, Ferron et al. 1998); however, woody debris likely only provides measurable cover during the leaf-on season, when not buried by snow. Measures of understory density, horizontal cover, and abundance of logs were greater in unthinned reference stands than stands treated with PCT, indicating that these structural attributes were associated with higher densities of hares on my study areas; untreated stands with more horizontal structure (i.e. stems, cover, and logs) supported the greatest densities of hare. A minimum of 40-60% understory horizontal cover has been suggested to maximize local densities of snowshoe hare in forest stands during winter (Wolfe et al. 1982, Litvaitis et al. 1985). Stands treated with PCT likely were below the structural threshold associated with higher densities of hares during my study. Thus, stands treated with PCT that also maintain understory complexity may mitigate the negative effects of thinning on densities of hare. To maximize post-treatment densities of snowshoe hare, forest managers could attempt to maintain greater horizontal cover (i.e. greater number of stems/ha) in thinned stands by reducing spacing distances between crop trees; however, silvicultural objectives of the thinning treatment could be compromised (Seymour 1993).

CONCLUSIONS

The stand-scale effects of PCT were incredibly consistent at reducing densities of snowshoe hare by nearly 50% from 1 to 11 years post-treatment during both leaf-off and leaf-on seasons and across 2 years of study. Although thinning appeared to reduce the density of snowshoe hare at the stand-scale, it may have a weaker, negative effect on hare numbers across the landscape than more widespread silvicultural practices that favor retention of overstory trees throughout the rotation, such as some forms of partial harvesting. Maintaining greater horizontal cover by reducing the spacing distance between crop trees in regenerating conifer stands treated with PCT may partially mitigate the negative effects of thinning on densities of snowshoe hare. However, the silvicultural objectives and the cost efficiencies of thinning could be compromised. Caution should be taken when applying these stand-scale results to indirect effects on forest carnivores because landscape-scale responses of hares to PCT may not directly translate into negative effects on foraging efficiency and density of species such as lynx, who likely respond to habitat at larger spatial scales. At the scale of the forested landscape, the effects of distribution and extent of intensive forest management, including PCT, on snowshoe hare are also poorly understood and might differ from the stand-scale effects studied here.

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CHAPTER 3

TEMPORAL EFFECTS OF PRECOMMERCIAL THINNING ON SMALL MAMMALS IN NORTHERN MAINE

ABSTRACT

Precommercial thinning (PCT) is being practiced increasingly throughout the Acadian forests of eastern North America to meet silvicultural objectives; however, the effects of this practice on wildlife, both immediately after treatment and several years later, are not well understood. Forest dependent small mammals have ecological roles as prey for numerous avian and mammalian predators, dispersers of seeds, fruit, and spores, and contribute to nutrient cycling. Researchers in the northwestern USA have suggested that thinning of young regenerating clearcuts may increase the abundance and diversity of some taxa of forest-dependent small mammals by increasing rates of forest development and by enhancing the ecological representation of mid-successional stands across managed landscapes. I examined the effects of PCT, from 1 to 16 years post-treatment, on abundances of mice, voles, shrews, and on within-stand structure in the commercial forests of northern Maine. I live-trapped small mammals on 24 herbicided clearcuts treated with PCT and 13 similar, unthinned stands during summers of 2000 and 2001. Thinning of mid-successional conifer stands resulted in increased abundances (red-backed voles, *Clethrionomys gapperi*, $P = 0.008$; masked shrews, *Sorex cinereus*, $P < 0.001$) or had no detectable effect on (deer mice, *Peromyscus maniculatus*, $P = 0.544$; short-tailed shrews, *Blarina brevicauda*, $P = 0.517$) the 4 most common species of small mammals in northern Maine. Several within-stand habitat characteristics associated with stand maturity, such as larger stem diameters and a partially open canopy, occurred

in thinned stands. Thus, PCT may accelerate development of habitat attributes typical of mid-successional conifer stands. At the scale of the forest stand, PCT produced within-stand habitat conditions favorable to small mammals, and may be an appropriate management tool to increase the abundances of red-backed voles and masked shrews, and may accelerate stand succession in intensively managed stands within the Acadian Forest. However, PCT will involve tradeoffs for early successional wildlife species associated with high stem densities, such as snowshoe hare (*Lepus americanus*) (Chapter 2).

INTRODUCTION

The Acadian forest, ranging from northern New England east through the maritime Canadian provinces, includes the ecological transition zone of eastern deciduous forest to the south and boreal forest to the north (Seymour and Hunter 1992). Commercial timberland is a primary economic use of this region and accounts for 86% of the land area of Maine (Maine Forest Service 1998), 82% of New Brunswick, 68% of Nova Scotia, and 35% of Quebec (Canadian Council of Forest Ministers 2002). Over the past 2 decades, commercial forestry in this region has evolved from extensive management towards more intensive silviculture. Currently, about 4% of Maine's commercial timberland is in high production silviculture, including precommercial thinning (PCT), herbicide release, and plantations (Maine Forest Service 1998). Similarly, the eastern Maritime Provinces in Canada have experienced increases in the land area under intensive management, with 1.2 to 1.5-fold increases from 1990-2000. One form of intensive forest management, PCT, increased from 4,352 ha to 9,950 ha in Maine (Maine Forest Service unpublished data, 2001), from 14,930 ha to 40,354 ha in New Brunswick, from 22,791 ha to 98,158 ha in Quebec, and from 3,228 ha to 8,113 ha in Nova Scotia (Canadian Council of Forest Ministers 2002), 1990-2000. Thus, thinning has affected an increasing percentage of regenerating forest habitat across the Acadian forest and this practice has been questioned in relation to its effects on early successional wildlife species such as snowshoe hare (*Lepus americanus*), the primary prey of the U.S. Federally threatened Canada lynx (*Lynx candadensis*) (Hickenbottom et al. 1999).

Precommercial thinning reduces the density of overstocked stands to minimize mortality from competition and to accelerate growth of residual trees (Ker 1987, Seymour 1984, Brissette and Frank 1999, Brissette et al. 1999). Characteristics of forest overstory (Ker 1987, McCormack and Lemin 1998, Brissette and Frank 1999, Chapter 4), understory (Doerr and Sandburg 1986, Newton et al. 1989, Wilson and Watts 1999, Lindgren and Sullivan 2001, Chapter 4), and microclimate (Reynolds et al. 1997) change dramatically after PCT and with stand succession. By reducing competition from crop trees via thinning, stem diameters (Harrington and Reukema 1983, Ker 1987, McCormack and Lemin 1998, Brissette and Frank 1999, Brissette et al. 1999, Pothier 2002) and crowns (McCormack and Lemin 1998, Brissette and Frank 1999, Brissette et al. 1999, Lindgren and Sullivan 2001, Sullivan et al. 2001) of residual crop trees increase rapidly, causing stands to bypass the stem exclusion stage of forest succession characterized by self-thinning (Smith et al. 1997). The reduction of competition among crop trees for nutrients, space, and light results in reduced mortality of residual stems (Ker 1987, Brissette and Frank 1999, Brissette et al. 1999); without mortality of large diameter trees, recruitment of CWD may be reduced (Carey and Johnson 1995, Hayes et al. 1997, Harrison 1999). These changes within stands could potentially influence, either positively or negatively, a variety of forest wildlife species (early to late seral) dependent on overstory, understory, structure, or coarse woody debris (CWD). Application of PCT to regenerating conifer stands reduces densities of snowshoe hare (Sullivan and Sullivan 1988, Chapter 2); however, studies in the Pacific Northwest have indicated that thinning of second growth forests may diversify the landscape and increase richness of wildlife species by accelerating stand succession (Carey and Johnson 1995, Hayes et al. 1997, Sullivan et al. 2001).

Forest dwelling voles (*Clethrionomys* spp.), mice (*Peromyscus spp.*, *Napeozapus spp.*), and shrews (Soricidae) are relevant taxa for examining responses to PCT because they are consumers of invertebrates, fungi, and vegetation (Hamilton 1941) and are prey for many avian (Mendall 1944) and mammalian carnivores (Soutiere 1979, Dibello et al. 1990, Cumberland et al. 2001). Additionally, small mammals may assist the revegetation of nonforested areas by dispersing spores of hypogeous fungi present in their feces (Maser et al. 1978, Kirkland 1990) and contribute to nutrient cycling (Brooks and Healy 1988). Small mammal abundances have been reported to be positively associated with some attributes of forest structure, including downed and decaying dead wood (Richens 1974, Hayes and Cross 1987, Carey and Johnson and 1995), microclimatic conditions associated with closed overhead cover and diverse ground structure (Miller and Getz 1977, Yahner 1986), and with characteristics of understory vegetation (Yahner 1986, Bowman et al. 2001). Habitat variables describing the structural attributes of mature forest at both the stand scale and microhabitat scale have been positively associated with densities of small mammals (Martell 1983b, Lachowski 1997). Thus, silvicultural practices that accelerate forest succession and reduce stand rotation, such as PCT, could accelerate the development of favorable habitat conditions for small mammals that prefer the overstory and understory characteristics of mature forest.

Stand thinning is designed to minimize natural mortality resulting from intra- and inter-specific competition among crop trees. This could reduce recruitment of CWD below levels required by small mammals, and might reduce abundance, age structure, or reproductive performance in affected populations. However, previous studies of the habitat relationships of red-backed voles (*Clethrionomys gapperi*), deer mice (*Peromyscus maniculatus*), short-tailed shrews (*Blarina brevicauda*), and masked shrews (*Sorex cinereus*) in commercial forests of Maine have uncovered few unequivocal relationships between population abundance and CWD (Lachowski 1997, Fuller 1999, Billig *in prep.*). These findings suggest that woody debris usually occurs above levels required by small mammals across a wide range of extensively managed and unmanaged stands in commercial forests of Maine. Alternatively, structures (e.g. slash) created from logging activities might serve as functional surrogates to CWD immediately after harvest. These inter-relationships among intensive silviculture (e.g. PCT), CWD, and forest dwelling small mammals require further study in eastern North America.

Understanding the response of small mammals to silvicultural prescriptions for longer than 2-3 years after treatment is necessary to evaluate the ecological effects of forest practices that influence long-term stand development. For example, initial changes in microclimate of stands directly after thinning could cause a decrease in small mammal populations, but populations could rebound as the growth of crop trees accelerates following treatment. Few studies have explored the temporal effects of PCT on small mammals longer than 4 years post-treatment (exception: Sullivan et al. 2001) and statistical replications have been limited (n ≤ 4) (Lautenschlager et al. 1997, Sullivan et al. 2001).

Published effects of PCT on forest dwelling small mammals have involved stands that were clearcut and thinned, but not treated with an herbicide (Lautenschlager et al. 1997, Sullivan et al. 2001); in the Acadian forest, PCT often occurs on stands that were previously herbicided (typically 3-10 years after clearcutting). Sullivan et al. (2001) presented results of effects of thinning on small mammals in British Columbia immediately after treatment and 10 years later; however, their study design did not allow for treatment effects to be distinguished from temporal variations in abundances of small mammals. Temporal effects potentially confound studies of small mammal responses to forest practices because densities of small mammals often exhibit significant inter-annual variation (Richens 1974, Krebs and Wingate 1976, Lachowski 1997, Bayne and Hobson 1998, Fuller 1999).

Stands previously treated with PCT in Maine have grown at a sufficient rate to allow for the first economically viable commercial entry as soon as 16 years after thinning (ages 30-35 years). Thus, I evaluated effects of PCT on small mammals at intervals of 1-2, 5-7, 9-12, and 14-17 years post-thinning in stands that were clearcut 17-33 years previously and treated with herbicides 2-19 years after harvest. My objectives were to retrospectively compare the relative abundances of small mammals and associated overstory and within-stand habitat attributes in herbicide treated clearcuts, with and without PCT. Generalizing the responses of wildlife to forest management across species of small mammals may be inappropriate because large changes in the densities of one or more dominant species may obscure changes in community composition or densities of individual species (Martell and Radvanyi 1977, Martell 1983b). I compared species-level abundance of red-backed voles, deer mice, short-tailed shrews, and masked shrews among regenerating, unthinned stands and similarly aged, thinned stands 1-16 years post-treatment. Overstory and within-stand habitat variables were also compared between thinned and unthinned stands and successional patterns in habitat and structural (e.g. CWD) characteristics of stands were documented from 1-16 years post-thinning.

Densities of animal populations are not always greatest in habitat types with the greatest habitat quality (Van Horne 1983). The proportion of individuals in a reproductive condition is frequently used as an indirect index of habitat quality for small mammals (Hobbs and Hanley 1990); therefore, I also compared lactation rates of female red-backed voles and deer mice between thinned and unthinned stands to evaluate effects of PCT on reproductive performance of these 2 dominant small mammals in the Acadian forest.

STUDY AREA

Seven townships in northern Maine (Days Academy Grant, Spencer Bay, T1 R13 WELS, T4 R 12, T4 R11, T5 R11, and Hersey) composed the study area (Figure 3.1). Hersey Township is in Aroostook County and the other 6 townships are in Piscataquis County. Most of the land in these towns is managed for pulpwood and sawtimber production by Plum Creek Timber, Fairfield, Maine; Great Northern Paper, Millinocket, Maine; and International Paper Company, Costigan, Maine. The study area spans 110 km east to west and 49 km north to south. Stands were chosen so that topography was relatively flat (< 15° slope).

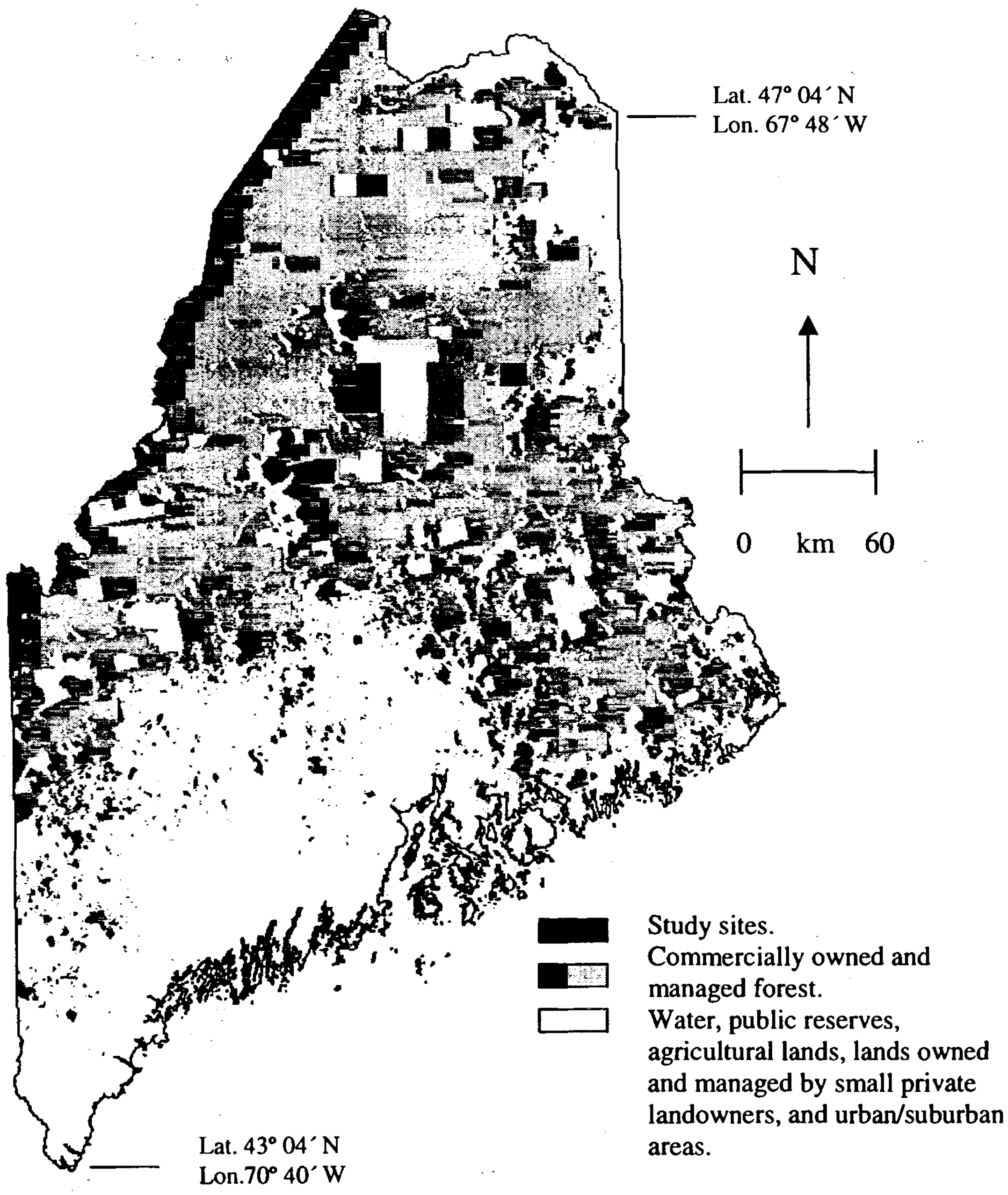

Figure 3.1. Location of study sites containing 37 stands where abundances of small mammals were investigated within 7 townships in the commercially owned and managed forests of northern Maine, 2000-2001.

Northern Maine is part of the Acadian forest, known also as the sub-boreal spruce-fir ecosystem (Seymour and Hunter 1992). Study sites were dominated by balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), and black spruce (*Picea nigra*), but also had minor components of white pine (*Pinus strobus*), larch (*Larix spp.*), white cedar (*Thuja occidentalis*), paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), and red maple (*Acer rubra*). The climate was generally cool and moist, with an annual mean temperature for the region of 3.3° C and 101 cm of average annual precipitation (Garoogian 2000). The area received an average of 2.75 m of snowfall yearly (averaged from 1970 to 2000) and the ground was usually snow-covered from December through April.

METHODS

I evaluated the site quality, tree density, diameter at breast height (dbh) of dominant trees, size, and spatial independence of stands before selecting study sites. Sites were considered spatially independent when separated by > 0.40 km or a body of water to minimize population exchange of small mammals (Bowman et al. 2000a). Site quality, which can strongly influence the rate of succession of conifer stands (Briggs and Lemin 1994), was estimated based on 4 to 6 soil cores sampled at 50-100 m intervals within the stand with a soil auger. According to Brigg's (1994) scale of forest productivity, site-quality ranged from 1 (highly productive) to 5 (unproductive). I attempted to minimize among-stand variation within a treatment × thinning class block by pairing treated and untreated stands based on year of initial clearcut, year of herbicide, time since PCT, site quality, topography and pre-thinning species composition (based on live trees and stumps in stands treated with PCT). Stands were paired retrospectively so were not treated as statistical pairs during analyses.

Treatment stands were clearcut (timber harvesting resulting in residual basal area of acceptable growing stock trees > 4.5 in. dbh of < 30 ft^2/acre) 1967-1983, aerially herbicided with Glyphosate (applied at a rate of ≈ 1.68 kg/ha acid equivalent) 1977-1988, and precommercially thinned with motor-manual brush-saws from 1984-1999. Unthinned reference stands were clearcut 1974-1982 and herbicided with Glyphosate (≈ 1.68 kg/ha acid equivalent) 1982-1988 (Table 3.1). The study design included 24 treatment stands that were surveyed for small mammal abundances at 5-year intervals since thinning (1-2 year post-thinning, n = 6; 5-7 years, n = 6; 9-12 years, n = 6; 14-17 years, n = 6) and 13 similar, unthinned stands (1 year, n = 5; 6 year, n =5; 11 year, n = 3), whose histories were comparable with treatment stands. I allowed some latitude (1-2 years) in separating stands into thinning classes so that I could maximize the number of stands studied. The study design was unbalanced; a greater number of stands were treated with PCT (n = 24) compared to unthinned stands (n = 13). I was unable to locate comparable, unthinned stands for the 16-year thinning class and located only 3 unthinned replicates for the 11-year thinning class. Nearly all stands that had been clearcut and herbicided prior to 1985 in my study areas had already been treated with PCT.

Small mammal trapping

I surveyed the relative abundances of red-backed voles, deer mice, short-tailed shrews, and masked shrews by live-trapping within 37 stands (Table 3.1) during June-August 2000 and 2001. I established 70 m by 70 m trapping grids with 64 trap stations at 10 m intervals (Figure 3.2). Grids were positioned > 50 m from edges of forest stands to

Table 3.1. Stand history, location, and site quality for 24 precommercially thinned stands and 13 unthinned stands located in 7 townships, northern Maine. (T = treated with PCT, C = unthinned stand). Site quality ranged from 1 (well drained, productive) to 5 (poorly drained, unproductive) according to Briggs (1994) classification guidelines.

Site number	Year of Clearcut	Year of Herbicide	Year of PCT	Township	Site Quality
1-1-T	1982	1988	1999	T 4 R 11	4+
1-2-T	1980	1983	1999	T4 R 12	3-
1-3-T	1977	1983	1999	T4 R 11	4+
1-4-T	1982	1988	1999	T4 R 11	4
1-5-T	1976	1983	1999	T4 R 12	4
1-6-T	1983	1988	1999	T 4 R 11	3
6-1-T	1979	1988	1994	Hersey	3+
6-2-T	1979	1988	1994	Hersey	2-
6-3-T	1987	1988	1994	Hersey	2
6-4-T	1974	1982	1994	T 5 R 11	3-
6-5-T	1976	1985	1995	T 5 R 11	3-
6-6-T	1979	1982	1994	T 5 R 11	3-
11-1-T	1975	1983	1989	T 1 R 13	3
11-2-T	1968	1987	1990	Spencer Bay	3-
11-3-T	1975	1983	1989	T 1 R 13	2-
11-4-T	1975	1986	1990	T 1 R 13	3
11-5-T	1975	1983	1989	T 1 R 13	2
11-6-T	1975	1984	1991	T 1 R 13	2-
16-1-T	1967	1986	1985	Spencer Bay	2-
16-2-T	1972	1980	1986	Days Acad.	3
16-3-T	1970	1977	1986	Days Acad.	2-
16-4-T	1969	1981	1986	Days Acad.	3+
16-5-T	1970	1981	1985	Days Acad.	3+
16-6-T	1968	1981	1984	Days Acad.	2-
1-1-C	1982	1988	n/a	T 4 R 11	4
1-2-C	1979	1983	n/a	T 4 R 11	3-
1-3-C	1981	1984	n/a	T 4 R 11	4+
1-4-C	1983	1988	n/a	T 5 R 11	4+
1-5-C	1976	1985	n/a	T 4 R 11	3-
6-1-C	1979	1988	n/a	Hersey	3+
6-2-C	1981	1988	n/a	Hersey	3+
6-4-C	1974	1982	n/a	T 5 R 11	4
6-5-C	1974	1985	n/a	T 4 R 12	3
6-6-C	1976	1983	n/a	T 4 R 11	4
11-1-C	1976	1982	n/a	T 5 R 11	3
11-3-C	1976	1982	n/a	T 5 R 11	3+
11-4-C	1974	1985	n/a	T 5 R 11	3

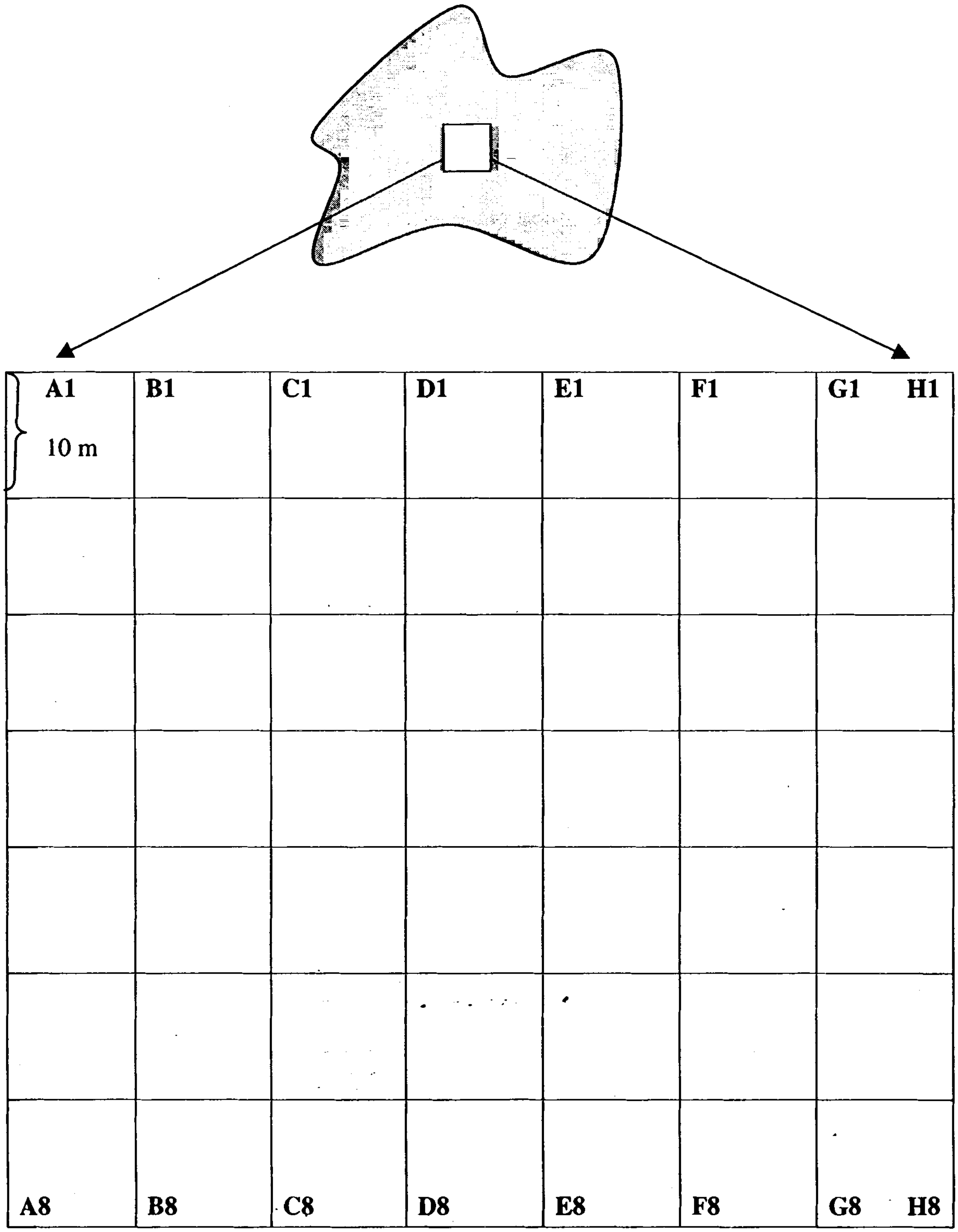

Figure 3.2. Small mammals were live-trapped during June-August 2000 and 2001 on 70 m by 70 m trapping grids established within PCT-treated (n = 24) and unthinned (n = 13) stands within 7 townships of northern Maine.

minimize edge-effects (Harris 1988, Fraver 1994). I placed one live-trap (B. N. Bolton, Inc. Vernon, B. C.; use of commercial names does not imply endorsement) baited with a mixture of rolled oats and peanut butter within 1 m of each trap station. Bolton live traps have an attached nest compartment to provide shelter and protection from predators. I placed 5 cotton balls in the nest compartment as material for nesting and placed the traps with the door facing downslope so that rainfall or condensation would drain. I covered traps with moss, leaves, and bark to provide additional thermal and visual protection.

I trapped each stand for 6 consecutive days and nights and tagged mice and voles with a unique, individually numbered ear-tag (Monel 1005-1; National Band and Tag Co., Newport, Kentucky). Short-tailed and masked shrews were not marked; therefore, only the number of captures was recorded for shrews. I recorded species, sex, age, and reproductive condition of each individual. I categorized small mammals as adult or juvenile by pelage color and relative size. I determined the reproductive condition of adult female mice and voles as lactating (mammaries swollen) or non-lactating (mammaries not swollen). Traps were checked from 0600 to 1300 hours, and after processing, animals were released at the trap site. The Institutional Animal Use and Care Committee, University of Maine, approved trapping and handling procedures. Field technicians took several safety precautions for hantavirus pulmonary syndrome. A baseline blood sample was drawn from technicians prior to handling of small mammals. Further, field technicians wore rubber gloves and full body coveralls when handling study animals, and traps were washed in a diluted bleach solution after each 6-day trapping session. Coveralls, traps, and trapping supplies were transported to and from study sites in an open-bed truck.

Within-stand habitat characteristics

I selected variables *a priori* that previous studies of habitat relationships of small mammals (Hamilton 1941, Miller and Getz 1977, Yahner 1986, Clough 1987, Hayes and Cross 1987, Carey and Johnson 1995, Lachowski 1997, Bowman et al. 2000b) have reported as important correlates or predictors of abundance. These variables included: total basal area, density of trees, total density of coarse woody debris, percent live ground cover, density of understory stems, and canopy density.

Habitat characteristics were measured within the small-mammal grids following the methods of Lachowski (1997) and Fuller (1999). I randomly selected 16 of the 64 trapping stations on the 37 trapping grids and oriented a 10-m by 2-m plot following a randomly selected compass direction at the center of each station. Within each plot I measured the diameter at breast height (dbh) of all coniferous trees and deciduous trees (≥ 7.6 cm dbh, ≥ 2 m height, > 45° from the ground) (DBH), and counted the number of herbaceous ground stems (HGSTEMS) (< 0.5 m height, < 7.6 cm dbh), number of deciduous and coniferous saplings (< 7.6 cm dbh, alive) at 1.5 m height (UNDERSTORY), the number of root masses (≥ 7.6 cm diameter), stumps (< 2 m height, ≥ 7.6 cm diameter), logs (≥ 1 m length, ≥ 7.6 cm diameter, < 45° from ground), and snags (≥ 7.6 cm dbh, ≥ 2 m height, > 45° from the ground) within the plot. I termed the number of logs/ha + stumps/ha + snags/ha as TOTDEBRIS. I measured the basal area of coniferous + deciduous trees (TOTBA) using a 2 m^2 / ha prism held at the center-point of the plot (Avery and Burkhart 2002). I measured percent canopy closure (CANOPY) at the 4 cardinal compass directions using a spherical densiometer held at waist height (Lemmon 1956).

Analysis of small mammal abundances

To determine if species-specific abundances met the parametric assumptions of Analysis of Variance (ANOVA), I examined across treatments and blocks for normality of residual errors using normal probability plots and Lilliefor's tests, and I examined data for constant variance using the modified Levene's test (Neter et al. 1996). I transformed data exhibiting heteroscedasticity (modified Levene's ≤ 0.10) or nonnormal errors (Lilliefor's ≤ 0.10) and then re-evaluated assumptions of normality and constant variance. The minimum number alive (MNA) of red-backed voles and MNA of deer mice were transformed using $\log_e$. Number of captures of short-tailed shrews (from 1-11 years post-treatment) met parametric assumptions following a square root transformation; however, number of captures of masked shrews did not meet assumptions after transformations and were analyzed using nonparametric alternatives to ANOVA.

To test whether the effects of PCT differed from effects of stand development, I conducted 2 separate analyses on the relative abundances (MNA and number of captures) of small mammals. I tested whether abundance of small mammals differed between stands treated with PCT and unthinned stands, from 1-11 years post-treatment, using a repeated-measures two-way ANOVA for each species (Zar 1999). I evaluated effects of treatment (PCT or unthinned), thinning class (1, 6, 11 years), year of sampling (2000 or 2001), and any interactions on the MNA index of abundance of red-backed voles, deer mice, and for the index of total number of captures for short-tailed shrews. I excluded the 16-year thinning class, which did not include any similar untreated stands, to avoid biasing effects and interactions with the 1, 6, and 11-year thinning classes.

Similarly, I used non-parametric alternatives to test whether number of captures of masked shrews differed between PCT and unthinned stands, by thinning class of stand, and between the 2 years of sampling. I examined for an effect of year by conducting a Wilcoxon signed rank test, while ignoring grouping factors (thinning class and treatment) (Zar 1999). Next, I summed the number of captures of masked shrews across 2000 and 2001 and ranked the resulting sum. I then conducted a two-way ANOVA with thinning class and treatment as main effects. I examined interaction terms with year in them by calculating the difference in number of captures between years, ranking the resulting data, and conducting a one-way ANOVA.

To evaluate changes in relative abundances of the 4 small mammal species in the PCT-treated stands through time, I conducted a repeated-measures ANOVA examining the effects of thinning class (1-year, 6-year, 11-year, 16-year post-thinning), year of sampling (2000 or 2001), and thinning class × year interaction with stands treated with PCT. I conducted this analysis on the MNA for both deer mice and red-backed voles. Non-parametric alternatives were necessary to analyze data for short-tailed and masked shrews. For shrews, I conducted a Wilcoxson signed rank test to determine if a year effect was present, and conducted a one-way ANOVA with thinning class as the main effect on the ranked sum of the number of captures in 2000 + 2001. I calculated the difference between years, ranked the resulting data, and conducted a one-way ANOVA to evaluate the presence of a year × thinning class interaction. I examined significant main effects for voles and mice *a posteriori* using pairwise comparisons using Tukey's honestly significant difference test (Zar 1999) and Bonferroni multiple contrasts for *a priori* selected pairwise comparisons for significant interaction terms (Neter et al. 1996).

Reproductive indices

I tested for differences in lactation rates of adult female deer mice and red-backed voles among treatment and control stands using a Chi-square test for proportions (Zar 1999). I captured few adult female small mammals during summer 2000; therefore, I pooled reproductive data for each species across years and stand-ages to maximize statistical power (the total number of adult female captures within each treatment ranged from 40-87).

Within-stand habitat analyses

The size of the trapping grid was approximately 1.0-2.5x the size of the average home range for red-backed voles and 0.3-3.0x for deer mice (Witt and Huntly 2001); therefore, within-stand habitat characteristics were described at the scale of the trapping grid. I averaged 6 overstory, understory, and CWD variables across the 16 sampling locations in each of 37 stands to produce an average value of each variable for each stand. Modified Levene's tests, Lilliefor's tests and normal probability plots were used to examine data for homoscedasticity and normal errors (Neter et al. 1996). DBH and UNDERSTORY were log transformed and CANOPY was arcsine transformed prior to analysis so that variables met parametric assumptions of ANOVA. I conducted a two-way ANOVA on the means of each habitat variable for the 1-year, 6-year and 11-year stands to examine for effects of thinning class (1-year, 6-year, 11-year), treatment (PCT or unthinned), and treatment × thinning class interaction. Significant pairwise differences among stand-ages were examined *a posteriori* with Tukey's honestly significant differences test (Zar 1999).

I tested for differences in habitat and structural variables among PCT stands of different (1-year, 6-year, 11-year, 16-year) ages since thinning by conducting a one-way ANOVA, with age-class as a main effect. Pairwise comparisons were conducted *a posteriori* using Tukey's honestly significant differences test (Zar 1999).

Sample sizes of thinned and unthinned stands ranged from only 3 to 6 within each class since thinning; thus, the probability of type II statistical error was relatively high. I attempted to balance type I and type II error by using $P < 0.10$ as my threshold for statistical inference.

RESULTS

Abundance of small mammals

I captured 600 red-backed voles (1,296 times), 399 short-tailed shrews, 386 masked shrews, 347 deer mice (824 times), 51 eastern chipmunks (*Tamias striatus*), 15 weasels (*Mustela spp.*), 11 red squirrels (*Tamiasciurus hudsonicus*), 10 woodland jumping mice (*Napeozapus insignis*), 5 smoky shrews (*Sorex fumeus*), 2 Southern bog lemmings (*Synaptomys cooperi*), and 1 meadow vole (*Microtus pennsylvanicus*) during 2000 and 2001, combined. Species except for red-backed voles, deer mice, short-tailed and masked shrews were excluded from further analyses of effects of PCT and thinning class on abundance because capture success was too low for a meaningful or statistically powerful analysis. Each of the 4 species of small mammal that were statistically evaluated exhibited different responses to treatment and thinning classes (Figures 3.3, 3.4, 3.5, 3.6, Table 3.2, 3.3), indicating strong effects of PCT and thinning class among red-backed voles, deer mice, short-tailed shrews, and masked shrews.

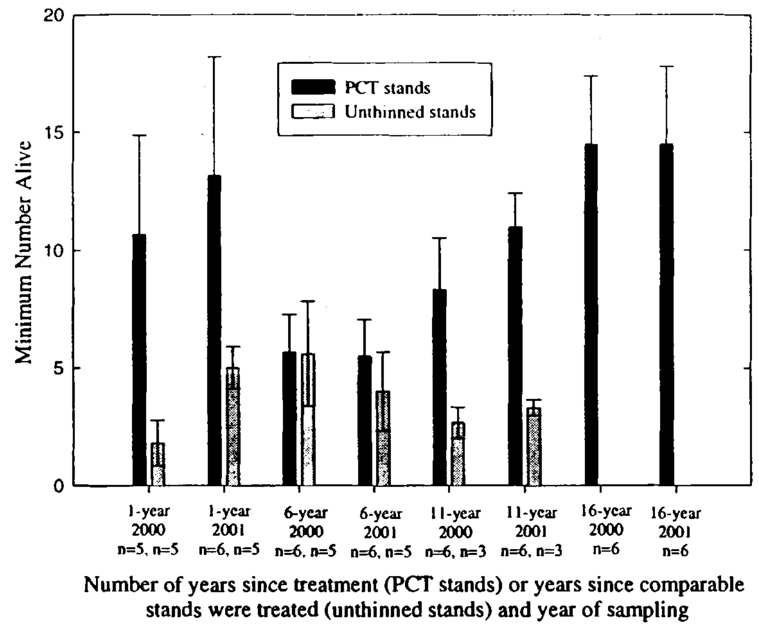

Figure 3.3. Mean minimum number alive (SE) of red-backed voles (*Clethrionomys gapperi*) in 24 stands treated with PCT and 13 unthinned stands during summer 2000 and 2001, northern Maine. Unthinned stands had similar years of clearcut and herbicide, and similar site quality to comparable PCT stands.

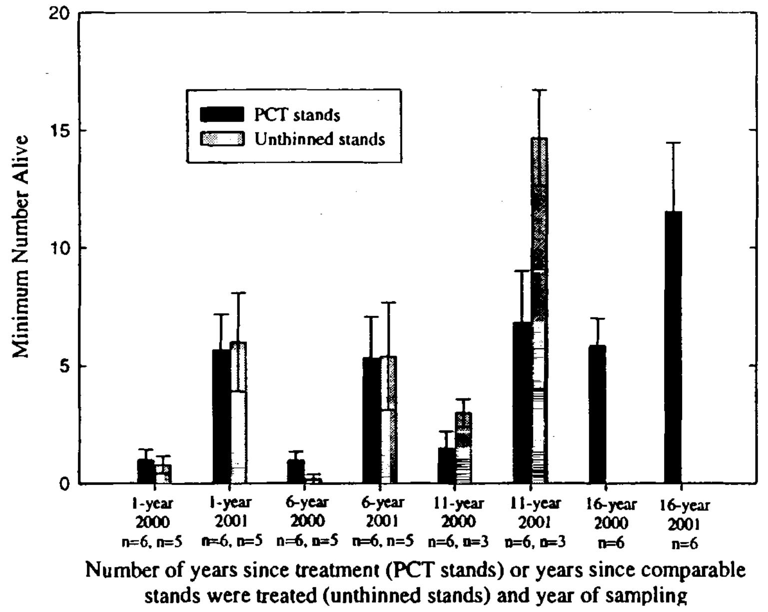

Figure 3.4. Mean minimum number alive (SE) of deer mice (*Peromyscus maniculatus*) in 24 stands treated with PCT and 13 similar unthinned stands during summer 2000 and 2001, northern Maine. Unthinned stands had similar years of clearcut and herbicide, and similar site quality to comparable PCT stands.

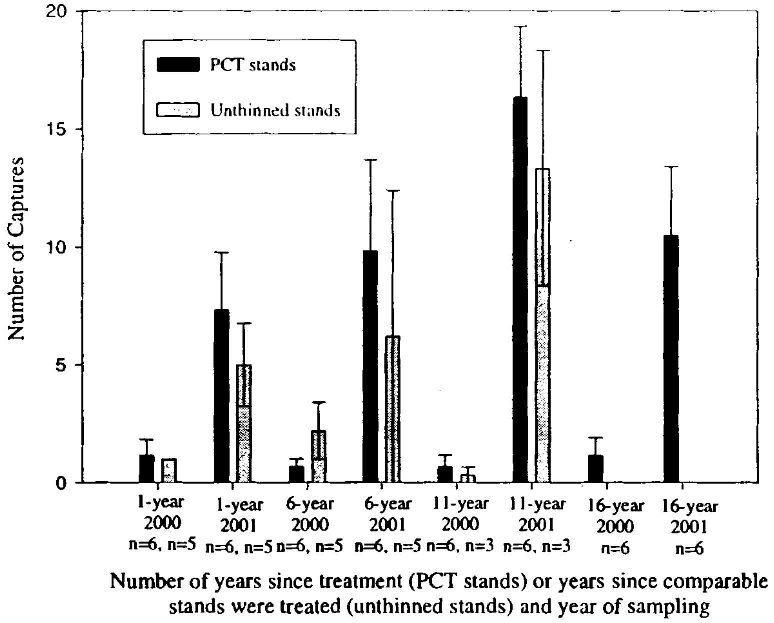

Figure 3.5. Total number of captures of short-tailed shrews (*Blarina brevicauda*) (SE) in 24 stands treated with PCT and 13 unthinned stands during summers 2000 and 2001, northern Maine. Unthinned stands had similar years of clearcut and herbicide, and similar site quality to comparable PCT stands.

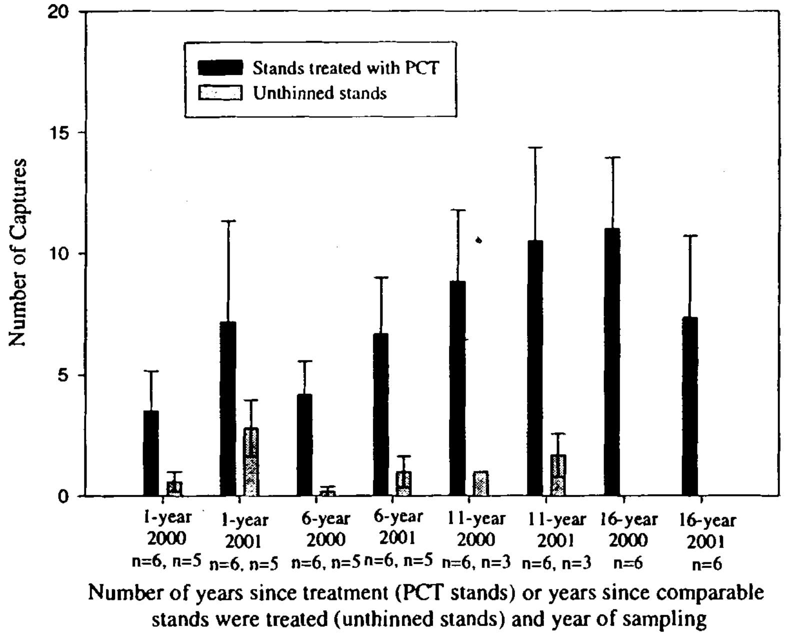

Figure 3.6. Total number of captures of masked shrews (*Sorex cinereus*) (SE) in 24 stands treated with PCT and 13 unthinned stands during summers 2000 and 2001, northern Maine. Unthinned stands had similar years of clearcut and herbicide, and similar site quality to comparable PCT stands.

Table 3.2. Comparisons of mean (SE) abundances (minimum number alive) of red-backed voles and deer mice and relative abundances (total number of captures) of short-tailed and masked shrews[a] on precommercially thinned stands (n = 18) and unthinned reference stands (n = 13) in northern Maine, 2000-2001. Data were analyzed using repeated-measures two-way Analysis of Variance; non-transformed means and standard errors are presented for transformed variables.[b]

	Species of small mammal[c]			
	Red-backed vole	Deer mouse	Short-tailed shrew	Masked shrew
Treatment				
F-Statistic	8.316	0.377	0.431	n/a
P-value	0.008	0.544	0.517	n/a
Abundance in PCT stands	9.06 (1.24)	3.56 (0.66)	6.00 (1.30)	6.81 (1.18)
Abundance in unthinned stands	3.84 (0.61)	4.42 (1.05)	4.35 (1.00)	1.19 (0.31)
Thinning class[d]				
F-Statistic	0.620	3.073	2.380	n/a
P-value	0.546	0.064	0.113	n/a
Abundance in 1-year stands	8.05 (1.96)	3.36 (0.80)	3.68 (0.95)	3.68 (1.28)
Abundance in 6-year stands	5.23 (0.82)	3.00 (0.84)	4.77 (1.32)	3.23 (0.90)
Abundance in 11-year stands	7.44 (1.15)	5.72 (1.35)	7.94 (2.16)	6.89 (1.81)
Year of sampling				
F-Statistic	3.815	29.271	51.175	n/a
P-value	0.062	< 0.001	< 0.001	n/a
Abundance in 2000	6.23 (1.12)	1.13 (0.23)	1.03 (0.26)	3.42 (0.86)
Abundance in 2001	7.52 (1.23)	6.71 (0.89)	9.58 (1.33)	5.48 (1.28)
Treatment × Thinning class				
F-Statistic	2.934	2.337	0.242	n/a
P-value	0.072	0.117	0.787	n/a

Table 3.2. Continued.

	Species of small mammal			
	Red-backed vole	Deer mouse	Short-tailed shrew	Masked shrew
Treatment × Year				
F-Statistic	0.389	0.277	1.175	n/a
P-value	0.539	0.604	0.289	n/a
Thinning class × Year				
F-Statistic	1.389	0.262	4.156	n/a
P-value	0.268	0.771	0.028	n/a
Treatment × Thinning class × Year				
F-Statistic	2.546	1.656	0.055	n/a
P-value	0.099	0.211	0.947	n/a

[a] Number of captures of masked shrews were not distributed normally; therefore a nonparametric analyses was conducted. Results are presented in the text.

[b] MNA of red-backed voles and deer mice were log transformed and number of captures of short-tailed shrews were square root transformed. The non-transformed mean and SE are presented here.

[c] Red-backed vole (*Clethrionomys gapperi*), deer mouse (*Peromyscus maniculatus*), short-tailed shrew (*Blarina brevicauda*), masked shrew (*Sorex cinereus*).

[d] Stands in the 1-year thinning class include stands (n = 6) that were treated with PCT in 1999 and unthinned stands (n=5). Stands in the 6-year thinning class include stands treated with PCT (n = 6) in 1994-1995 and unthinned stands (n = 5). Stands in the 11-year thinning class include stands (n = 6) that were treated with PCT 1989-1991 and unthinned stands (n = 3). Unthinned stands had similar years of clearcut and herbicide, and similar site quality to comparable PCT stands.

Table 3.3. Comparison of mean (SE) abundances (minimum number alive) of red-backed voles and deer mice and median (range) of number of captures of short-tailed shrews and masked shrews across 4 thinning classes of stands treated with PCT (1-year post-treatment, n = 6; 6-years post-treatment, n = 6; 11 years post-treatment, n = 6; 16 years post-treatment, n = 6) in northern Maine, 2000-2001. Means were compared using one-way ANOVA and medians were compared using nonparametric analyses[a]; non-transformed means and standard errors are presented for deer mice.

	Species of small mammal[b]			
	Red-backed vole	Deer mouse	Short-tailed shrew[a]	Masked shrew[a]
Thinning class[c]				
F-statistic	1.837	3.423	1.755	1.567
P-value	0.173	0.037	0.188	0.228
1-year	11.917 (3.156)	3.333 (1.032)	3 (0-18)	1.5 (0-25)
6-years	5.583 (1.062)	3.167 (1.072)	1.5 (0-27)	5 (0-17)
11-years	9.667 (1.305)	4.167 (1.359)	6 (0-28)	9.5 (1-25)
16-years	14.500 (2.091)	8.667 (1.738)	3.5 (0-22)	9.5 (0-20)
Year of sampling				
F-statistic	1.042	14.259	Z = 4.154	Z = 0.383
P-value	0.320	< 0.001	< 0.001	0.702
2000	9.792 (1.507)	2.333 (0.547)	0 (0-4)	4.5 (0-19)
2001	11.042 (1.652)	7.333 (1.135)	9.5(0-28)	5 (0-25)
Thinning class × Year				
F-statistic	0.397	3.502	2.017	0.599
P-value	0.757	0.034	0.144	0.623

[a] Presence of a year-effect for shrews was tested for using a Wilcoxsin signed rank test. An effect of age-class was tested for using a one-way ANOVA on the ranked sum of the number of captures in 2000 + 2001 and an age-class × year interaction term was tested for with the difference in abundances between years.

[b] Red-backed vole (*Clethrionomys gapperi*), deer mouse (*Peromyscus maniculatus*), short-tailed shrew (*Blarina brevicauda*), masked shrew (*Sorex cinereus*).

[c] Stands in the 1-year age-class include stands (n = 6) that were treated with PCT in 1999. Stands in the 6-year age-class include stands treated with PCT (n = 6) in 1994-1995. Stands in the 11-year age-class include stands (n = 6) that were treated with PCT 1989-1991.

I did not detect an effect of thinning class of stands on voles (P = 0.546), but there was a significant treatment × thinning class interaction (P = 0.072) (Table 3.2). Although red-backed voles were 2.5× more abundant in stands treated with PCT than unthinned stands (P = 0.008), the effect of PCT was not consistent across thinning-classes. Thinned stands had greater numbers of voles in the 1-year (P < 0.001) and 11-year age-class (P < 0.005), but treatments had similar abundances in the 6-year thinning class (P > 0.600). There was significant inter-annual variation in abundances of voles; a greater number were captured during 2001 (n = 233) than 2000 (n = 193) (P = 0.062). A significant year × thinning class × treatment interaction (P = 0.099) was observed indicating that the effects of PCT on voles were inconsistent across thinning classes of stands and years of sampling. Within solely PCT stands, from 1 to 16 years post-treatment, I did not detect an effect of year since thinning (thinning class, P = 0.173), year of sampling (P = 0.320), or a thinning class × year interaction term (P = 0.757) on the abundance of red-backed voles (Table 3.3).

Differences between the MNA of deer mice in thinned and unthinned stands was not significant (P = 0.544) from 1 to 11 years post-treatment (Table 3.2). Abundances of deer mice were different among thinning classes (P = 0.064); however interpretations were confounded by a significant (P = 0.034) thinning class × year interaction. The 16-year thinning class had 2.1-2.7× greater abundance of deer mice than each of the 3 younger thinning classes (Table 3.3). Across all thinning classes, abundance of deer mice was nearly 4× greater in 2001 (n = 277) than in 2000 (n = 70) (P < 0.001) (Table 3.3).

Treatment and thinning class of stands did not have a detectable effect on the number of captures of short-tailed shrews from 1 to 11 years post-treatment (P > 0.100).

There was, however, a marked change (9.2×) in shrew abundance between 2000 and 2001 ($P < 0.001$). Additionally, there was an inconsistent effect of thinning class on abundance of short-tailed shrews across the 2 years sampled (thinning class × year interaction, $P = 0.028$). During 2000, the 3 thinning classes had similar abundances ($P > 0.10$), but during 2001 the 11-year age-class had greater numbers of shrews than the 1-year age-class ($P < 0.01$).

Masked shrews responded strongly and positively to thinning ($P < 0.001$) and abundances were 5.7× greater in thinned stands than in similar reference stands, from 1 to 11 years post-treatment. I did not detect a significant effect of year of sampling or thinning class on masked shrews ($P > 0.10$); however, the treatment × thinning class interaction was significant ($P = 0.092$), indicating that there was an inconsistent effect of PCT across the 3 thinning classes. Pairwise comparisons indicated that stands treated with PCT had greater numbers of masked shrews than in unthinned stands in the 6-year ($P < 0.001$) and 11-year ($P < 0.001$) thinning classes, but not within the 1-year stands ($P = 0.82$).

Reproductive indices

No significant difference ($\chi^2 = 0.93$, $P = 0.34$) in the proportion of lactating adult female red-backed voles was observed between stands treated with PCT (41%, n = 187, 90 % C.I. 33 – 48 %) and unthinned reference stands (30%, n = 40, 90 % C.I. 16 –46 %). A greater proportion of adult female deer mice were lactating ($\chi^2 = 9.18$, $P < 0.001$) on unthinned stands (58 %, n = 43, 90 % C.I. 42 –72 %) than in thinned stands (31 %, n = 108, 90 % C.I. 23-41 %).

Habitat in PCT versus unthinned stands

Of the 6 *a priori* selected microhabitat variables, average diameter at breast height of trees was 1.15× greater (P = 0.003), total basal area was 1.38× greater (P = 0.002), and understory density was 1.40× greater (P = 0.022) within small mammal grids that had been treated with PCT, compared to grids within unthinned stands with a similar history of clearcutting and herbiciding (Table 3.4). Canopy closure was greater in unthinned stands than in stands treated with PCT up to 11-years post-treatment (P = 0.009). Canopy closure differed among thinning classes (P = 0.040); pairwise comparisons indicated that the 11-year thinning class had greater canopy closure than the 1-year thinning class (P = 0.070). Total understory density differed by thinning class, and the 6-year thinning class had a greater density of understory stems/ha than the 1-year (P = 0.008) or 11-year (P = 0.023) thinning classes.

Temporal effects of PCT on within-stand habitat characteristics

Average dbh, canopy closure, and total basal area generally increased with thinning class (Table 3.5). The 1-year thinning class had a lower dbh than the 6, 11, or 16-year thinning class (P = 0.080). Canopy closure (P = 0.011) and total basal area (P = 0.076) were greater in the 16-year thinning class than the 1-year thinning class. The 16-year thinning class also had greater total basal area than the 6-year thinning class (P = 0.018). Abundance of coarse woody debris was greater 11 years after treatment compared to 16 years post-thinning in PCT-treated stands (P = 0.005), but there were not differences in total amount of CWD between treatments (P = 0.180) or among thinning classes (1-year, 6-year, 11-year; pooled across treatments) (P = 0.231). Density of understory stems was greater 6-years post thinning than 1-year post-thinning (P = 0.001).

Table 3.4. Comparison of means (SE) for 6 habitat variables selected *a priori* between precommercially thinned stands (n = 18) and unthinned reference stands (n = 13) in northern Maine, 2000-2001. Differences in means by treatment for each variable were tested using two-way Analysis of Variance; non-transformed means and standard errors are presented for transformed variables[a].

	DBH[b]	CANOPY[c]	HGSTEM[d]	TOTDEBRIS[e]	TOTBA[f]	UNDERSTORY[g]
Treatment						
F-Statistic	11.171	8.417	1.321	1.900	12.351	5.928
P-value	0.003	0.009	0.261	0.180	0.002	0.022
PCT (n = 18)	12.7 (0.4)	74.68 (2.85)	400,398 (47,545)	1,531 (132)	20.19 (0.99)	3,376 (507)
No PCT (n = 13)	10.5 (0.2)	81.35 (2.17)	279,865 (56,379)	2,038 (172)	26.11 (2.09)	2,397 (676)
Thinning-class[h]						
F-Statistic	2.521	3.672	0.070	1.553	1.623	9.248
P-value	0.101	0.040	0.933	0.231	0.217	0.001
1-year (n = 11)	10.6 (0.3)	69.87 (5.07)	323,563 (74,625)	1,946 (257)	20.49 (1.81)	1,642 (271)
6-year (n = 11)	11.9 (0.7)	75.1 (2.4)	301,463 (42,658)	1,602 (121)	21.4 (2.7)	5,028 (990)
11-year (n = 9)	12.0 (0.5)	82.13 (3.18)	376,191 (89,445)	2,063 (157)	24.32 (1.45)	2,125 (429)
Treatment × thinning class						
F-Statistic	6.256	0.767	0.639	1.611	0.587	3.619
P-value	0.006	0.439	0.566	0.220	0.563	0.042

[a] DBH and UNDERSTORY were log transformed prior to analysis.

[b] DBH = average diameter breast height (cm) of closest tree (≥ 7.6 cm dbh, ≥ 2 m height, > 45° from horizontal, alive) in each quarter.

[c] CANOPY = average overhead percent canopy closure during summer.

[d] HGSTEMS = number of herbaceous ground stems (< 0.5 m height, < 7.6 cm dbh, alive) per ha.

[e] TOTDEBRIS = number of (snags + logs + stumps + root masses) per ha.

[f] TOTBA = Basal area of hardwood trees + softwood trees + snags (m^2/ha).

[g] UNDERSTORY = total number of understory stems (number of saplings (≤ 7.6 cm dbh, alive) at 1.5 m height per ha.

[h] Stands in the 1-year thinning class include stands (n = 6) that were treated with PCT in 1999 and similar unthinned stands (n=5). Stands in the 6-year thinning class include stands treated with PCT (n = 6) in 1994-1995 and similar unthinned stands (n = 5). Stands in the 11-year thinning class include stands (n = 6) that were treated with PCT 1989-1991 and similar unthinned stands (n = 3). Unthinned stands had similar years of clearcut and herbicide, and similar site quality to comparable PCT stands.

Table 3.5. Comparisons (one-way ANOVA) of mean (SE) values for 6 habitat variables across 4 thinning classes[a] based on years since precommercial thinning within 24 herbicided, regenerating clearcut stands treated with PCT in northern Maine. Non-transformed means and standard errors are presented for transformed variables[b].

Factor	DBH[c]	CANOPY[d]	HGSTEM[e]	TOTDEBRIS[f]	TOTBA[g]	UNDERSTORY[h]
Thinning class						
F-statistic	8.120	4.336	0.861	5.079	4.462	6.569
P-value	0.001	0.017	0.478	0.009	0.015	0.030
1-year	10.5 (0.3)	62.33 (8.05)	325,927 (84,972)	1,578 (303)	18.15 (2.43)	1,630 (494)
6-year	13.4 (0.8)	72.68 (3.52)	323,792 (72,761)	1,490 (147)	16.56 (1.28)	5,848 (1,330)
11-year	12.5 (0.6)	77.66 (3.28)	454,073 (18,424)	2,115 (239)	21.92 (0.93)	2,745 (400)
16-year	14.5 (0.7)	86.04 (1.76)	497,802 (101,478)	943 (101)	24.15 (1.53)	3,281 (796)

[a] Stands in the 1-year thinning class include stands (n = 6) treated with PCT. Stands in the 6-year thinning class include stands treated with PCT (n = 6) in 1994-1995. Stands in the 11-year thinning class include stands (n = 6) treated with PCT 1989-1991. Stands in the 16-year thinning class include stands (n = 6) treated with PCT in 1984-1986.

[b] DBH and UNDERSTORY were log transformed and CANOPY was arcsine transformed prior to analysis.

[c] DBH = average diameter breast height (cm) of closest tree ($\geq$ 7.6 cm dbh, $\geq$ 2 m height, > 45° from horizontal, alive) in each quarter.

[d] CANOPY = average overhead percent canopy closure during summer.

[e] HGSTEMS = number of herbaceous ground stems (< 0.5 m height, < 7.6 cm dbh, alive) per ha.

[f] TOTDEBRIS = number of (snags + logs + stumps + root masses) per ha.

[g] TOTBA = Basal area of hardwood trees + softwood trees + snags (m^2/ha).

[h] UNDERSTORY = total number of understory stems (number of saplings ($\leq$ 7.6 cm dbh, alive) at 1.5 m height per/ha.

DISCUSSION

PCT positively affected or produced no detectable effect on abundances of the 4 most common species of voles, mice, and shrews on my study areas. From 1-11 years post-thinning, the abundances of red-backed voles and masked shrews were greater in stands treated with PCT and abundances of deer mice were not significantly affected by thinning. A trend of greater abundances of short-tailed shrews in stands treated with PCT was evident; however, high variation between stands and low abundances likely prevented statistical differences for that species. Short-tailed shrews, red-backed voles, and deer mice exhibited large inter-annual variation. Despite substantial annual variation in densities within treatments, abundances of deer mice increased with thinning class within regenerating conifer stands in northern Maine.

Reducing competition among crop trees via precommercial thinning accelerated stand development in regenerating clearcut stands with a prior history of gylphosate application. Stands treated with PCT acquired some attributes of more mature forest (without PCT) such as greater stem diameters, diverse understories, and a more broken canopy layer. The silvicultural response of forest stands treated with PCT was consistent with previous reports (Brissette et al. 1999, Brissette and Frank 1999, Lindgren and Sullivan 2001, Sullivan et al. 2001, Pothier 2002); significant increases in dbh of trees, canopy density, and basal area were observed from 1 to 16 years post-treatment.

The acceleration of stand development that occurs within PCT-treated stands was favorable or neutral for common species of small mammals in the Acadian forest. By producing stands containing some characteristics of more mature forest (broken canopy, larger stem diameters), PCT has the potential to increase heterogeneity of forest stand conditions across the mid-successional dominated landscapes that presently occur throughout much of the Acadian forest (Maine Forest Service 1998). As forest rotations associated with intensive management become increasingly shorter, the acceleration of mature stand conditions via PCT across significant portions of the forest landscape could help mitigate some effects of intensive silviculture on small mammals.

Within-stand habitat structure

I observed larger trees, a more open canopy, and more understory stems in stands treated with PCT. The growth of overstory trees and temporary opening of the overstory layer that occurred from 1-6 years post-thinning produced within-stand habitat characteristics more typical of conifer stands in later seral stages, when compared to unthinned stands. Penetration of sunlight allowed understory stems to flourish temporarily from 1-6 years post-treatment, but by 11-years post-PCT understory stem density had declined. Advanced regeneration was released initially from competition and shading in thinned stands; however, a delayed self-thinning response occurred from 6-11 years post-thinning.

Coarse woody debris has often been touted as an element of forested stands that is necessary to maintain small mammal communities. Downed and dead woody material has been suggested to provide subnivian access in winter, habitat for invertebrates, escape cover from predators, growing surface for fungi, and to mediate microclimate by retaining moisture (Hamilton 1941, Hayes and Cross 1987, Hagan and Grove 1999, Fraver et al. 2002). The total density of logs, snags, stumps, and root masses did not differ between thinned and unthinned stands, or among thinning classes of stands; however, 16-year post-PCT stands had less CWD than 11-year post-PCT stands, suggesting that CWD may be lost to decay but not recruited in PCT stands after 11-years post-thinning. Many of the highest small mammal numbers were observed in thinned stands, and especially in the 16-year stands, indicating that CWD may not be limiting from the perspective of forest-dwelling voles, mice, and shrews in regenerating clearcuts or in intensively managed stands. This finding is consistent with other studies in Maine, which have detected few strong relationships among abundances of small mammals and CWD throughout a range of forest types, thinning classes, and harvesting regimes (Lachowski 1997, Fuller 1999, S. Billig, *In prep.*).

Red-backed voles

Red-backed voles have been reported to have ecological relevance as indicators of late successional forest, because their greatest densities often occur in mature or over-mature stands (Martell 1983b, Nordyke and Buskirk 1991). Contrary to those results, voles were abundant across three thinning classes of mid-successional stands in the Acadian forest and I observed no significant effect of thinning class on abundances. Greater abundances of voles were observed in stands treated with PCT; additionally, the proportion of female voles lactating on thinned stands was not detectably different than the proportion lactating on unthinned stands, indicating that habitat quality for voles may have been comparable between treatments. Red-backed voles were the most common species of small mammal within stands 14-33 years post clearcutting (13-24 years post-herbicide treatment). Therefore, the mesic conifer-dominated Acadian forest may accumulate habitat characteristics typical of mature forest more rapidly than in conifer stands of Ontario (Martell 1983b) and the central Rocky Mountains (Nordyke and Buskirk 1991). Abundance of red-backed voles in PCT stands temporarily declined at 6-

years post-treatment, which coincided with the greatest density of understory stems (Table 3.4, 3.5). These results are inconsistent with findings from Wyoming, where understory cover was positively associated with abundance of red-backed voles in conifer stands of various successional stages (Nordyke and Buskirk 1991).

Deer mice

Deer mice are widely considered a habitat generalist and have been reported to respond positively to reduction of the forest overstory following clearcut harvesting (Martell and Radvanyi 1977, Martell 1983a, Martell 1983b, Morrison and Anthony 1988, Kirkland 1990, Sullivan et al. 1999). However, previous studies have indicated that deer mice exhibit little response to PCT of conifer stands (Lautenschlager et al. 1997, Sullivan et al. 2001). Consistent with previous research, I observed that abundances of deer mice were similar among PCT-treated and unthinned stands on my study areas. The greatest abundance of deer mice was observed in the 11 year thinning class, which, pooled across years, was 1.56x greater than the 6-year and 1.40x greater than the 1-year thinning classes. Further, across the 4 classes of stands treated with PCT, the 16-year post-PCT stands had the greatest numbers of deer mice in both 2000 and 2001. The positive effects of thinning class on numbers of deer mice were consistent between years of sampling despite a nearly 4-fold increase in total number of individuals from 2000 to 2001. These observations that populations of deer mice on my study area reached their greatest densities in older stands indicate that attributes of stand maturity may have had a greater influence on densities of deer mice than PCT. Previous investigations of forest-dwelling small mammals have also detected greater abundances of deer mice in older stands than in regenerating stands in the commercial forests of Maine (Lachowski 1997, Fuller 1999).

Although densities of adult female deer mice were similar between thinned (averaged 2.3/grid) and unthinned conifer (averaged 1.7/grid) stands, a greater proportion of adult female deer mice were lactating in unthinned stands compared to similar PCT-treated stands. Reproductive output of deer mice may have been affected by treatment; deer mice often have aggressive intra-specific interactions (Martell 1983a), which may lead to subordinate, non-reproductive individuals occupying areas with lower habitat quality (Van Horne 1983). The observed difference in lactation rates of adult female deer mice between thinned and unthinned stands suggest that habitat quality could be greater in stands without PCT; however, additional information on survival and reproductive success is necessary to evaluate this hypothesis.

Short-tailed shrews

Short-tailed shrews did not significantly respond to thinning from 1-11 years post-treatment or to thinning class, either pooled across treatments or within only the PCT-treated stands from 1-16 years after thinning. However, small numbers of individuals captured/grid in addition to large variation of abundances of short-tailed shrews between grids, may have precluded my detection of a positive effect of PCT. *B. brevicauda* are reported to reach their greatest densities in stands with complex understories with abundant herbaceous vegetation (Miller and Getz 1977, Brooks and Healy 1988, Healy and Brooks 1988, Kirkland 1990), which may be related to positive associations between insects and diversity of plant species and structure (Murdoch et al. 1972). Although 6-year stands had the greatest density of herbaceous vegetation, I did not detect greater abundances of shrews in those stands, which suggests that prey was distributed evenly among treatment and thinning classes, or was not limiting across all sites. Abundance of short-tailed shrews in my study areas was likely related to sub-stand scale attributes other than those that are associated with thinning. The changes in forest structure that occur after thinning and with stand maturation apparently do not exert a strong influence on relative abundance of *B. brevicauda*.

Masked shrews

PCT produced positive and long-lasting effects on the relative abundance of masked shrews in regenerating conifer stands in northern Maine. Number of captures were 4.38 and 10.21× greater in stands treated with PCT than similar unthinned stands up to 11-years post-treatment when data were pooled across thinning classes. In contrast to the greater numbers of masked shrews that I observed in thinned versus unthinned stands, combined densities of masked shrews and pygmy shrews (*Sorex hoyi*) were similar among herbicided stands and stands thinned with brush-saws (but not herbicided) 1-2 years post-treatment in Ontario (Lautenschlager et al. 1997). Application of herbicide has substantial and long-lasting effects on composition and abundance of tree species within stands (Newton et al. 1989, Daggett and Wagner, *In prep.*); therefore, inconsistencies reported between this study and results reported from Ontario likely resulted from the application of either herbicide or PCT, but not both treatments on study sites in Canada.

The positive effects of PCT on masked shrews that I observed suggests that microhabitat structure associated with thinning enhances abundance of masked shrews across a range of thinning classes, from 1 to 11-years post-thinning. Herbaceous vegetation often flourishes after PCT (Hurst et al. 1982, Bell et al. 1997, Thomas et al. 1999, Lindgren and Sullivan 2002), because opening of the canopy allows sunlight to reach the forest floor. Dense herbaceous vegetation may have provided cover to shrews, supported greater densities of foliar-insect prey (Murdoch et al. 1972), or been associated with moister microclimate (Miller and Getz 1977).

CONCLUSIONS

Small mammals had species-specific responses to both PCT and stand development, which complicates prescriptions of forest management activities to increase densities and diversity within small mammal communities. These results indicate that PCT, across an 11-year range since treatment, positively or neutrally affects the abundance of the 4 most common species of small mammals (red-backed voles, deer mice, short-tailed shrews, masked shrews) in the commercial forests of northern Maine. Greater abundances of red-backed voles and masked shrews occurred in stands treated with PCT than in unthinned stands, from 1 to 11-years post-treatment, whereas deer mice and short-tailed shrews did not appear to be affected by PCT. Thinning increased or maintained overall abundances of forest-dwelling small mammals across a range of years since treatment, suggesting that PCT produces positive and long-term responses within the small mammal community. However, lactation rates for deer mice were lower in thinned stands. Additionally, several habitat attributes (e.g. basal area, dbh, canopy closure) that are positively associated with degree of stand maturity were greater in stands treated with PCT than in unthinned stands.

Additional to attaining silvicultural and economic objectives, forest managers may be able to increase the abundance of small mammals across commercial forest landscape via PCT. An increase in the number of small mammals could also have positive effects on other trophic levels, including forest-dependent predators, such as

American Marten (*Martes americana*) (Lachowski 1997) if other structural requirements for denning, rest sites, escape cover (Buskirk 1984, Payer and Harrison 2000), and subnivian access (Sherburne and Bissonette 1994) are present. Increased rates of stand development associated with PCT may help compensate for the short rotations (< 60 years) commonly applied to intensively managed stands in the Acadian forest (Seymour and Hunter 1992). Maintaining significant portion of the landscape in PCT, however, may involve trade-offs for early-successional dependent forest mammals such as snowshoe hare (Sullivan and Sullivan 1988, Chapter 2) and their predators (e.g. Canada lynx (*Lynx canadensis*)). Although this study evaluated stand-scale effects of PCT, broader landscape-scale evaluations of PCT are needed to reconcile silvicultural objectives with desired balances between conflicting habitat needs of early (e.g. snowshoe hare) and mid-successional (e.g. red-backed voles, masked shrews) wildlife species.

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CHAPTER 4

HABITAT AND STRUCTURAL DIFFERENCES BETWEEN PRECOMMMERCIALLY THINNED AND UNTHINNED CONIFER STANDS: IMPLICATIONS FOR WILDLIFE

ABSTRACT

Effects of precommercial thinning (PCT) in young, high-density forest stands on the growth and yield of crop trees has been well-studied, but effects on habitat characteristics, structural attributes, and wildlife populations is lacking. I examined the dominant changes in habitat characteristics and forest structure that occur with PCT and stand development in commercial spruce-fir stands within the Acadian forest of northern Maine. I selected 30 regenerating, herbicide-treated conifer stands (17 treated with PCT) of 3 thinning classes (1, 6, or 11-years) in 6 townships and measured 27 variables that described the characteristics and structure of the understory, overstory, woody debris, or ground cover on 20 circular plots per stand. I conducted a two-way Analysis of Variance (ANOVA) on the stand-scale means of each habitat variable to examine for the effect of treatment (treated with PCT or unthinned) or thinning class (1, 6, or 11-years). Variables with a F-statistic > 2.0 for either main effect were retained for inclusion into a principal components analysis (PCA). Two separate PCAs were conducted; 1 included variables that differed by treatment, and 1 included variables that differed among thinning classes. Changes in vegetation structure that occur with PCT were described by 3 principal components, which accounted for > 80% of the variation: near-ground cover, overstory cover, and understory structure. Horizontal cover, an overstory to understory contrast, and a gradient of herbaceous vegetation described differences in habitat and forest

structure among thinning classes; these components described > 75% of the variation that occurred with development of forest stands. The application of PCT accelerated some characteristics of stand development, resulting in a reduction of understory structure and complexity. However, PCT and the shorter rotations associated with intensively managed stands may reduce recruitment of logs and coarse woody debris (CWD). Species-specific responses of wildlife will likely be associated with the changes in forest structure that occur with PCT and stand development; species that are associated with early successional habitat, including snowshoe hare (*Lepus americanus*) and shrub-nesting songbirds, have been documented to respond negatively to thinning. Other forest-wildlife associated with more mature forest, however, such as red-backed voles (*Clethrionomys gapperi*), and perhaps spruce grouse (*Falcipennis candadensis*), may increase their densities following PCT.

INTRODUCTION

Precommercial thinning (PCT) of overstocked, regenerating conifer stands has been practiced increasingly in Maine and other jurisdictions within the Acadian forest of eastern North America (Maine Forest Service 1994-2001, Canadian Council of Forest Ministers 2002) to reduce competition, increase growth rates, and to shorten rotation length. In the late 1980's, forest landowners thinned about 2,400 hectares of densely stocked, regenerating clearcuts each year in Maine; by 2000 the total acres of land treated with PCT each year had risen to > 8,100 hectares a year, or 3.5% of the total silvicultural activity for the state (Maine Forest Service 2000-2002). The eastern Maritime Provinces of Canada have also experienced large increases in the land area treated with PCT; from 1990 to 2000 the acreage treated with PCT each year increased by 2.5-fold in Nova

Scotia, 2.7-fold in New Brunswick, and 4.3-fold in Quebec (Canadian Council of Forest Ministers 2002). Although the application of PCT to regenerating clearcuts has increased across the commercial forest landscape of the Acadian forest, the ecological effects of PCT on structural attributes of forest stands and the potential influences of structural changes on forest-dependent wildlife have been studied little.

The silvicultural response of crop trees to PCT have been well-documented; thinning increases stem diameters (Harrington and Reukema 1983, Ker 1987, McCormack and Lemin 1998, Brissette and Frank 1999, Brissette et al. 1999, Pothier 2002), increases crown size (McCormack and Lemin 1998, Brissette and Frank 1999, Brissette et al. 1999, Lindgren and Sullivan 2001, Sullivan et al. 2001), decreases mortality of crop trees (Ker 1987, Brissette and Frank 1999, Brissette et al. 1999), increases merchantable volume (Ker 1987), and may reduce rotation length (Sullivan et al. 2001). In contrast, the immediate and long-term ecological changes in habitat characteristics and forest structure that are associated with PCT of overstocked conifer stands are poorly understood. Most studies of structural and habitat changes associated with PCT have focused on short-term (1-3 years post-treatment) changes in understory and overstory characteristics and have been conducted on stands that were thinned, but not previously treated with herbicide (Bell et al. 1997, Sullivan and Lindgren 2001), which is a general practice throughout much of the Acadian forest. The application of herbicide several years before thinning likely has strong effects on overstory and understory responses to subsequent PCT (Dagget and Wagner *In prep.*). Understanding the long-term changes in forest overstory and understory structural attributes and habitat characteristics that occur after PCT of conifer stands is a prerequisite to evaluating biological consequences, to making informed forest management decisions, and to establishing ecological policies.

Manipulation of stem densities in regenerating clearcut stands may have negative consequences for species associated with early successional habitat (Hayes et al. 1997). In contrast, PCT of regenerating stands may diversify second and third growth forests by more rapidly producing stands with characteristics of forest in later seral stages (Carey and Johnson 1995, Hayes et al. 1997, Sullivan et al. 2001). The objectives of this study were to describe the biological changes across a range of intervals since treatment, in habitat characteristics and structural attributes between PCT and non-PCT treated clearcuts with a previous history of herbicide treatment in northern Maine. Instead of focusing on diversity of plant species after thinning (Thomas et al. 1999, Lindgren and Sullivan 2001), the goal of this effort was to describe structural attributes relevant to predicting responses of forest-dependent wildlife to PCT and to stand development in herbicide-treated clearcuts.

STUDY AREA

The study area was located within the matrix of commercial, mixed northern hardwoods-spruce-fir forest of northern Maine. I sampled 30 stands distributed across 6 townships in northern Maine, which spanned 102 km east to west and 49 km north to south. Stands were located in the town of Hersey, T4 R 11 WELS, T 5 R 11 WELS, T4 R 12 WELS, T1 R 13 WELS, and Spencer Bay. These townships were extensively clearcut-harvested during and following the spruce-budworm outbreak of the 1980's and many clearcuts were treated with an aerial herbicide to promote softwood regeneration. Great Northern Paper Company, Millinocket, Maine; Plum Creek Timber, Fairfield, Maine; and International Paper Company, Costigan, Maine managed those townships for pulpwood and timber production. The study area receives abundant precipitation (101 cm annually), with an average of 276 cm falling annually as snowfall, and seasons include mild summers (July mean maximum = 25° C) and cold winters (January mean minimum = -19° C) (Garoogian 2000).

I sampled stands that had been clearcut (timber harvesting resulting in residual basal area of acceptable growing stock trees > 4.5 in. dbh of < 30 ft^2/acre) 1968-1982, treated with an aerial herbicide (e.g. Glyphosate at ≈ 1.68 kg/ha acid equivalent) 1982-1988, and either precommercially thinned with brush-saws 1989-1999 (n = 17) or unthinned (n = 13) (Table 4.1). Balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), and black spruce (*Picea nigra*) were the dominant tree species, but stands also had small components of white pine (*Pinus strobus*), larch (*Larix spp.*), white cedar (*Thuja occidentalis*), paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*) and red maple (*Acer rubra*). Chapter 2 contains a more detailed description of the study sites.

METHODS

Stands were selected based on stand history, size, spatial independence, and site quality. I selected stands that were > 8 ha in size (median = 22.2 ha, range 8.5-74.3 ha) and were separated from each other by > 0.40 km. Site quality was estimated based on 4 to 6 soil cores sampled at 50-100 m intervals within each stands with a soil auger to avoid confounding effects of site quality affecting the rate of development (Briggs and Lemin 1994). I assigned a site quality value to each stand ranging from 1 (highly productive) to 5 (unproductive) based on Brigg's (1994) scale of forest productivity.

Table 4.1. Stand history, location, and site quality for 17 precommercially thinned (PCT) stands and 13 unthinned stands in northern Maine that were sampled for structural attributes and habitat characteristics. (T = stand treated with PCT, C = untreated stand). Site quality ranged from 1 (well drained, productive) to 5 (poorly drained, unproductive) according to Briggs (1994) classification guidelines.

Site number	Year of Clearcut	Year of Herbicide	Year of PCT	Township	Site Quality
1-1-T	1982	1988	1999	T 4 R 11	4+
1-2-T	1980	1983	1999	T4 R 12	3-
1-3-T	1977	1983	1999	T4 R 11	4+
1-4-T	1982	1988	1999	T4 R 11	4
1-5-T	1976	1983	1999	T4 R 12	4
6-1-T	1979	1988	1994	Hersey	3+
6-2-T	1979	1988	1994	Hersey	2-
6-4-T	1974	1982	1994	T 5 R 11	3-
6-5-T	1976	1985	1995	T 5 R 11	3-
6-6-T	1979	1982	1994	T 5 R 11	3-
11-1-T	1975	1983	1989	T 1 R 13	3
11-2-T	1968	1987	1990	Spencer Bay	3-
11-3-T	1975	1983	1989	T 1 R 13	2-
11-4-T	1975	1986	1990	T 1 R 13	3
11-5-T	1975	1983	1989	T 1 R 13	2
11-6-T	1975	1984	1991	T 1 R 13	2-
11-7-T	1975	1986	1989	Spencer Bay	2-
1-1-C	1982	1988	n/a	T 4 R 11	4
1-2-C	1979	1983	n/a	T 4 R 11	3-
1-3-C	1981	1984	n/a	T 4 R 11	4+
1-4-C	1983	1988	n/a	T 5 R 11	4+
1-5-C	1976	1985	n/a	T 4 R 11	3-
6-1-C	1979	1988	n/a	Hersey	3+
6-2-C	1981	1988	n/a	Hersey	3+
6-4-C	1974	1982	n/a	T 5 R 11	4
6-5-C	1974	1985	n/a	T 4 R 12	3
6-6-C	1976	1983	n/a	T 4 R 11	4
11-1-C	1976	1982	n/a	T 5 R 11	3
11-3-C	1976	1982	n/a	T 5 R 11	3+
11-4-C	1974	1985	n/a	T 5 R 11	3

The study design included 17 PCT-treated stands that were sampled for habitat characteristics and structural attributes at 5 year intervals (1-2 year post thinning, n = 5; 5-7 years, n = 5; 9-12 years, n = 7) and 13 similar unthinned stands (1 year, n = 5; 6 year, n = 5; 11 year, n = 3) whose year of clearcut and herbicide treatment were comparable to treatment stands. I allowed 1-2 years of latitude in separating stands into thinning classes to maximize the number of stands studied. The ratio of PCT-treated to unthinned stands in the 11-year thinning class was unbalanced because I was unable to locate more than 3 unthinned stands that met my criteria of similar site quality, year of clearcut, and year of herbicide-treatment. Treatment stands were paired with an unthinned stands with similar site quality, year of clearcut and year of herbicide to avoid gross biases arising from temporal variation in years of treatment. Stands were not statistically paired and were not treated as paired during analyses.

Habitat sampling

Vegetation structure was measured on 20 fixed-area nested plots centered on 4, 400 m transects separated by 65 m and located > 50 m from stand edges (Chapter 2). I centered 5 plots per 400 m of transect at random locations along the transects and distributed plots in a stratified-random design. I used 25 m^2 circular plots within thinned stands and 10 m^2 circular plots within unthinned stands to sample approximately the same number of crop trees, and to maximize number of sample plots across varying stand densities. Within each plot I measured 27 habitat variables to describe the structure of the overstory, understory, woody debris, or ground-level herbaceous vegetation.

Within each plot, I counted the number of coniferous and deciduous overstory trees ($\geq$ 7.6 cm dbh, > 1.0 m height, alive) and measured the diameter breast height (dbh), total height, and the height from the ground to the lowest living branch. Heights were measured using a telescoping height pole. I calculated the live crown ratio of overstory trees as the [(total height – height to crown) / total height]. I also measured the number, type (coniferous or deciduous), dbh, total height, and height to crown for all understory stems (< 7.6 cm dbh, >1 m height, alive) within the plot and calculated the average live crown ratio of the understory. The number of stem cover units (SCU) was computed by summing the number of coniferous understory stems × 3.0 plus the number of deciduous understory stems (Litvaitis et al. 1985).

I counted the number and type (coniferous or deciduous) of woody, regenerating stems (≥ 0.2 m, < 1.0 m, alive) on a 1.0-m diameter nested subplot that was centered within each of the 20 plots/stand. The density of stems/ha in each stands was calculated by summing the total number of regenerating stems, understory stems, and overstory stems and dividing by the number of ha sampled within each stand. The percent of ground covered by grass and forbs, moss, rock, vegetative litter, and other vegetation was also visually estimated in the 1.0-m subplot.

Horizontal vegetation cover was quantified with a 2.0 m cover pole with alternating 0.1 m red and white bands. Following a random compass bearing separated by 180°, the distance to horizontal cover was measured from the center point as the distance where ≥ 25 % of all red and white bands were visually obstructed. I estimated the number and volume of downed logs with a modified version of the planar intersection method used by Payer and Harrison (2000). I established a 20-m randomly oriented transect with the midpoint at the center of each sampling station. I quantified the number of logs that crossed the transect and were ≥ 1.0 m length, ≥ 7.6 cm diameter (at the point of intersection), and ≤ 45° from the ground. Only sound to moderately decayed logs were considered, so that extremely decayed logs were excluded from sampling. Overhead canopy cover was measured with a spherical densiometer; 4 readings in the 4 cardinal compass directions at 1.0 m height (estimated height of mid-winter snowpack) were taken at the center of each plot and averaged to a single value for each plot (Lemon 1956).

Statistical analyses

Analysis of variance

I calculated an average value for each habitat variable within each stand and treated the stand as the unit of replication. Residual errors of each variable were examined for normality and homoscedasticity across stands and I transformed all non-normal data (modified Levene's test < 0.10 and/or Lilliefor's test < 0.10) with $\log_e$, square root, or cube root transformations to meet the parametric assumptions of analysis of variance (ANOVA) (Neter et al. 1996). Next, I conducted a two-way ANOVA on the means of each habitat variable with treatment (PCT or unthinned) and thinning class (1, 6, or 11-years post-treatment) as the main effects. Post hoc, Tukey's honestly significant difference tests were used to examine pairwise differences among thinning classes of habitat variables with significant thinning class effects (Zar 1999).

Principal components analysis

I eliminated all habitat variables with a F-statistic < 2.0 for treatment (PCT or unthinned) or for thinning class (1, 6, or 11-years) from further analyses; however a large number of variables had significant treatment or thinning class effects based on this initial screening procedure. High dimensionality of large and complex multivariate data sets causes interpretation of results to be difficult (McGarigal et al. 2000). To reduce the dimensionality of the habitat variables, I conducted 2 separate principal component analyses (PCA) to describe the variation in habitat structure between treatments and thinning classes: 1) habitat variables that differed between thinned and unthinned stands, and; 2) habitat variables that differed among the 3 thinning classes of stands, regardless of thinning history. PCA is an ordination technique that creates new components that are linear combinations of original variables. These linear combinations of variables, or components, maximize variation among observations in ordination space to more simplistically explain the data with a smaller number of variables.

I included normally distributed (e.g. transformed when necessary) habitat variables for each stand that were standardized by subtracting the mean and dividing by the standard deviation of that variable to the PCA. Standardization of variables was required because the scales of measurement differed among structural variables and this prevents dominance by variables with large variation (Pielou 1984). After computing the principal components, I used scree plots, relative variance criterion, and the latent root criterion to determine how many components to retain (McGarigal et al. 2000). For both analyses, I used a varimax rotation to aid in interpretation of loadings and components. I examined rotated factor loadings to interpret and provide biologically relevant names for the principal components. Variables with loadings (after rotation) of > 0.60 or < -0.60 were considered to have strong effects on that component; these thresholds roughly correspond to variables that account for about 40% of the variance in the component (Tabachnik and Fidell 1983, McGarigal et al. 2000). Ordination diagrams using the first

3 components from each analysis were constructed with Gaussian confidence ellipses for the sample (P = 0.70) (SPSS 1997).

RESULTS

Analysis of variance

Fourteen of 27 habitat variables that I measured differed between thinned and unthinned stands (F > 2.0); however, those showing the greatest differences in magnitude were stem cover units, total number of understory stems, total number of stems, and the number of logs, which were 3.8, 2.9, 2.2, and 2.2 times greater in unthinned stands, respectively. Other variables that differed between treatment types were the understory height, understory height to crown, understory live crown ratio, average dbh of the understory, number of understory conifer stems, total number of overstory stems, log volume, average dbh of the overstory, canopy density, and the horizontal vegetation distance (Table 4.2).

Twelve of 27 habitat variables differed among the thinning classes (F > 2.0). These included the average dbh of understory stems, the height of understory stems, the number of deciduous understory stems, the total number of understory stems, the average dbh of overstory stems, the height of overstory stems, the total number of overstory stems, the total stem density, the percent ground cover of grass and forbs, the percent ground cover of other herbaceous vegetation, the number of logs, and the log volume (Table 4.3). In general, the dbh and height of understory trees and overstory trees were greatest in the 11-year stands (P < 0.10). The greatest number of deciduous understory stems and total stem density occurred in the 6-year thinning class (P < 0.10). I observed

Table 4.2. The effect of treatment (PCT vs. unthinned) on mean (SE) values of 27 habitat variables sampled within 17 precommercially thinned stands and 13 unthinned reference stands with a previous history of clearcutting followed by herbicide (Glyphosate) application in northern Maine. Non-transformed means and standard errors are presented for transformed variables. Comparisons yielding a calculated F-statistic ≥ 2.0 are depicted in bold.

				Overstory Type	
Variable	Transformation	F	P	PCT	Unthinned
Average dbh of understory stems (cm)		**11.545**	**0.002**	3.2 (0.1)	3.8 (0.1)
Height of understory stems (m)		**49.801**	**< 0.001**	3.1 (0.1)	4.2 (0.1)
Height to crown of understory stems (m)		**19.567**	**< 0.001**	0.9 (0.1)	1.5 (0.1)
Live crown ration of understory stems (value from 0-1.0)	Ln	**5.280**	**0.031**	0.68 (0.02)	0.62 (0.02)
Number of understory conifer stems (#/ha)	Ln	**34.528**	**< 0.001**	1,471 (705)	7,101 (820)
Number of understory deciduous stems (#/ha)	Ln	0.053	0.485	1,675 (409)	1,896 (475)
Total number of understory stems (#/ha)	Ln	**32.471**	**< 0.001**	3,146(707)	8,997 (821)
Stem cover units (#/ha)	Ln	**38.445**	**< 0.001**	6,089 (2,037)	21,199 (2,367)
Average dbh of overstory stems (cm)		**7.897**	**0.010**	12.1 (0.3)	10.8 (0.4)
Height of overstory stems (m)		0.000	0.983	8.1 (0.2)	8.1 (0.2)
Height to crown of overstory stems (m)		0.700	0.412	1.4 (0.1)	1.6 (0.2)
Live crown ratio of overstory (value from 0-1.0)		1.870	0.184	0.84 (0.02)	0.80 (0.02)
Number of overstory conifer stems (#/ha)		1.832	0.188	1,199 (98)	1,402 (114)
Number of overstory deciduous stems (#/ha)	Ln	1.645	0.212	75 (37)	151 (43)
Total number of overstory stems (#/ha)		**3.064**	**0.093**	1,274 (104)	1,553 (121)
Number of coniferous regenerating stems (#/ha)		0.334	0.569	299 (70)	361 (81)
Number of deciduous regenerating stems (#/ha)		0.710	0.408	571 (92)	690 (107)
Total number of regenerating stems (#/ha)		1.344	0.258	870 (102)	1,051 (119)
Total number of stems (#/ha)	Ln	**36.422**	**< 0.001**	5,289 (730)	11,601 (849)
Percent ground cover of grass and forbs (%)	Square root	1.510	0.231	5 (1)	3 (1)
Percent ground cover of rock (%)	Ln	0.137	0.714	1 (0)	1 (0)
Percent ground cover of litter (%)		1.249	0.275	64 (3)	69 (4)
Percent ground cover of other herbaceous vegetation (%)		0.675	0.419	13 (2)	11 (1)
Horizontal vegetation distance (m)		**12.570**	**0.002**	10.0 (0.4)	7.6 (0.5)
Number of logs (#/transect)	Ln	**25.196**	**< 0.001**	1.6 (0.3)	3.5 (0.3)
Log volume (m^3/transect)	Cube root	**14.793**	**0.001**	0.24 (0.12)	0.79 (0.14)
Canopy density (%)		**2.447**	**0.131**	78.2 (2.5)	84.1 (2.8)

Table 4.3. The effect of thinning class (1-year, 6-year, or 11-year) on mean (SE) values of 27 habitat variables sampled within 17 precommercially thinned stands and 13 unthinned reference stands with a previous history of clearcutting followed by herbicide (Glyphosate) application in northern Maine. Non-transformed means and standard errors are presented for transformed variables. Comparisons yielding a calculated F-statistic ≥ 2.0 are depicted in bold.

Variable	Transformation	F	P	Thinning Class		
				1-year (n = 10)	6-year (n = 10)	11-year (n =10)
Average dbh of understory stems (cm)		**11.678**	**< 0.001**	3.9 (0.1)	3.0 (.1)	3.6 (0.15)
Height of understory stems (m)		**8.956**	**0.001**	3.9 (0.1)	3.2 (0.1)	3.8 (0.1)
Height to crown of understory stems (m)		1.135	0.338	1.3 (0.1)	1.1 (0.1)	1.3 (0.1)
Live crown ration of understory stems (value from 0-1.0)	Ln	0.155	0.857	0.66 (0.02)	0.65 (0.02)	0.65 (0.02)
Number of understory conifer stems (#/ha)	Ln	0.772	0.473	4632 (908)	4778 (908)	3448.8 (991)
Number of understory deciduous stems (#/ha)	Ln	**2.855**	**0.077**	1578 (526)	2773 (526)	1004 (574)
Total number of understory stems (#/ha)	Ln	**3.241**	**0.057**	6210 (910)	7551 (910)	4453 (993)
Stem cover units (#/ha)	Ln	1.849	0.179	15474 (2622)	17107 (2622)	11351 (2861)
Average dbh of overstory stems (cm)		**5.425**	**0.011**	10.5 (0.4)	11.4 (0.4)	12.4 (0.4)
Height of overstory stems (m)		**13.314**	**< 0.001**	7.4 (0.2)	7.9 (0.2)	9.0 (0.2)
Height to crown of overstory stems (m)		1.423	0.261	1.4 (0.2)	1.3 (0.2)	1.7 (0.2)
Live crown ratio of overstory (value from 0-1.0)		0.978	0.391	0.81 (0.02)	0.84 (0.02)	0.80 (0.02)
Number of overstory conifer stems (#/ha)		1.911	0.17	1348 (126)	1102 (126)	1452 (138)
Number of overstory deciduous stems (#/ha)	Ln	1.854	0.178	129 (47.5)	72 (48)	137 (52)
Total number of overstory stems (#/ha)		**2.416**	**0.111**	1477 (134.2)	1174 (134)	1589 (147)
Number of coniferous regenerating stems (#/ha)		0.699	0.507	332 (90)	408 (90)	250 (98)
Number of deciduous regenerating stems (#/ha)		0.517	0.603	722 (119)	625 (119)	544 (130)
Total number of regenerating stems (#/ha)		1.07	0.359	1054 (131)	1033 (131)	795 (143)
Total number of stems (#/ha)	Ln	**2.642**	**0.092**	8741 (940)	9758 (940)	6837 (1026)
Percent ground cover of grass and forbs (%)	Square root	**2.317**	**0.12**	2 (1)	5 (1)	3 (2)
Percent ground cover of rock (%)	Ln	0.055	0.947	1 (1)	0 (1)	1 (1)
Percent ground cover of litter (%)		1.971	0.161	65 (4)	61 (4)	72 (4)
Percent ground cover of other herbaceous vegetation (%)		**3.076**	**0.065**	13 (2)	16 (2)	8 (2)
Horizontal vegetation distance (m)		1.811	0.185	8.6 (0.6)	8.2 (0.6)	9.7 (0.6)
Number of logs (#/transect)	Ln	**2.389**	**0.113**	2.9 (0.4)	2.8 (0.4)	2.0 (0.4)
Log volume (m^3/transect)	Cube Root	**2.362**	**0.116**	0.79 (0.15)	0.48 (0.15)	0.27 (0.16)
Canopy density (%)		0.588	0.563	78.8 (3.2)	80.7 (3.2)	83.9 (3.4)

the greatest total number of overstory stems in the 11-year stands. Measures of logs were greater in the 1-year thinning class than the 11-year thinning class ($P < 0.10$) and herbaceous vegetation other than grass and forbs was greatest in 6-year stands.

Four variables, the average dbh of understory stems, the number of deciduous understory stems, the live crown ration of understory stems, and the number of coniferous regenerating stems had significant (F-statistics > 2.0) treatment × stand-thinning interactions. This study was not designed with adequate sample sizes to describe the complex interactions between treatment and thinning class; therefore, variables with significant interaction terms were excluded from PCA models.

Principal components analysis

Three principal components described 83.2 % of the variability of the habitat data between thinned and unthinned stands (Table 4.4). The first Principal component (PC1) in this analysis included positively loaded variables that described the density of the understory and downed woody structure and negatively loaded variables that were associated with sparse understory cover (labeled "near-ground cover"). PC2 included positively loaded variables (> 0.60) that described overstory structure and cover (labeled "overhead cover"). The third principal component (labeled "understory structure") was positively associated with understory height and the dbh of the understory. Principal components 4 – 14 had eigenvalues < 1.0 and contributed little (< 18 % of variation Ordination diagrams for this analysis portrayed that the greatest differences in forest structure between thinned and unthinned stands occurred with near-ground cover, and greater similarity between treatments was evident with overhead cover and understory structure (Figure 4.1).

Table. 4.4. Loadings of stand-scale habitat variables that separated thinned and unthinned regenerating conifer stands (n = 30) into 3 principal components after varimax rotation. Habitat variables were sampled within 30 forest stands (17 precommercially thinned, 13 unthinned) in northern Maine, June – August, 2001-2002.

Habitat variable	Principal Components		
	PC1 – Near-ground cover	PC2 – Overhead cover	PC3 – Understory structure
Stem cover units	0.9501	0.1601	0.1341
Understory stem density	0.9365	0.2437	-0.0484
Total stem density	0.9038	0.3738	0.0047
Understory conifer density	0.8590	0.1012	0.3369
Vegetation distance	-0.7927	-0.0662	-0.0240
Log volume/transect	0.7609	0.0421	0.1676
Logs/transect	0.7275	-0.0308	0.4158
Dbh of overstory	-0.6259	0.1790	-0.5515
Canopy density	0.0484	0.9409	-0.0022
LCR of understory	-0.3191	-0.8782	0.2001
Understory height to crown	0.3384	0.7741	0.4537
Overstory stem density	-0.1519	0.6624	0.5371
Dbh of understory	0.1007	-0.0584	0.9573
Height of understory	0.2932	0.3010	0.8360
Eigenvalue	6.9916	2.5319	2.1292
% Variance explained	41.4344	21.8761	19.9227

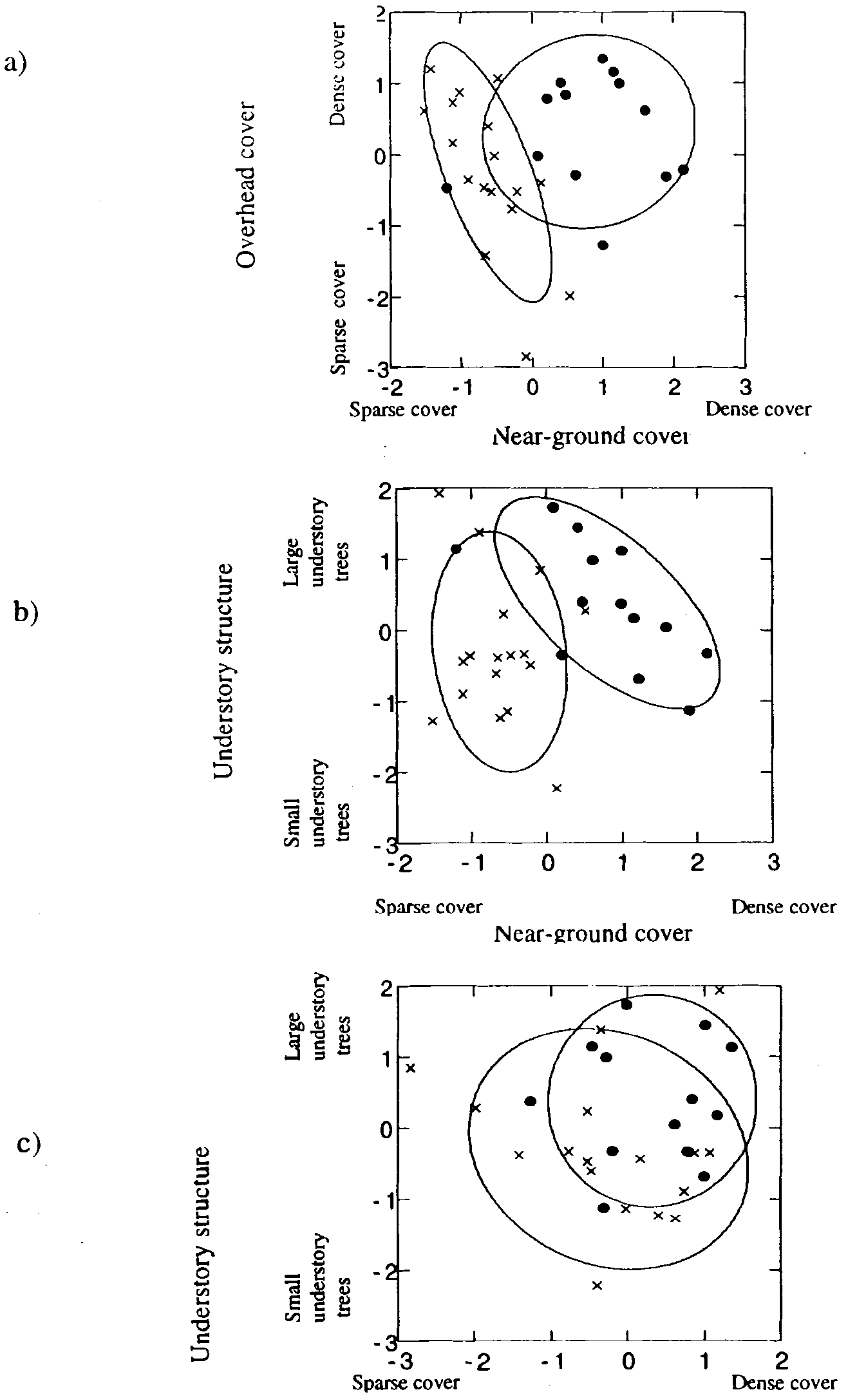


Figure 4.1. Ordination diagrams for 3 dominant (eigenvalue > 1.0) principal components describing the heterogeneity of stand-scale forest structure between 17 stands treated with PCT (x symbol) and 13 unthinned stands (• symbol). Gaussian confidence ellipses (P = 0.70) are shown centered around the sample means.

Three principal components also described the variation in habitat variables across the 3 thinning class intervals. The remaining 9 components cumulatively added 25% to the total explained variance and were not included in further discussion. Highly loaded variables onto the first principal component described vegetation characteristics associated with low-level horizontal structure (Table 4.5). PC1 (labeled "horizontal cover") included strong positive loadings from total stem density, the density of understory stems, and 2 measures of coarse woody debris (logs and log volume). The principal component with the second largest eigenvalue included large positive loadings for the average dbh of overstory trees, the density of deciduous trees in the understory, and overstory height (Table 4.5). Further, PC2 had strong negative loadings with the average dbh and height of the understory. This component described the relationship of forest structure between the overstory and understory (labeled "overstory to understory contrast"). Lastly, the component with the third largest eigenvalue described the presence of ground-level herbaceous vegetation (labeled "herbaceous vegetation gradient"). PC3 included positive associations with the density of overstory trees and strong negative loadings of the percent cover of other vegetation and grass and forbs. Ordination diagrams of the 3 principal components suggest that stands in the 1-year thinning class interval had more variable horizontal cover, overstory trees, and herbaceous vegetation than stands in the 6 or 11-year thinning class intervals (Figure 4.2). In each of the 3 diagrams, the 1-year stands overlapped older thinning classes, but the 6 and 11-years stands separated more distinctly from each other based on confidence ellipses of ordination scores.

Table. 4.5. Loadings of stand-scale habitat variables that separated regenerating conifer stands (n = 30) of 3 thinning classes (1-year, n = 10; 6-year, n = 10; 11-year, n = 10) into 3 principal components after varimax rotation. Habitat variables were sampled within 30 forest stands (17 precommercially thinned, 13 unthinned) in northern Maine, June – August, 2001-2002.

Habitat variable	Principal Components		
	PC1 – Horizontal cover	PC2 – Overstory to understory contrast	PC3 – Herbaceous vegetation gradient
Total stem density	0.9533	0.0440	0.1557
Understory stem density	0.9504	0.0557	0.0263
Log volume/transect	0.7645	-0.2318	-0.0142
Logs/transect	0.7580	-0.4352	0.0130
Dbh of overstory	-0.5306	0.7284	0.1173
Dbh of understory	0.0687	-0.8743	0.3173
Deciduous understory density	0.4824	0.6947	-0.0152
Height of overstory	-0.2810	0.6792	0.5253
Height of understory	0.3524	-0.6023	0.4960
Overstory stem density	0.0428	-0.1986	0.8335
% Other herbaceous vegetation	0.1541	-0.2207	-0.7193
% Grass and forbs	-0.2926	0.1843	-0.6023
Eigenvalue	4.5468	2.3199	2.1465
% Variance explained	31.7032	24.7673	18.6393

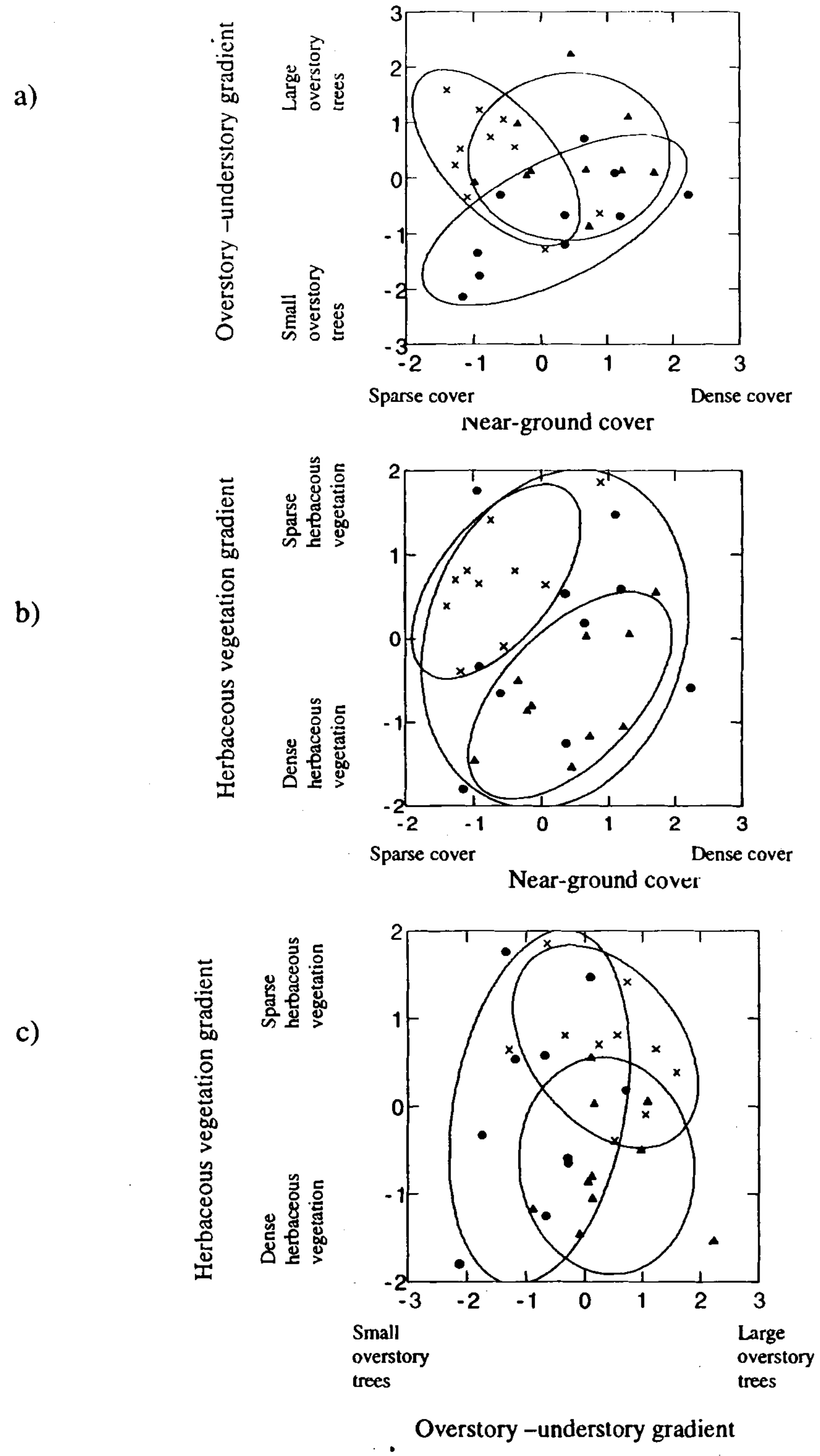


Figure 4.2. Ordination diagrams for 3 dominant (eigenvalue > 1.0) principal components describing the heterogeneity of stand-scale forest structure between stands of 3 thinning classes, including 1-year stands, n = 10 (• symbol); 6-year stands, n = 10 (▲ symbol); and 11-year stands, n = 10 (× symbol). Gaussian confidences ellipses are shown (P = 0.70) centered around sample means.

DISCUSSION

Multivariate comparisons of habitat characteristics among thinned and unthinned stands at different stages of post-clearcut and herbicide succession indicated that major gradients in forest structure resulted from differences in horizontal structure, overstory structure, understory size, and ground-level herbaceous vegetation. Stand-scale habitat characteristics describing near-ground horizontal cover were most important for describing the differences between thinned and unthinned regenerating clearcuts, and among stands of 3 different thinning classes, indicating that reductions of cover occurred with both treatment with PCT and development of stands through time. Near-ground cover and horizontal cover described 41.3 and 31.7% of the variation, respectively in forest structure that differed by treatments and thinning classes. In contrast to reported increases in structural diversity after PCT of non-herbicided forest (Thomas et al. 1999, Lindgren and Sullivan 2001, Daggett and Wagner, *In prep.*), these results suggest that simplification of understory structure was the primary outcome of the application of PCT to conifer stands that had been previously aerially sprayed with herbicides. Further, a reduction of horizontal cover in the understory also was associated with stand development through time, and thinning seemed to accelerate the simplification of horizontal structure associated with normal stand development in herbicide-treated clearcuts.

Structural differences between thinned and unthinned stands

Among variables loaded highly (> 0.60 or < -0.60) onto the first principal component (near-ground cover), 4 variables described stem densities (+), 2 variables quantified number and volume of downed logs (+), 1 variable described horizontal visual obscurity (-), and 1 variable quantified the size of overstory trees (-) (Table 4.4). This component best illustrated the differences between thinned and unthinned forest structure, with unthinned stands consistently receiving higher scores (denser cover) than similar stands treated with PCT from 1 to 11 years post-treatment (Figure 4.1, 4.3a). Therefore, the reduction in "near-ground cover" that is associated with stands treated with PCT is the primary attribute that explains the variation among thinned and unthinned forest in northern Maine.

These results conflict with studies of thinning of non-herbicided conifer stands in Washington (Thomas et al. 1999), British Columbia (Lindgren and Sullivan 2001), Quebec (Bujuold 2002), and Maine (Daggett and Wagner, *In prep.*) that reported strong regrowth of deciduous understories and associated understory cover following PCT. A long-term study of the effects of herbicide and PCT on stand structure in Maine indicated that recovery of understory structure occurred by 10-years post-treatment in stands that were thinned with brush-saws, but not in stands that were both herbicided and thinned (Daggett and Wagner *In prep.*). My study sites in northern Maine were treated with aerial herbicide to kill competing deciduous vegetation 3-16 years prior to thinning, which accounts for the disparity of understory response to PCT among studies. Coniferous understory stems were 3.5 × more abundant than deciduous understory stems in unthinned stands, suggesting that because deciduous stems were a minor component of stands prior to PCT, they would have little chance for recovery after treatment. Herbicide treatment suppresses regrowth of deciduous saplings for up to at least 11 years post-thinning in Maine.

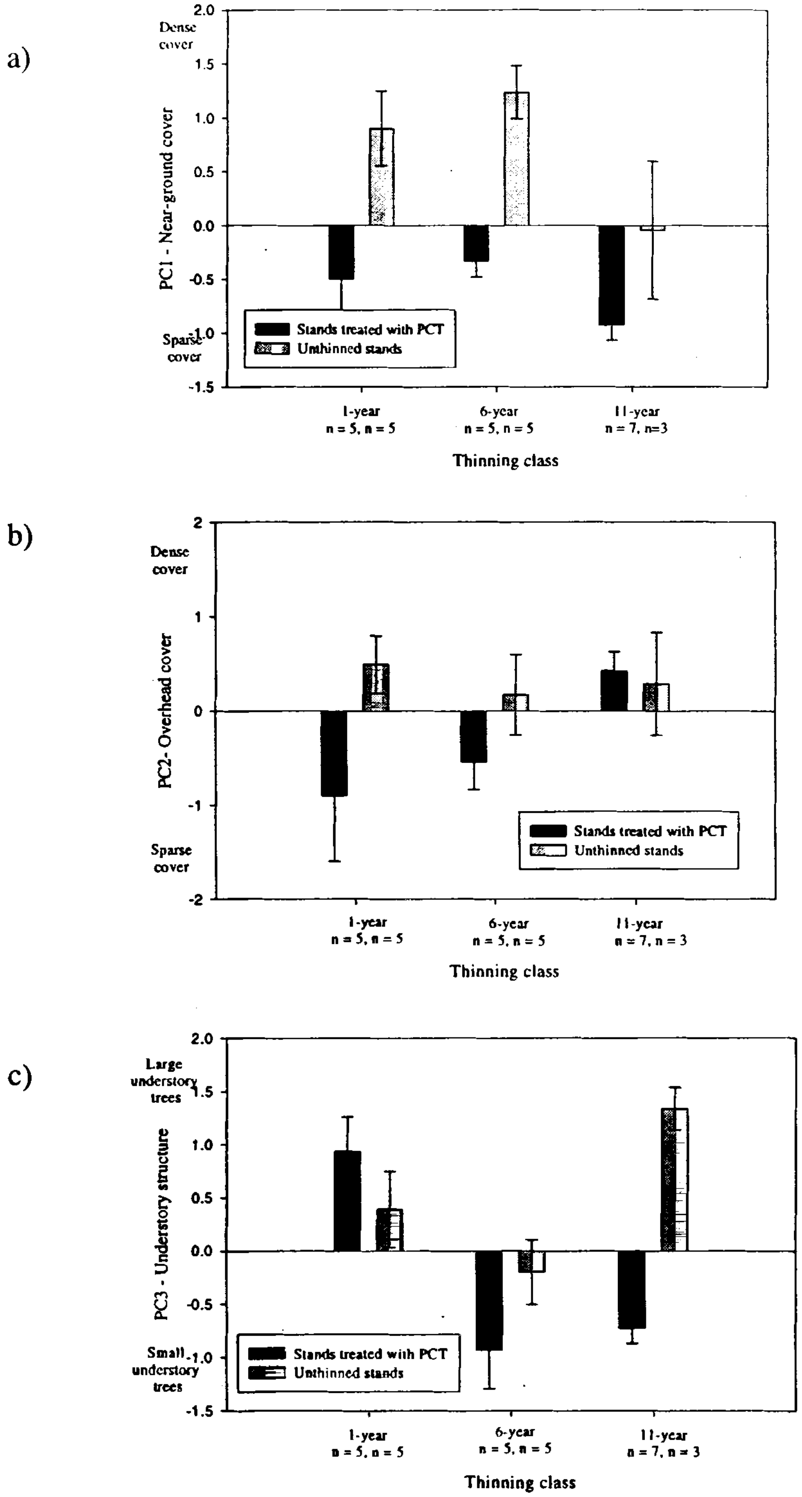
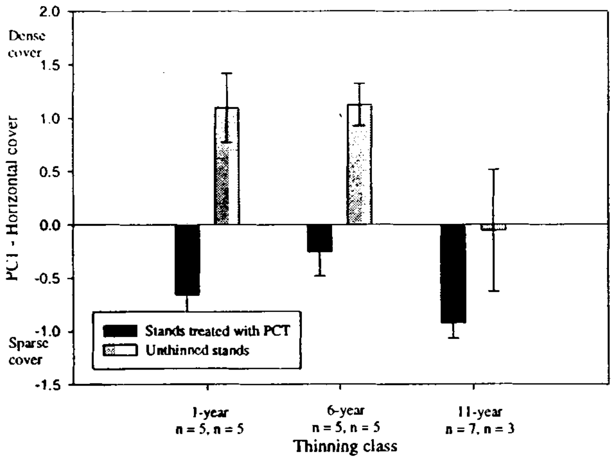
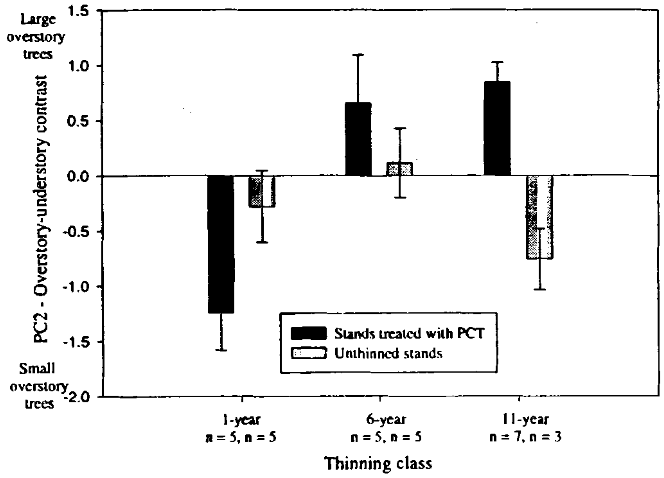


Figure 4.3. Mean principal component scores (SE) by treatment (treated with PCT, n = 17; unthinned, n = 13) and thinning class (after treatment interval, 1-year, n = 10; 6-years, n = 10; or 11-years, n = 10) for principal components describing > 15 % of heterogeneity of vegetation structure among treatments (Figure 4.3a-c) and thinning classes (Figure 4.3d-f) for 30 forest stands with a history of clearcut harvesting followed by herbicide (glyphosate) treatment in northern Maine, June – August, 2001-2002.

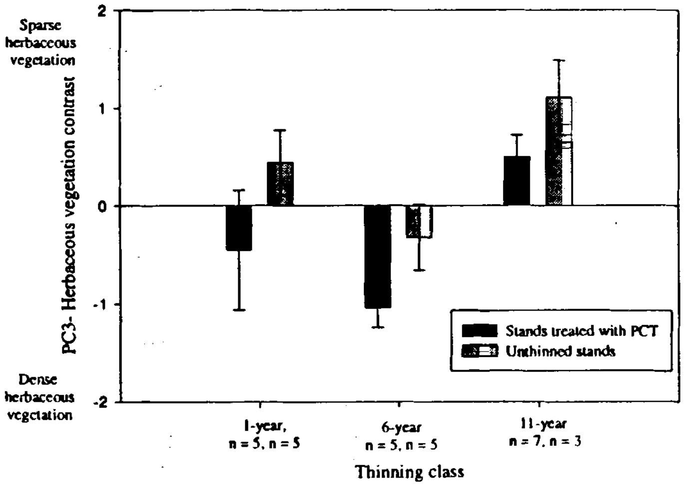
d)


2.0
Dense cover
1.5
1.0
0.5
0.0
-0.5
-1.0
Sparse cover
-1.5
PC1 - Horizontal cover
Stands treated with PCT
Unthinned stands
1-year
n = 5, n = 5
6-year
n = 5, n = 5
11-year
n = 7, n = 3
Thinning class

e)


Large overstory trees
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
Small overstory trees
-2.0
PC2 - Overstory-understory contrast
Stands treated with PCT
Unthinned stands
1-year
n = 5, n = 5
6-year
n = 5, n = 5
11-year
n = 7, n = 3
Thinning class

f)


Sparse herbaceous vegetation
2
1
0
-1
Dense herbaceous vegetation
-2
PC3- Herbaceous vegetation contrast
Stands treated with PCT
Unthinned stands
1-year,
n = 5, n = 5
6-year
n = 5, n = 5
11-year
n = 7, n = 3
Thinning class

The variable with the greatest loading (0.9501) onto near-ground cover was stem cover units, which weights the cover provided from conifer saplings 3 times greater than cover from deciduous saplings (Litvaitis et al. 1985). Although this relationship was developed to describe habitat-relationships of snowshoe hare (*Lepus americanus*), the greater value of coniferous saplings in providing horizontal visual obscurity, thermal protection, and overhead cover likely affects other forest-wildlife that are associated with high stem densities. Near-ground cover in unthinned stands was markedly greater than in PCT-treated stands 1-year and 6-years post-thinning, but by 11-years after treatment, cover decreased to amounts similar to treated stands. Additionally, the high positive loading of variables describing downed logs with near-ground cover and the small component scores (sparse cover) of thinned stands, indicate that woody debris is reduced in stands treated with PCT. Thinning may reduce accumulation of woody debris because natural mortality is reduced and because snags are often removed for safety or operational concerns (Hayes et al. 1997, Harrison 1999).

Overhead cover, which was the second principal component, described the vegetative structure provided by a developed canopy layer. Variables with the highest loadings included a high percentage of canopy density (+) and large density of overstory (dbh ≥ 7.6 cm, alive) trees (+). Among treatments and thinning classes, the differences in overhead cover between thinned and unthinned stands was most pronounced in the 1 and 6-year thinning class, but the treatments converged to similar component scores by 11-years post-treatment (Figure 4.3b). The short-lived disparity in overhead cover probably occurred because manipulation of stem densities initially reduced canopy closure (Wilson and Watts 1999, Lindgren and Sullivan 2001), but overstory crowns closed by 11-years post-treatment.

Lastly, the size of the understory trees (stem diameters and height) was reflected by the third principal component, understory structure. Understory structure appeared similar between thinned and unthinned stands (Figure 4.1b, c); however, distinct patterns were apparent when separated by thinning class and treatment (Figure 4.3c). Soon after PCT (1-year thinning class), both thinned and unthinned stands had similar structure of trees < 7.6 cm dbh, but understories followed distinctly unique successional trajectories to 11-years post-treatment. In thinned stands, understory trees rapidly increased stem diameters and heights after a reduction of competition. Trees that were < 7.6 cm dbh (the separation point between understory and overstory trees in this study) at 1-year post-treatment had graduated into the overstory (≥ 7.6 cm dbh) by 6 and 11 years post-treatment. Saplings that did not respond to thinning remained a stunted part of the understory. In contrast to the accelerated development and reduced understory structure of PCT stands, unthinned stands slowly accumulated understory structure (height and stem growth) to 11-years post-treatment. Understory stem densities were nearly 3× greater in unthinned stands than PCT stands, and the severe competition for space, light, and nutrients that result from being overstocked may have retarded the structural development of these trees (Brissette et al. 1999, Lindgren and Sullivan 2001).

Stands treated with PCT were characterized as having little near-ground structure, an overstory that closed by 11-years post-treatment, and few understory stems that were small and short. In contrast, unthinned stands of otherwise similar characteristics initially had higher amounts of near-ground cover that decreased with time, a consistently developed overstory through time, and slowly developing understory trees resulting from high competition. PCT of regenerating conifer stands consistently reduced horizontal cover from 1-11 years post-treatment, but increased temporal and spatial heterogeneity of the canopy by temporarily opening the overstory layer. Within-stand structure varied less through time and overstory structure accumulated much slower in unthinned stands.

Changes in forest structure with stand development

Near-ground cover described the greatest amount of variation between thinned and unthinned conifer stands. Further, a similar component (horizontal cover) weighted by many of the same variables accounted for the greatest variation (31.7%) of forest structure among stands of 3 thinning classes (Table 4.5). Therefore, horizontal cover described a major portion of the changes in forest structure associated with both thinning and stand development through time. Unthinned stands were associated with more dense horizontal cover than stands treated with PCT during the 1-year and 6-year thinning classes, but both unthinned stands converged to more similar amounts of cover by 11-years post treatment (Figure 4.3d). Both thinned and unthinned stands had less horizontal cover in the 11-year stands than in younger stands, which implies that competition-induced suppression of the understory and decomposition of logs occurred as both thinned and unthinned stands succeeded from early to mid-succession. This process allowed stands to succeed to a mature or overmature stage that may be necessary to provide sustainable numbers of logs in managed forests (Hagan and Grove 1999). Further, shorter rotations in intensively managed stands may lead to long-term reductions in near-ground structural diversity and CWD.

The contrast between overstory and understory structure explained the second greatest amount of variation (24.8%) in forest structure among stand thinning classes. Large values of this component described stands with developed overstories and underdeveloped understories; likewise, small values corresponded to stands with large and tall understory trees and little overstory structure. Thinned stands had markedly greater overstory structure in the 6-year and 11-year thinning classes than in 1-year thinning classes (Figure 4.3e). Further, thinned stands also had greater overstory structure than similar untreated stands in the 2 older thinning classes. Unthinned stands gained little overstory structure from 1 to 11-years post-treatment, which indicates the application of PCT was responsible for the accelerated height and diameter growth (Harrington and Reukema 1983, Ker 1987, McCormack and Lemin 1998, Brissette and Frank 1999, Brissette et al. 1999, Pothier 2002). The increased number of large overstory trees in addition to the retention of small understory stems in stands treated with PCT suggests that stratification of canopy layers occurs by 11 years after thinning and that vertical height diversity is enhanced by subsequent growth and development after thinning (Figure 4.3c,e).

The herbaceous vegetation gradient, the third principal component, described the inverse relationship between amounts of herbaceous vegetation and overstory cover. Density and diversity of ground-level herbaceous vegetation often relates to the amount of light able to penetrate to the forest floor, so that stands with developed overstories have sparse ground-level vegetation (Grelen et al. 1972, Thomas et al. 1999, Lindgren and Sullivan 2002). Consistent with many previous studies, thinned stands had denser herbaceous vegetation than unthinned stands by only 1-year post-treatment (Hurst et al.

1982, Bell et al. 1997, Thomas et al. 1999, Lindgren and Sullivan 2002) because herbaceous vegetation can respond quickly to changes in light and microclimate (Figure 4.3f). Density of herbs was even greater in thinned stands by 6-years post-treatment, but was sparse after closure of the canopy in the 11-year PCT stands. Herbaceous vegetation in unthinned stands was less variable, but did exhibit the greatest values in the 6-year stands, possibly from increased sunlight from small canopy gaps created as trees died.

In general, stands in the 1-year thinning class, regardless of thinning history, were distinguished by highly variable amounts of horizontal cover (dense cover in unthinned stands, sparse cover for thinned stands) and ground-level herbaceous vegetation. PCT reduced many variables associated with horizontal structure, and allowed the penetration of sunlight to the forest floor, positively influencing the amount of herbaceous vegetation. Moderate densities of horizontal cover, moderate sizes of overstory trees, and dense herbaceous vegetation characterized regenerating conifer stands in the 6-year thinning class. Lastly, stands in the 11-year thinning class had little horizontal cover, large overstory trees, and sparse ground level vegetation. Thus, the successional pathway of regenerating conifer stands included a reduction of horizontal cover, growth of overstory structure, and decreasing herbaceous vegetation as stands developed.

Potential effects of thinning and stand development on wildlife

The changes in vegetation structure with PCT and stand succession indicate that large differences in forest structure exist between thinned and unthinned stands, and that changes vary temporally. Wildlife species respond to changes in forest structure rather than stand age (Carey and Johnson 1995, Hayes et al. 1997). Therefore, thinned and unthinned stands of similar ages may potentially support different wildlife communities.

Wildlife associated with the structure of dense, early-successional forest will likely be negatively affected by PCT, but other species that use mature forest may receive positive benefits. Thus, I hypothesize that wildlife will exhibit species-specific responses to alteration of forest structure from PCT and stand succession.

Across their geographic range, snowshoe hare are consistently reported to reach their greatest densities in mid-successional, overstocked conifer stands with high levels of visual obscurity (Wolff 1980, O'Donoghue 1983, Pietz and Tester 1983, Litvaitis et al. 1985, Litvaitis et al. 1990, Koehler 1990, Fuller 1999, Hoving 2001). Therefore, the reduction in near-ground cover associated with PCT would be expected to negatively affect densities of snowshoe hare. A companion study of snowshoe hare on the same 30 forest stands measured during this study indicated that hare densities were 2 to 2.5 times greater on unthinned stands versus similar stands treated with PCT in leaf-off (October – May) and leaf-on (June – September) seasons, respectively (Chapter 2). A similar reduction in densities of snowshoe hare was observed by 4-years post-PCT in British Columbia (Sullivan and Sullivan 1988).

Spruce grouse (*Falcipennis candadensis*), a conifer dependent species, have special conservation statuses near at the southern edge of their distribution: they are state-listed as endangered in New York and Vermont, classified as a non-game breeding bird in New Hampshire, and are not legally harvested in Maine (A. Weik, Maine Department of Inland Fisheries and Wildlife, pers. comm.). Spruce grouse reportedly utilize mid-successional conifer forest with characteristics typical of post-PCT treated stands, including well-developed middle stories and tree heights of 7-14 m (Boag and Schroeder 1992). Previous research conducted in Maine indicated that summer habitat of adult female spruce grouse with broods is characterized by denser ground vegetation and a more open canopy than during other seasons (Allan 1985). My observations of spruce grouse during June–August, 2001 are consistent with the literature; across the same 30 stands sampled for forest structure in this study, I observed 19 adults (8 F, 11 M) in the 17 stands treated with PCT and 7 adults (3 F, 4 M) in the 13 unthinned stands during morning visits on 6 consecutive days per stand, July-August 2001. Further, 7 of 8 females in the PCT stands were observed with broods, whereas none of the females in unthinned stands were seen with young. These observations suggest that positive effects of PCT on summer habitat of spruce grouse may exist, and that these relationships could warrant further exploration.

Numerous strong relationships have been documented between forest songbirds and habitat structure (MacArthur and MacArthur 1961, McShea and Rappole 2000, Kirk and Hobson 2001), and changes in cover and structural diversity associated with PCT and stand succession could influence abundance, diversity, nesting success, and community composition of songbirds. Species of birds that require a diverse understory for nest concealment, foraging, or perching would be expected to decrease in abundance after PCT. In Ontario, after vegetation management, the greatest decrease in bird density was observed in stands that were manually thinned with brush-saws, as compared among herbicide and thinning treatments (Woodcock et al. 1997). They reported that shrub-nesting birds, such as the chestnut-sided warbler (*Dendroica pensylvanica*) and veery (*Catharus fuscescens*), declined in abundance 1-year after thinning due to the removal of nesting and foraging structure. Whereas PCT may be associated with reduced abundance of some species, total diversity of songbirds was greater on commercially thinned deciduous stands in Massachusetts (DeGraaf et al. 1991) and would be predicted to be higher on my thinned 11-year stands based on greater vertical height diversity (MacArthur and MacArthur 1961). If the maintenance of shrub-nesting songbird community is a management goal, it is unlikely to be reached if stands are treated with PCT. In contrast, if overall diversity of bird species was the primary objective, thinning may indirectly enhance songbird diversity by increasing heterogeneity of forest stands across landscapes that are dominated by early-successional forest. These hypotheses should be further evaluated using field investigations.

Abundances of forest-dependent small mammals reportedly respond positively to volume of coarse woody debris (CWD) (Richens 1974, Hayes and Cross 1987, Carey and Johnson and 1995) and characteristics of mature forest, such as closed canopies and large diameter trees (Martell 1983, Nordyke and Buskirk 1991, Lachowski 1997). I observed that stands treated with PCT were associated with lower abundances of downed logs, but had larger and more developed overstory trees. Strong, unequivocal relationships between CWD and densities of small mammals have not been reported for Maine (Fuller 1999, Billig *In prep.*), so I would not expect small mammals to be strongly affected by reductions in CWD associated with thinning. North American studies of the effects of PCT have reported positive effects (Lautenschlager et al. 1997, Chapter 3) or no detectable effect (Lautenschlager et al. 1997, Sullivan et al. 2001, Chapter 3) on abundances of forest-dwelling small mammals, but responses were species-specific. I observed greater numbers of red-backed voles and masked shrews in stands treated with PCT; however, abundances of deer mice and short-tailed shrews were not affected by thinning (Chapter 3). Therefore, the application of PCT to regenerating stands appears to be compatible with maintaining or enhancing densities of small mammals at the scale of the forest stand.

CONCLUSIONS

The consideration of ecological integrity into silvicultural programs mandates that forest management systems be examined for their effects on biodiversity in addition to reaching economic, social, or silvicultural objectives. Intensive forest management, such as PCT, is reported to be in disagreement with ecological forestry, which has the maintenance of intact ecosystems as its primary goal (Seymour and Hunter 1999). By definition, intensive forest management simplifies forest structure by removing or killing vegetation that competes with crop trees (Seymour and Hunter 1999), and recommendations for maintaining biodiversity generally include temporal, spatial, and structural heterogeneity (Brokaw and Lent 1999, Spies and Turner 1999). Although stands treated with PCT may be incompatible with retaining the ecological communities of untreated forest, the changes in forest structure that occur with PCT and stand succession will likely positively influence some species.

This study was the first that I am aware of to examine the major changes in vegetation structure that occur after PCT of regenerating conifer stands up to 11-years post-treatment, and to relate these findings to effects on wildlife. In comparison to unthinned conifer stands, stands thinned with brush saws in northern Maine were associated with lower levels of near-ground cover, an overstory that developed complexity by 11-years post-treatment, and a lack of understory structure. The forest structure in regenerating stands treated with PCT may have negative effects on densities of early successional species, such as snowshoe hare and some species of shrub-nesting songbirds. Wildlife that use conifer stands with less dense understories and overstories dominated by large trees, have been or likely will be positively affected by PCT; these include red-backed voles and possibly, spruce grouse.

This study was descriptive in nature and generalizations of vegetative responses of forest structure to other geographic areas and thinning treatments should be conducted cautiously. Further, the 30 stands in this study were all treated with an aerial application of herbicide several years prior to thinning, which suppressed regrowth of understory structure and deciduous vegetation for nearly 20 years post-application. Thus, the temporal and spatial changes in forest structure as well as the indirect effects on populations of wildlife that occurred during this study will likely differ from stands that are released with brushsaws, but without prior application of herbicide.

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APPENDICES

APPENDIX A. Captures of snowshoe hares in northern Maine

Table A1. Number of captures and recaptures of snowshoe hares live-trapped within 8 forest stands (4 treated with PCT) in northern Maine, May-June 2001-2002.

		Number of initial captures		Number of recaptures	
Stand	Dates trapped	Male	Female	Male	Female
0-4-C	5/8/01-5/27/01	24	15	47	32
0-3-C	5/13/01-5/28/01	27	28	77	75
0-1-T	6/2/01-6/15/01	11	6	26	13
5-4-T	6/2/01-6/15/01	7	10	12	23
10-7-T	5/4/02-5/17/02	7	3	13	8
10-1-T	5/5/02-5/18/02	14	9	58	40
0-1-C	5/23/02-6/04/02	20	18	67	70
0-2-C	5/23/02-6/04/02	23	19	94	96

APPENDIX B. Densities of snowshoe hare pellets in regenerating clearcuts, with and without PCT, northern Maine, 2000-2002.

Table B1. Snowshoe hare pellet densities (pellets/ha/day) during leaf-off (October – April) and leaf-on (May-September) of 2000 – 2002 among 17 PCT stands and 13 unthinned stands, from 1 – 11 years post-treatment in northern Maine.

Thinning class[a]	Treatment[b]	Replicate	Year and season Leaf-off 2000-2001	Leaf-on 2001	Leaf-off 2001-2002	Leaf-on 2002
1	T	1	449.37	148.10	198.57	37.20
1	T	2	524.08	154.42	82.76	70.56
1	T	3	445.51	283.70	461.62	54.64
1	T	4	161.42	291.78	380.46	49.83
1	T	5	508.02	172.42	129.16	45.79
1	C	1	1062.30	748.75	915.94	136.39
1	C	2	889.02	395.25	817.49	45.27
1	C	3	1043.82	394.77	769.54	193.93
1	C	4	714.87	263.10	208.72	221.88
1	C	5	442.91	338.07	312.54	72.44
6	T	1	65.50	58.52	88.84	53.78
6	T	2	289.05	177.80	116.22	59.03
6	T	4	252.38	102.79	291.21	65.68
6	T	5	432.97	143.10	242.15	104.82
6	T	6	125.55	175.56	83.20	64.53
6	C	1	424.78	274.60	189.91	99.04
6	C	2	478.61	188.87	344.21	108.23
6	C	4	555.22	298.84	435.03	218.60
6	C	5	432.21	183.93	297.47	77.88
6	C	6	980.29	695.27	447.82	204.91
11	T	1	507.79	160.12	463.20	149.11
11	T	2	285.84	108.39	93.82	92.86
11	T	3	372.95	166.55	282.72	75.27
11	T	4	729.14	248.15	324.27	200.68
11	T	5	93.39	68.75	162.71	72.29

Table B1. Continued.

Thinning class[a]	Treatment[b]	Replicate	Year and season			
			Leaf-off 2000-2001	Leaf-on 2001	Leaf-off 2001-2002	Leaf-on 2002
11	T	6	547.14	150.24	171.96	87.92
11	T	7	90.59	34.80	64.48	25.06
11	C	1	812.99	612.94	500.94	141.83
11	C	3	522.04	403.51	297.03	136.81
11	C	4	514.86	246.06	211.25	91.97

[a] Thinning class, 1 = stands 1-2 years post-PCT and unthinned stands with similar management histories; 6 = stands 6-7 years post-PCT and unthinned stands with similar management histories, 11 = stands 11 years post-PCT and unthinned stands with similar management histories.

[b] Treatment, T = stands treated with PCT, C = unthinned stands.

APPENDIX C. Geographic location of snowshoe hare pellet transects, northern Maine.

Table C1. Coordinates (Universal transverse mercators (UTMs)) (km) of the endpoints of snowshoe hare pellet transects located within 30 regenerating conifer stands (17 treated with PCT) in northern Maine, 2002. UTMs are within zone 19 and using WGS – 1984 datum.

	UTM coordinates of transect endpoints					
Stand	Transect 1	Transect 2	Transect 3	Transect 4	Transect 5	Transect 6
1-1-T	5095.494 N, 488.61 E; 5095.478 N, 488.212 E	5095.429 N, 488.598 E; 5095.383 N, 488.202 E	5095.363 N, 488.604 E; 5095.331 N, 488.206 E	5095.299 N, 488.592 E; 5095.267 N, 488.196 E		
1-2-T	5092.382 N, 478.775 E; 5092.779 N, 478.804 E	5092.382 N, 478.837 E; 5092.785 N, 478.874 E	5092.378 N, 478.900 E; 5092.778 N, 478.945 E	5092.619 N, 478.622 E; 5092.819 N, 478.635 E	5092.810 N, 478.565 E; 5092.623 N, 478.556 E	
1-3-T	5094.789 N, 490.012 E; 5094.776 N, 490.410 E	5094.724 N, 490.020 E; 5094.700 N, 490.418 E	5094.659 N, 490.008 E; 5094.645 N, 490.407 E	5094.597 N, 490.017 E; 5094.590 N, 490.415 E		
1-4-T	5093.049 N, 488.287 E; 5093.074 N 487.907 E	5092.986 N, 488.286 E; 5093.032 N, 487.881 E	5092.920 N, 488.280 E, 5092.959 N, 487.881 E	5092.855 N, 488.279 E; 5092.888 N, 487.872 E		
1-5-T	5096.338 N, 476.868 E; 5095.942 N, 476.844 E	5096.342 N, 476.802 E; 5095.933 N, 476.789 E	5096.347 N, 476.738 E; 5095.949 N, 476.723 E	5096.356 N, 476.673 E; 5095.946 N, 476.673 E		
6-1-T	5105.805 N, 551.162 E; 5106.002 N, 551.459 E	5105.860 N, 551.127 E; 5106.062 N, 551.459 E	5105.914 N, 551.092 E; 5106.101 N, 551.370 E	5105.968 N, 551.056 E; 5106.138 N, 551.315 E	5106.070 N, 551.093 E; 5106.245 N, 551.194 E	
6-2-T	5106.129 N, 553.758 E; 5106.427 N, 553.786 E	5106.443 N, 553.711 E; 5106.139 N, 553.693 E	5106.437 N, 553.645 E; 5106.142 N, 553.627 E	5106.455 N, 553.575 E; 5106.148 N, 553.566 E	5106.151 N, 553.503 E; 5106.112 N, 553.328 E	5106.091 N, 553.503 E; 5106.054 N, 553.319 E
6-4-T	5102.022 N, 485.878 E; 5102.525 N, 485.692 E	5102.026 N, 485.938 E; 5102.528 N, 485.750 E	5102.011 N, 486.008 E; 5102.512 N, 485.804 E			
6-5-T	5101.705 N, 491.213 E; 5102.095 N, 491.229 E	5102.083 N, 491.289 E; 5101.696 N, 491.276	5101.752 N, 491.344 E; 5102.050 N, 491.359 E			

Table C1. Continued.

	UTM coordinates of transect endpoints					
Stand	Transect 1	Transect 2	Transect 3	Transect 4	Transect 5	Transect 6
6-6-T	5102.587 N, 487.103 E; 5102.873 N, 486.697 E	5102.647 N, 487.130 E; 5102.927 N, 486.720 E	5102.693 N, 487.130 E; 5102.917 N, 486.846 E	5102.754 N, 487.205 E; 5102.870 N, 487.045 E		
11-1-T	5064.626 N, 466.853 E; 5064.743 N, 467.230 E	5064.689 N, 466.838 E; 5064.812 N, 466.838 E	5064.753 N, 466.823 E; 5064.866 N, 467.202 E	5064.812 N, 466.804 E; 5064.919 N, 467.198 E		
11-2-T	5059.281 N, 460.977 E; 5059.614 N, 460.665 E	5059.337 N, 461.013 E; 5059.507 N, 460.861 E	5059.393 N, 461.043 E; 5059.528 N, 460.923 E	5059.262 N, 461.003 E; 5059.025 N, 461.289 E	5059.090 N, 461.313 E; 5059.315 N, 461.037 E	
11-3-T	5066.237 N, 466.444 E; 5066.392 N, 466.077 E	5066.303 N, 466.473 E; 5066.444 N, 466.096 E	5066.355 N, 466.499 E; 5066.476 N, 466.227 E	5066.415 N, 466.527 E; 5066.490 N, 466.353 E	5066.473 N, 466.558 E; 5066.596 N, 466.283 E	
11-4-T	5058.468 N, 473.995 E; 5058.753 N, 474.267 E	5058.422 N, 474.043 E; 5058.620 N, 474.250 E	5058.378 N, 474.088 E; 5058.624 N, 474.343 E	5058.335 N, 474.088 E; 5058.624 N, 474.343 E		
11-5-T	5066.641 N, 467.802 E; 5066.228 N, 467.609 E	5066.670 N, 467.744 E; 5066.295 N, 467.584 E	5066.702 N, 467.684 E; 5066.365 N, 467.684 E	5066.725 N, 467.628 E; 5066.380 N, 467.477 E		
11-6-T	5059.640 N, 471.511 E; 5059.607 N, 471.910 E	5059.575 N, 471.510 E; 5059.544 N, 471.915 E	5059.513 N, 471.504 E; 5059.488 N, 471.901 E	5059.448 N, 471.500 E; 5059.418 N, 471.906 E		
11-7-T	5064.115 N, 464.753 E; 5064.086 N, 465.150 E	5064.181 N, 464.763 E; 5064.141 N, 465.163 E	5064.244 N, 464.767 E 5064.209 N, 465.163 E	5064.306 N, 464.771 E; 5064.278 N, 465.172 E		
1-1-C	5096.084 N, 487.558 E; 5096.427 N, 487.726 E	5096.096 N, 487.624 E; 5096.439 N, 487.785 E	5096.084 N, 487.688 E; 5096.084 N, 487.688 E	5096.091 N, 487.754 E; 5096.436 N, 487.908 E		
1-2-C	5095.450 N, 490.476 E; 5095.439 N, 490.873 E	5095.514 N, 490.489 E; 5095.497 N, 490.890 E	5095.579 N, 490.486 E; 5095.544 N, 490.882 E	5095.642 N, 490.500 E; 5095.625 N, 490.895 E		

Table C1. Continued.

	UTM coordinates of transect endpoints					
Stand	Transect 1	Transect 2	Transect 3	Transect 4	Transect 5	Transect 6
1-3-C	5098.003 N,	5098.005 N,	5098.007 N,	5098.008 N,		
	484.474 E;	484.412 E;	484.344 E	484.279 E;		
	5097.608 N,	5097.597 N,	5097.613 N,	5097.603 N,		
	484.446 E	484.386 E	484.316 E	484.255 E		
1-4-C	5103.425 N,	5103.430 N,	5103.420 N,	5103.427 N,		
	485.144 E;	485.075 E;	485.009 E;	484.940 E;		
	5103.798 N,	5103.806 N,	5103.793 N,	5103.795 N,		
	485.000 E	484.945 E	485.009 E	484.940 E		
1-5-C	5097.453 N,	5097.467 N,	5097.459 N,	5097.471 N,		
	492.866 E;	492.931 E;	492.996 E;	493.058 E;		
	5097.851 N,	5097.865 N,	5097.856 N,	5097.870 N,		
	492.851 E	492.933 E	492.980 E	493.048 E		
6-1-C	5105.214 N,	5105.218 N,	5105.220 N,			
	553.732 E;	553.667 E;	553.603 E;			
	5105.620 N,	5106.024 N,	5105.612 N,			
	553.716 E	553.712 E	553.635 E			
6-2-C	5104.686 N,	5104.625 N,	5104.663 N,	5104.608 N,		
	549.498 E;	549.492 E;	549.594 E;	549.569 E;		
	5104.780 N,	5104.716 N,	5104.510 N,	5104.455 N,		
	549.114 E	549.096 E	549.959 E	549.946 E		
6-4-C	5101.453 N,	5101.452 N,	5101.472 N,	5101.472 N,		
	486.054 E;	486.120 E;	486.182 E;	486.248 E,		
	5101.057 N,	5101.057 N,	5101.076 N,	5101.076 N,		
	486.107 E	486.171 E	486.233 E	486.248 E		
6-5-C	5097.507 N,	5097.500 N,	5097.498 N,	5097.493 N,	5097.391 N,	
	479.638 E;	479.700 E;	479.766 E;	479.829 E;	479.889 E;	
	5097.102 N,	5097.191 N,	5097.317 N,	5097.089 N,	5097.097 N,	
	479.617 E	479.696 E	479.758 E	479.817 E	479.875 E	
6-6-C	5095.919 N,	5095.986 N,	5096.046 N,	5096.357 N,	5096.400 N,	
	491.591 E;	491.595 E;	491.591 E;	491.234 E;	491.258 E;	
	5096.098 N,	5096.167 N,	5096.227 N,	5096.255 N,	5096.319 N,	
	491.237 E	491.228 E	491.238 E	491.416 E	491.418 E	
11-1-C	5100.937 N,	5100.929 N,	5100.918 N,	5100.905 N,	5100.897 N,	
	491.883 E;	491.948 E;	492.012 E;	492.070 E;	492.134 E,	
	5100.580 N,	5100.605 N,	5100.626 N,	5100.604 N,	5100.602 N,	
	491.832 E	491.912 E	491.976 E	492.026 E	492.094 E	
11-3-C	5100.623 N,	5100.634 N,	5100.645 N,	5100.656 N,		
	492.858 E;	492.793 E;	492.729 E;	492.662 E;		
	5100.227 N,	5100.227 N,	5100.249 N,	5100.252 N,		
	492.827 E	492.767 E	492.701 E	492.638 E		

Table C1. Continued.

	UTM coordinates of transect endpoints					
Stand	Transect 1	Transect 2	Transect 3	Transect 4	Transect 5	Transect 6
11-4-C	5103.423 N, 491.704 E; 5103.634 N, 492.029 E	5103.363 N, 491.735 E; 5103.576 N, 492.082 E	5103.430 N, 491.636 E; 5103.040 N, 491.576 E	5103.437 N, 491.572 E; 5103.037 N, 491.502 E		

APPENDIX D. Minimum number alive and number of captures of small mammals, northern Maine.

Table D1. Number of initial captures of red-backed voles and deer mice, and total number of captures of shrews during June – August 2000 and 2001 within 37 trapping grids among 7 treatment- thinning class combinations in 7 townships in northern Maine.

			Year of sampling							
			2000				2001			
Thinning Class[a]	Treatment[b]	Replicate	RBV[c]	DM[d]	SS[e]	MS[f]	RBV[c]	DM[d]	SS[e]	MS[f]
1	T	1	3	0	2	4	16	2	5	14
1	T	2	31	3	0	1	37	5	6	1
1	T	3	10	0	4	4	9	2	4	0
1	T	4	8	1	0	1	5	12	1	2
1	T	5	4	1	0	0	5	6	18	1
1	T	6	8	1	1	11	7	7	10	25
1	C	1	0	0	1	0	3	12	1	0
1	C	2	1	1	1	1	6	2	11	2
1	C	3	3	2	1	0	4	1	2	6
1	C	4	0	1	1	0	8	9	6	5
1	C	5	5	0	1	2	4	6	5	1
6	T	1	6	0	0	5	3	8	8	0
6	T	2	0	0	1	3	12	10	0	5
6	T	3	4	1	0	5	4	9	4	5
6	T	4	11	1	0	1	8	0	13	17
6	T	5	9	2	2	10	4	1	7	5
6	T	6	4	2	1	1	2	4	27	8
6	C	1	1	0	0	0	2	14	6	2
6	C	2	6	0	1	1	7	2	7	0
6	C	4	13	0	0	0	9	3	9	3
6	C	5	7	1	6	0	1	6	2	0
6	C	6	1	0	4	0	1	2	7	0
11	T	1	2	0	0	3	9	2	18	25
11	T	2	3	0	3	17	6	1	11	14

Table D1. Continued.

			Year of sampling							
			2000				2001			
Thinning Class[b]	Treatment[c]	Replicate	RBV[c]	DM[d]	SS[e]	MS[f]	RBV[c]	DM[d]	SS[e]	MS[f]
11	T	3	11	0	1	15	16	13	11	1
11	T	4	11	3	0	3	10	4	9	16
11	T	5	7	2	0	14	13	13	21	5
11	T	6	16	4	0	1	12	8	28	2
11	C	1	4	3	0	1	4	11	4	0
11	C	3	2	4	1	1	3	15	21	2
11	C	4	2	2	0	1	3	18	15	3
16	T	1	25	3	0	0	21	0	4	0
16	T	2	10	4	0	6	5	10	15	20
16	T	3	19	5	4	11	13	7	10	1
16	T	4	10	7	0	19	23	16	3	8
16	T	5	6	5	3	18	5	19	22	1
16	T	6	17	11	0	12	20	17	9	14

[a] Thinning class, 1 = stands 1 year since treatment or stands with similar history of clearcutting, herbiciding, and site quality that were not thinned, 6 = 6 years since treatment or stands with similar history of clearcutting, herbiciding, and site quality that were not thinned, 11 = 11 years since treatment or stands with similar history of clearcutting, herbiciding, and site quality that were not thinned , 16 = 16 years since treatment.

[b] T = treated with PCT, C = unthinned stand.

[c] RBV = red-backed vole.

[d] DM = deer mouse.

[e] SS = short-tailed shrew.

[f] MS = masked shrew.

APPENDIX E. Geographic location of small mammal trapping grids within regenerating conifer stands, northern Maine.

Table E1. Township, ownership, and coordinates of the center point of small mammal trapping grids within 24 precommercially thinned and 13 similar, unthinned regenerating conifer stands in northern Maine. Universal trahsverse mercators (UTMs) are provided for zone 19 and WGS – 1984 datum.

Stand	Township	Land owner	Latitude - Longitude	UTM coordinate
1-1-T	T 4 R 11	Great Northern Paper	46°00'45.30666''N 69°09'06.75407 W	5095457.006 N 488242.547 E
1-2-T	T4 R 12	Great Northern Paper	45°59'11.44249''N 69°16'23.82878''W	5092585.166 N 478833.712 E
1-3-T	T4 R 11	Great Northern Paper	46°00'19.47527''N 69°07'33.90162''W	5094656.285 N 490237.933 E
1-4-T	T4 R 11	Great Northern Paper	45°59'23.02101''N 69°09'08.42909''W	5092928.953 N 488228.301 E
1-5-T	T4 R 12	Great Northern Paper	46°01'06.87746''N 69°18'00.45932''W	5096155.319 N 476768.209 E
1-6-T	T4 R 11	Great Northern Paper	49°59'56.66411''N 69°07'17.57484''W	5093951.718 N 490588.056 E
6-1-T	Hersey	International Paper	46°06'19.08670''N, 68°20'16.81348''W	5105960.354 N 551162.533 E
6-2-T	Hersey	International Paper	46°06'26.50177''N 68°18'20.99903''W	5106210.414 N 553646.849 E
6-3-T	Hersey	International Paper	46°05'32.81159''N 68°19'13.92464''W	5104543.533 N 552524.840 E
6-4-T	T 5 R 11	Great Northern Paper	46°04'11.27331''N 69°06'46.11927''W	5102304.673 N 485802.022 E
6-5-T	T 5 R 11	Great Northern Paper	46°04'11.27331''N 69°06 46.11927''W	5101808.777 N 491275.781 E
6-6-T	T 5 R 11	Great Northern Paper	46°04'42.16172''N 69°09'57.17069''W	5102769.287 N 487173.619 E
11-1-T	T 1 R 13	Plum Creek Timber	45°44'49.40830''N 69°26'00.27581''W	5066035.841 N 466287.480 E
11-2-T	T 1 R 13	Plum Creek Timber	45°41'11.75821''N 69°30'06.75490''W	5059349.978 N 460919.688 E
11-3-T	T 1 R 13	Plum Creek Timber	45°44'08.00600''N 69°25'29.26869''W	5064754.506 N 466950.658 E

Table E1. Continued.

Stand	Township	Land owner	Latitude - Longitude	UTM coordinate
11-4-T	T 1 R 13	Plum Creek Timber	45°40’44.42015”N 69°19’53.22495”W	5058437.236 N 474186.950 E
11-5-T	T 1 R 13	Plum Creek Timber	45°45’03.69945”N 69°24’54.61439”W	5066469.364 N 467708.500 E
11-6-T	T 1 R 13	Plum Creek Timber	45°41’20.37399”N 69°21’46.77091”W	5099557.467 N 471735.640 E
16-1-T	Spencer Bay	Plum Creek Timber	45°43’31.40681”N 69°27’28.84729”W	5063639.257 N 464359.956 E
16-2-T	Days Academy Grant	Plum Creek Timber	45°42.46.19090”N 69°40.35.82062”W	5062364.429 N 407337.645 E
16-3-T	Days Academy Grant	Plum Creek Timber	45°42’04.31443”N 69°39’57.84492”W	5061065.176 N 448147.923 E
16-4-T	Days Academy Grant	Plum Creek Timber	45°42’23.65636”N 69°39’11.69910”W	5061653.872 N 449150.672 E
16-5-T	Days Academy Grant	Plum Creek Timber	45°43’25.12562”N 69°37’44.98749”W	5063535.882 N 451040.494 E
16-6-T	Spencer Bay	Plum Creek Timber	45°42’37.67044”N 69°34’50.97244”W	5062042.908 N 454791336 E
1-1-C	T 4 R 11	Great Northern Paper	46°01’07.28114”N 69°09’37.83206”W	5096136.517 N 487575.610 E
1-2-C	T 4 R 11	Great Northern Paper	46°00’45.25239”N 69°07’20.08491”W	5095451.383 N 490536.368 E
1-3-C	T 4 R 11	Great Northern Paper	46°02’05.94640”N 69°12’03.07320”W	5097954.198 N 484457.242 E
1-4-C	T 5 R 11	Great Northern Paper	46°05’03.24662”N 69°11’33.47639”W	5103424.702 N 485106.685 E
1-5-C	T 4 R 11	Great Northern Paper	46°01’53.74408”N 69°05’34.11513”W	5097562.174 N 492817.617 E
6-1-C	Hersey	International Paper	46°05’59.76304”N 68°18’24.56659”W	5105384.495 N 553577.458 E
6-2-C	Hersey	International Paper	46°05’37.27979”N 68°21’39.64881”W	5104655.497 N 549394.586 E
6-4-C	T 5 R 11	Great Northern Paper	46°03’57.30549”N 69°10’48.17648”W	5108387.254 N 486074.690 E
6-5-C	T 4 R 12	Great Northern Paper	46 01 48.35087”N 69 15 45.13566”W	5097425.038 N 479682.127 E

Table E1. Continued.

Stand	Township	Land owner	Latitude - Longitude	UTM coordinate
6-6-C	T 4 R 11	Great Northern Paper	46°01'04.32650''N 69°06'39.50821''W	5096038.791 N 491409.754 E
11-1-C	T 4 R 11	Great Northern Paper	46°03'37.56601''N 69°06'10.43538''W	5100767.417 N 492040.994 E
11-3-C	T 5 R 11	Great Northern Paper	46°03'33.11034''N 69°05'38.04697''W	5100629.040 N 492736.714 E
11-4-C	T 5 R 11	Great Northern Paper	46°05'07.38142''N 69°06'20.47879''W	5103539.710 N 491828.888 E

APPENDIX F. Within-stand habitat and structural characteristics throughout thinned and unthinned stands, northern Maine.

Table F1. Median values (range) for overstory, understory, and coarse wood debris variables measured during the leaf-on season on 70 m × 70 m small mammal trapping grids within 37 stands distributed among 7 treatment-thinning class stand types throughout 7 townships in northern Maine.

	Overstory Types						
Variable	1-year PCT n=6	1-year unthinned n=5	6-year PCT n=6	6-year unthinned n=5	11-year PCT n=6	11-year unthinned n=3	16-year PCT n=6
LOGS[a]	906.25 (406.25 –1,781.25)	1,437.50 (688-2,500)	769.88 (375-1,406.25)	812.50 (719-1563)	1,078.13 (375-1,406)	812.50 (656-906)	250.00 (63-531)
LOGVOL[b]	44.21 (7.75-128.27)	55.94 (36.43-83.49)	15.90 (12.56-47.43)	34.31 (23.37-57.25)	39.48 (5.92-59.91)	32.14 (18.77-36.22)	12.29 (3.81-27.63)
STUMPS[c]	484.34 (344-875)	687.5 (438-1,156)	531.25 (281-938)	656.25 (469-781)	1,093.75 (563-1,250)	937.5 (875-1250)	593.75 (188-969)
STVOL[d]	22.29 (11.28-46.74	65.12 (21.72-75.57)	11.38 (2.97-46.10)	33.27 (23.02-69.76)	37.62 (22.77-85.48)	48.10 (47.13-97.66)	19.61 (8.35-83.18)
DBH[e]	10.50 (9.29-11.57)	10.67 (9.33-12.13)	13.27 (10.92-15.70)	10.10 (9.56-10.42)	12.34 (10.75-14.88)	11.11 (10.43-11.37)	15.07 (11.83-16.08)
LITTER[f]	3.17 (1.96-3.64)	2.50 (1.79-4.37)	3.16 (1.88-4.24)	2.24 (0.94-2.42)	1.85 (1.47-4.3)	1.81 (1.77-2.98)	2.18 (2.00-2.49)
CANOPY[g]	63.49 (42.27-88.43)	79.58 (72.28-87.87)	72.09 (63.80-87.19)	77.75 (67.84-85.84)	77.68 (68.85-90.64)	92.54 (85.61-95.09)	86.38 (80.34-91.18)
VVD[h]	4.00 (3.15-4.50)	4.66 (4.56-4.75)	4.12 (3.08-4.84)	4.80 (4.61-4.88)	4.19 (3.41-4.61)	4.65 (4.60-4.72)	3.59 (2.51-4.85)
DECIDTR[i]	94 (0-250)	0 (0-62.5)	16 (0-594)	63 (0-125)	0 (0-0)	125 (0-250)	15.63 (0-125)

Table F1. Continued.

Variable	Overstory Types 1-year PCT n=6	1-year unthinned n=5	6-year PCT n=6	6-year unthinned n=5	11-year PCT n=6	11-year unthinned n=3	16-year PCT n=6
CONTR[j]	860 (438-1,938)	1,000 (719-1,281)	734 (375-1,219)	1,156 531-1,906)	1,156 (844-1,531)	2,000 (1,844-2,125)	1,109 (813-1,594)
HGSTEM[k]	259,125 (146,438-680,188)	180,969 (107,906-854,406)	417,016 (36,531-478,125)	332,625 (168,562-356,656)	348,688 (143,625-774,563)	290,906 (46,125-324,250)	516,188 (227,531-765,969)
WGST[l]	31,766 (10,344-62,094)	25,000 (5,344-43,438)	23,031 (14,219-37,438)	24,750 (18,281-46,625)	23,906 (3,656-52,156)	40,625 (27,406-44,375)	67,234 (41,906-81,656)
DECST[m]	1,078 (281-1,719)	969 (250-1,406)	3,250 (906-4,844)	1,344 (63-6,438)	1,328 (500-1,875)	188 (0-219)	9,751 (406-2,938)
CONST[n]	219 (0-2,625)	875 (219-1,469)	1,156 (0-3,188)	781 (188-5,594)	1,297 (438-3,250)	531 (63-1,656)	1,797 (281-4,250)
HWBA[o]	1.25 (0-5.5)	1.63 (0.3-3.4)	1.94 (0.6-15.8)	3.50 (0.8-11.1)	0.69 (0.3-1.3)	2.38 (2-3.4)	1.38 (0.5-3.8)
SWBA[p]	15.63 (9.9-22.5)	20.75 (15.8-27.3)	14.38 (7.6-17.3)	20.50 (12.9-32.3)	21.31 (17.1-24.3)	26.88 (22.1-28.9)	22.19 (18-28.9)
SNAGBA[q]	0.38 (0-1.9)	0.75 (0.4-2)	0.25 (0-1.9)	0.25 (0.1-1.5)	0.56 (0.4-2)	0.63 (0-1)	0.06 (0-0.5)
LIVEGC[r]	35.09 (29.75-52.19)	35.63 (12.63-52.06)	42.75 (20.31-72.5)	29.69 (22.81-55.31)	34.84 (33.75-57.81)	25.31 (22.81-29.06)	37.84 (20.69-52.5)

Table F1. Continued.

Variable	Overstory Types 1-year PCT n=6	 1-year unthinned n=5	 6-year PCT n=6	 6-year unthinned n=5	 11-year PCT n=6	 11-year unthinned n=3	 16-year PCT n=6
RTMS/HA[s]	63 (0-313)	31 (0-312)	31 (0-125)	63 (0-250)	16 (0-156)	94 (94-156)	16 (0-62.5)
TOTDEB[t]	1,781 (563-2,375)	2,250 (1,438-3,281)	1,563 (906-1,813)	1,594 (1,344-2,500)	2,172 (1,312.5-2,781.25)	1,906 (1,656-2,063)	953 (594-1,250)
TOTBA[u]	18.44 (10.8-24.9)	23.00 (18-32)	16.69 (13.1-20.1)	25.50 (16.8-43.6)	22.44 (19.1-24.3)	30.25 (25.5-31.6)	24.56 (18.9-29.9)
TOTSTEM[v]	2,438 (938-5,750)	2,656 (1,938-3,469)	5,640 (3,875-13,156)	3,469 (2,469-8,781)	3,859 (2,219-5,250)	2,781 (2,219-4,000)	3,703 (3,031-8,375)

[a] LOGS = number of logs (≥ 1 m length, ≥ 7.6 cm diameter, < 45° from horizontal) per ha.

[b] LOGVOL = volume of logs (m^3/ha) (≥ 1 m length, ≥ 7.6 cm diameter, < 45° from horizontal) per ha.

[c] STUMPS = number of stumps (< 2 m height, ≥ 7.6 cm diameter).

[d] STUMPVOL = volume of stumps (m^3/ha) (< 2 m height, ≥ 7.6 cm diameter) per ha.

[e] DBH = average dbh (cm) of closest tree (≥ 7.6 cm dbh, ≥ 2 m height, > 45° from horizontal, alive) in each quarter.

[f] LITTER = average litter depth (cm).

[g] CANOPY = average overhead percent canopy closure during summer.

[h] VVD = understory lateral foliage density (average of four measures of visual obscurity in each of four height classes (0-0.5m, 0.5-1.0 m, 1.0-1.5 m, 1.5-2.0 m)).

[i] DECIDTR = number of deciduous trees (≥ 7.6 cm dbh, ≥ 2 m height, > 45° from horizontal, alive) per ha.

[j] CONTR = number of coniferous trees (≥ 7.6 cm dbh, ≥ 2 m height, > 45° from horizontal, alive) per ha.

[k] HGSTEM = number of herbaceous ground stems (< 0.5 m height, < 7.6 cm dbh, alive) per ha.

[l] WGST = number of woody ground stems (< 0.5 m height, < 7.6 cm dbh, alive) per ha.

[m] DECST = number of deciduous saplings (≤ cm dbh, alive) at 1.5 m height per ha.

[n] CONST = number of coniferous saplings (≤ cm dbh, alive) at 1.5 m height per ha.

[o] HWBA = basal area (m^2/ha) of deciduous trees .

[p] SWBA = basal area (m^2/ha) of coniferous trees.

Table F1. Continued.

[q] SNAGBA = basal area (m^2/ha) of snags (≥ 7.6 cm dbh, ≥ 2 m height, > 45° from horizontal, dead).
[r] LIVEGC = percent live ground cover.
[s] RTMS/HA = number of root masses (≥ 7.6 cm dbh at root collar) per ha.
[t] TOTDEB = number of (snags + logs + stumps + root masses) per ha.
[u] TOTBA = HWBA + SWBA + SNAGBA (m^2/ha).
[v] TOTSTEM = number of coniferous trees (≥ 7.6 cm dbh, ≥ 2 m height, > 45° from horizontal, alive) + number of deciduous trees (≥ 7.6 cm dbh, ≥ 2 m height, > 45° from horizontal, alive) + number of coniferous saplings (≤ 7.6 cm dbh, alive at 1.5 m height) + number of deciduous saplings (≤ 7.6 cm dbh, alive at 1.5 m height) per ha.

APPENDIX G. Median and range of stand-level structural variables in thinned and unthinned regenerating clearcuts, from 1 – 11 years post-treatment.

Table G1. Median values (range) for extensive overstory, understory, and coarse woody debris variables measured during the leaf-on season on 4, 400-m transects within 30 stands (17 PCT stands, 13 unthinned stands) among 6 treatment-thinning class stand types in northern Maine.

	Overstory types					
Variable	1-year PCT n=5	1-year unthinned n=5	6-year PCT n=5	6-year unthinned n=5	11-year PCT n=7	11-year unthinned n=3
DBH <7.6[a]	4.3 (3.6-4.6)	3.6 (2.9-4.4)	2.9 (2.2-3.0)	3.4 (3.0-3.8)	2.9 (2.5-3.2)	4.3 (3.9-4.8)
HT<7.6[b]	3.6 (3.4-4.6)	4.0 (3.4-4.8)	2.6 (2.5-2.9)	3.9 (3.0-4.2)	2.8 (2.7-3.2)	4.9 (4.2-5.1)
CROWN<7.6[c]	1.0 (0.5-1.7)	1.5 (1.2-2.0)	0.7 (0.6-1.0)	1.4 (0.9-1.7)	1.0 (0.8-1.4)	1.5 (1.1-2.0)
UNDERLCR[d]	0.72 (0.63-0.85)	0.60 (0.57-0.67)	0.68 (0.58-0.80)	0.59 (0.56-0.75)	0.63 (0.57-0.70)	0.70 (0.55-0.70)
#CONTR<7.6[e]	1,600 (1,060-3,400)	8,350 (1,350-14,300)	1,180 (420-1,580)	7,300 (5050-11,950)	1,200 (580-2,420)	4,250 (1,100-11,100)
#DECTR<7.6[f]	960 (100-1,600)	2,200 (600-3,850)	1,760 (800-8,800)	2,000 (850-6,150)	1,440 (580-2,040)	700 (600-850)
TOTUNDER[g]	2,580 (1,620-4,780)	8,950 (5,200-16,500)	2,940 (2,120-8,500)	12,950 (7,300-13,850)	2,780 (1,780-3780)	4,850 (1,800-11,950)
SCU[h]	6,400 (4,140-11,580)	26,650 (7,900-45,100)	5,300 (4,200-9,340)	28,050 (18,600-37,550)	4,960 (3,200-8,460)	13,350 (4,000-34,150)

Table G1. Continued.

Variable	Overstory types 1-year PCT n=5	1-year unthinned n=5	6-year PCT n=5	6-year unthinned n=5	11-year PCT n=7	11-year unthinned n=3
DBH >7.6^{i}	10.4 (9.9-11.3)	10.0 (9.1-11.8)	12.0 (11.0-14.8)	10.7 (9.5-11.5)	12.9 (11.9-15.3)	11.0 (10.0-13.3)
HT>7.6^{j}	7.1 (6.3-7.8)	7.5 (6.4-8.7)	7.9 (7.4-8.7)	7.9 (7.0-8.8)	9.0 (8.2-10.1)	8.9 (8.7-9.1)
CROWN>7.6^{k}	1.4 (0.5-2.3)	1.3 (0.9-2.2)	1.2 (0.5-1.3)	1.5 (0.7-2.5)	2.0 (0.9-2.5)	1.5 (1.4-2.2)
OVERLCR^{l}	0.80 (0.71-0.91)	0.85 (0.71-0.87)	0.85 (0.84-0.94)	0.83 (0.72-0.9)	0.81 (0.76-0.9)	0.77 (0.71-0.84)
#CONTR>7.6^{m}	1,220 (460-2,140)	1,450 (1,150-1,950)	1,100 (640-1,380)	1,150 (500-1,750)	1,420 (920-1,540)	1,550 (1,450-1,700)
#DECTR>7.6^{n}	60 (0-260)	0 (0-700)	20 (20-100)	150 (0-150)	20 (0-260)	150 (100-300)
TOTOVER^{o}	1,280 (460-2,400)	1,650 (1,450-1,950)	1,200 (660-1,460)	1,150 (550-1,900)	1,420 (1,180-1,760)	1,750 (1,700-1,800)
#CONREGEN^{p}	340 (40-680)	100 (0-900)	200 (80-340)	500 (50-1,100)	340 (40-580)	200 (0-350)
#DECREGEN^{q}	520 (280-600)	850 (100-1,550)	460 (220-1,080)	750 (200-1,100)	560 (240-1,340)	450 (300-750)

Table G1. Continued.

	Overstory types					
Variable	1-year PCT n=5	1-year unthinned n=5	6-year PCT n=5	6-year unthinned n=5	11-year PCT n=7	11-year unthinned n=3
TOTREGEN[r]	920	1,300	760	1,150	920	800
	(640-1,040)	(200-1,750)	(560-1,280)	(650-1,850)	(280-1,680)	(300-950)
TOTSTEM[s]	5,120	10,800	5,080	15,350	5,000	7,500
	(3,960-6,420)	(8,350-19,700)	(3,800-10,040)	(9,100-16,900)	(4,280-6,520)	(3,850-14,550)
% G & F[t]	3	0	6	2	2	1
	(0-8)	(0-3)	(2-12)	(2-10)	(0-16)	(0-9)
% MOSS[u]	18	12	11	17	15	16
	(13-27)	(8-31)	(3-42)	(3-34)	(10-32)	(10-21)
% GROUND[v]	0	1	0	0	0	0
	(0-1)	(0-2)	(0-1)	(0-3)	(0-2)	(0-0)
% ROCK[w]	1	1	0	0	1	0
	(0-4)	(0-7)	(0-0)	(0-1)	(0-2)	(0-1)
% LITTER[x]	59	76	55	69	78	69
	(46-83)	(55-87)	(32-81)	(51-78)	(63-80)	(65-79)
% OTHER[y]	17	12	20	10	5	5
	(5-23)	(1-19)	(7-24)	(9-26)	(2-9)	(0-25)
VEGDIST[z]	9.7	7.1	9.7	6.4	10.4	7.6
	(9.1-10.6)	(5.3-9.9)	(8.0-11.3)	(6.4-8.1)	(8.4-15.5)	(6.3-11.9)

Table G1. Continued.

	Overstory types					
	1-year PCT	1-year unthinned	6-year PCT	6-year unthinned	11-year PCT	11-year unthinned
Variable	n=5	n=5	n=5	n=5	n=7	n=3
LOGS[aa]	700 (440-1,280)	1,300 (1,000-2,300)	540 (460-1,140)	1,400 (600-2,600)	300 (220-1,100)	1,150 (1,100-1,250)
LOGVOL[ab]	94 (22-280)	309 (58-928)	100 (44-147)	251 (74-625)	42 (30-70)	196 (103-212)
CANOPY[ac]	73.72 (53.29-92.25)	85.02 (78.61-90.91)	76.43 (70.58-84.35)	87.21 (71.34-92.50)	88.05 (74.82-93.87)	83.23 (69.24-93.81)

[a] DBH<7.6 = average diameter at breast height (dbh) (cm) of stems < 7.6 cm, >1.0 m ht, alive.
[b] HT<7.6 = average height (m) of stems < 7.6 cm, >1.0 m ht, alive.
[c] CROWN<7.6 = average height (m) from ground to lowest living branches of crown, of stems < 7.6 cm, >1.0 m ht, alive.
[d] UNDERLCR = average ratio of length of crown to total height of stems < 7.6 cm, >1.0 m ht, alive.
[e] #CONTR<7.6 = number of conifer trees/ha < 7.6 cm, >1.0 m ht, alive.
[f] #DECTR<7.6 = number of deciduous trees/ha < 7.6 cm, >1.0 m ht, alive.
[g] TOTUNDER = #CONTR<7.6 + #DECTR<7.6 per ha.
[h] SCU = (3 × #CONTR<7.6) + (1 × #DECTR<7.6) per ha.
[i] DBH>7.6 = average diameter at breast height (dbh) (cm) of stems ≥ 7.6 cm, >1.0 m ht, alive.
[j] HT>7.6 = average height (m) of stems ≥ 7.6 cm, >1.0 m ht, alive.
[k] CROWN>7.6 = average height (m) from ground to lowest living branches of crown, of stems ≥ 7.6 cm, >1.0 m ht, alive.
[l] OVERLCR = average ratio of length of crown to total height of stems ≥ 7.6 cm, >1.0 m ht, alive.
[m] #CONTR>7.6 = number of conifer trees/ha ≥ 7.6 cm, >1.0 m ht, alive.
[n] #DECTR>7.6 = number of deciduous trees/ha ≥ 7.6 cm, >1.0 m ht, alive.
[o] TOTOVER = #CONTR≥7.6 + #DECTR≥7.6 per ha.
[p] #CONREGEN = number of regenerating conifer stems > 0.2 and <1.0 m height per ha.
[q] #DECREGEN = number of regenerating deciduous stems > 0.2 and <1.0 m height per ha.
[r] TOTREGEN = #CONREGEN + #DECREGEN
[s] TOTSTEM = TOTUNDER + TOTOVER + TOTREGEN
[t] % G & F = percentage of the ground covered by grass and forbs.
[u] %MOSS = percentage of the ground covered by mosses.

Table G1. Continued.

[v] %GROUND = percentage of the ground that is bare ground.
[w] %ROCK = percentage of the ground covered by bare rock.
[x] %LITTER = percentage of the ground covered by leaf litter and twigs.
[y] %OTHER = percentage of the ground covered by other living vegetation.
[z] VEGDIST = average understory lateral foliage density (average distance that an entire 2.0 m pole is obscured)
[aa] LOGS = number of logs per ha.
[ab] LOGVOL = volume of logs (m^3/ha) (>1 m length, ≥ 7.6 cm diameter at point of intersection, < 45° from horizontal)
[ac] CANOPY = average overhead percent canopy cover closure at 1.0 m height during summer.

APPENDIX H. Relationship between snowshoe hare density and total stem density in regenerating conifer stands, northern Maine.

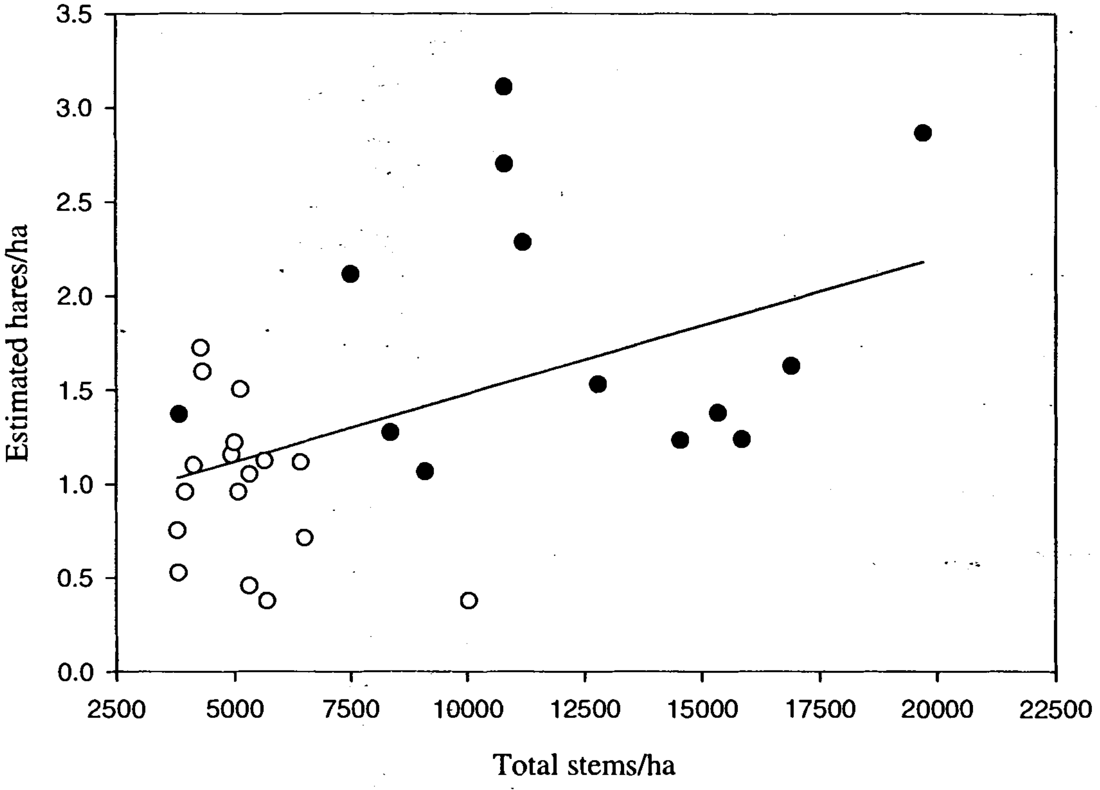

Figure H1. Relationship of snowshoe hare densities to total stem densities within 30 regenerating conifer stands (17 treated with PCT, ○ symbol; 13 unthinned stands, ● symbol), northern Maine, 2000-2002. Hare densities were predicted using pellet densities averaged across 2 leaf-off seasons with the modified Litvaitis-Long model (Chapter 1). Total stem densities were calculated by summing the number of overstory, understory, and regenerating stems/ha.

BIOGRAPHY OF THE AUTHOR

Jessica Anne Homyack was born in Reading, Pennsylvania on 25 March 1977. She was raised in the heart of Lancaster County in the village of Blainsport, Pennsylvania and graduated from Cocalico High School in 1995. Jessica attended West Virginia University from 1995 to 1999 and graduated *magna cum laude* in May 1999 with a Bachelor of Science in Wildlife and Fisheries Resources. At West Virginia University, Jessica held several elected positions in the Student Chapter of The Wildlife Society and was voted the Outstanding Senior in the Wildlife and Fisheries Program.

Jessica began a graduate program in the Department of Wildlife Ecology at the University of Maine in April, 2000. She received the George F. Dow Award for 2003. Jessica is a candidate for the Master of Science degree in Wildlife Ecology from The University of Maine in May, 2003.