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The effects of clearcutting on snowshoe hare (*Lepus americanus*) relative abundance in central Labrador

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Abstract

To assess the effects of clearcutting on snowshoe hare (*Lepus americanus*) relative abundance, we surveyed pellets in 1 m^2 circular plots and, vegetation and browse surveys in 4.5 m^2 circular plots among four different aged clearcut (30, 20, 10, 5 years post-harvest) and mature forests (>150 years old) in central Labrador, Canada. Data were modelled at three grain sizes: transect (4400 m^2), plot (314 m^2) and subplot scales (4.5 m^2). *Betula papyrifera*, distance from mature forest edge, tree and herb cover as well as remotely sensed forest inventory data were used as predictors for hare pellets. We found pellet abundance was 5 and 37 times greater (new and old pellets, respectively) in clearcut stands 30 years old than the next highest in 20 year old cuts. There were few hare pellets in the remaining stand ages. *B. papyrifera* was the most proportionately used browse species and most important of our fine-detailed vegetation in predicting hare pellets. The coarse-detailed, forest inventory and topographic data better predicted hare pellets than the fine-detailed vegetation data.

Keywords: Browse; Clearcut; Labrador; *Lepus americanus*; Pellet counts; Relative abundance; Snowshoe hare

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1. Introduction

A major concern of forest harvesting is the effects of altered forest structure and successional patterns on biodiversity. In addition to removing the overstory canopy, successional patterns are altered through disturbance to understory vegetation and soil (Donnelly and Shane, 1986; Greene et al., 1999; Stone, 2002; Simon and Schwab, 2005). Since most terrestrial animals require vegetation for food and cover, plant succession results in differing animal communities through time. Edges between uncut forest and clearcuts often produce a variety of plant species and structures over small areas (Yahner, 1988). As a result, these edges often support diverse animal communities due to the simultaneous availability of

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cover and forage (Yahner, 1988). However, edges may also support high predator densities (Dijak and Thompson, 2000; Forsey and Baggs, 2001) suggesting reduced habitat quality for prey species such as snowshoe hares, hereafter hares (Forsey and Baggs, 2001).

The nature and magnitude of logging effects on hare requirements depend upon time since harvesting (Telfer, 1974; Monthey, 1986; Ferron et al., 1998). The immediate effect of clearcutting is that some hares relocate while home ranges increased for hares that remained due to reduced habitat quality (Ferron et al., 1998). An important habitat attribute for hare survival is a dense understory cover to escape predation (Litvaitis et al., 1985; Wolff et al., 1982). Therefore, clearcut avoidance continues until woody vegetation reaches protective cover heights of >2 m (Sullivan and Moses, 1986; Ferron et al., 1998; de Bellefeuille et al., 2001). The dense understories in 10–30-year-old regenerating conifer stands provide prime hiding cover for hares (Wolff, 1980; Fuller and Heisey, 1986; Rogowitz, 1988; Ferron and Ouellet, 1992; Ferron et al., 1998).

Plant regeneration during the later stages of stand initiation after harvesting provides abundant hare forage (Sullivan and Moses, 1986; Rogowitz, 1988). In winter, hares forage on bark, twigs and leaves of low growing trees and shrubs, e.g., *Abies* spp., *Betula* spp., *Picea* spp., *Salix* spp. (Dodds, 1960; de Vos, 1964; MacCracken et al., 1988; Ferron and Ouellet, 1992). In spring and summer, hares consume nutrient-rich new growth of woody plants, e.g., those listed above, as well as *Ledum groenlandicum*, *Vaccinium* spp. and herbs, e.g., *Cornus canadensis*, *Equisetum* spp., *Trifolium* spp. (Dodds, 1960; MacCracken et al., 1988) in the order of emergence. Relative to other stand types, regenerating clearcuts 11–30 years of age have abundant forage and therefore high hare abundance (Parker, 1984; Monthey, 1986; Ferron et al., 1998). Hare abundance may return to pre-disturbance levels in harvested sites over time (Ferron et al., 1998). Further, mature forest-clearcut edges provide hare with cover and food in close proximity suggesting high quality habitat (Meslow and Keith, 1968; Wolff, 1980; Buehler and Keith, 1982; Litvaitis et al., 1985; Radvanyi, 1987; Forsey and Baggs, 2001). However, these benefits may be offset by increased predator densities near edges (Dijak and Thompson, 2000; Forsey and Baggs, 2001).

Hares have considerable ecological, recreational, and economic values throughout their range (de Bellefeuille et al., 2001). In Labrador, hares and their predators provide recreation, subsistence food and economic benefit for residents. Thus, there is interest in logging effects and increased access from hunters and predators due to larger road networks, on hare densities (Forest Management District 19A Planning Team, 2003). Many studies report that harvesting causes increased hare densities following sufficient regeneration, but this time varies geographically, upwards to 30 years, likely due to different successional patterns (Wolff, 1980; Fuller and Heisey, 1986; Rogowitz, 1988; Ferron and Ouellet, 1992; Ferron et al., 1998). This may be a short time frame relative to natural disturbances and hare population cycles but represents a significant portion of a hunter's lifespan. Thus, forest managers must ensure sufficient forest of the appropriate structure to support the traditional hunting needs of local communities. This necessitates site-specific understanding of hare abundance relative to forest harvesting regimes.

To evaluate the effects of harvesting on hares, we assessed their relative abundance in mature forests and regenerating clearcuts and related their abundance to vegetation structure. Such models can be linked to forest succession models to predict hare habitat quality under various management scenarios. However, fine-detailed vegetation descriptions are difficult to collect so we modelled hare abundance using coarse-detailed forest inventory and topographic maps—data routinely available to forest managers. As ecological patterns and processes change with scale (Weins, 1989; Legendre and Legendre, 1998), modeling was conducted at three grain sizes: subplot (4.5 m^2), plot (314 m^2), and transect (4400 m^2) and the efficacy of both the fine- and coarse-detailed models were compared.

2. Study area

We conducted pellet surveys from 28 June to 10 August 2004 within 40 km of Happy Valley, Goose Bay (53°19′N, 60°25′W) Newfoundland and Labrador, Canada (Fig. 1). All transects were located in the High Boreal Forest Ecoregion of Labrador (Meades, 1990) which contains the most productive forests for

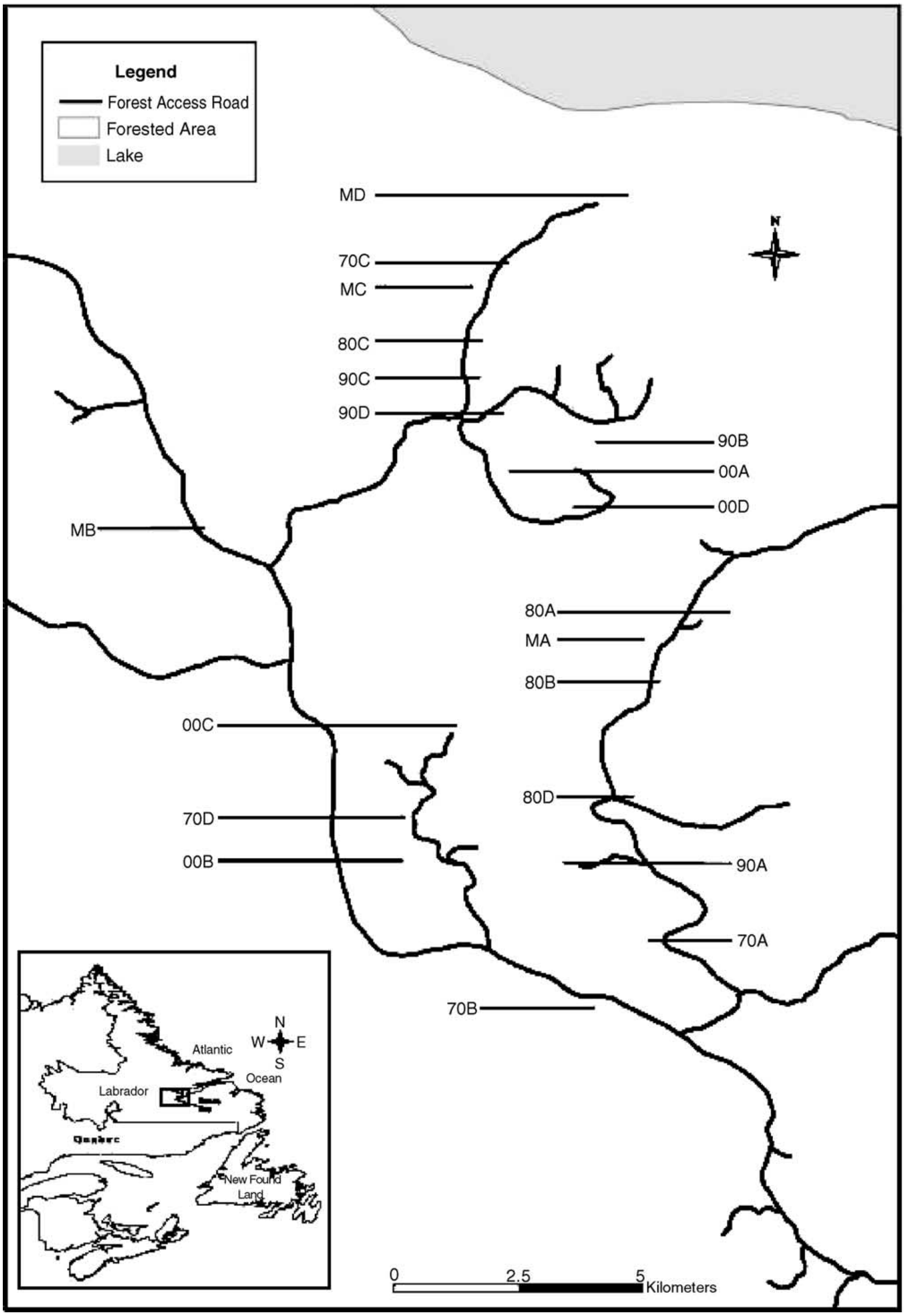

Fig. 1. Study area showing transect locations, number refers to year of harvest where 00 = 2000; 90 = 1990; 80 = 1980; 70 = 1970 and M = mature.

commercial timber in Labrador (Wilton, 1959; Lopoukhine et al., 1975) and is accessed by forest harvesting roads (Fig. 1). The moderately rolling terrain is dominated by *Picea mariana*/*Pleurozium schreberi* forest (Lopoukhine et al., 1975) at the higher elevations and *Abies balsamea*/*P. mariana*/*Betula* spp. forest at slightly lower elevations.

This area experiences a mean annual temperature of −0.5 °C (monthly mean range: −18.1 to 15.4 °C) and precipitation amounts of 949 mm, half of which falls as snow (Environment Canada Climate Normals: http://www.msc-smc.ec.gc.ca; viewed 27 September 2004). Snow generally remains on the ground from October through June. Portions of this study area have been commercially harvested from the late 1960s until present (Forest Management District 19A Planning Team, 2003). The rotation age is 120 years and *P. mariana* usually dominates the overstory of regenerating stands when *P. mariana* forests are harvested, but with increased proportions *A. balsamea*, particularly on moist slopes (Simon and Schwab, 2005).

3. Methods

3.1. Study design

We established 20, 250 m transects in different stands, with four transects representing each of five stand ages: clearcut in the mid-1970s, mid-1980s, mid-1990s, after 2000, or uncut mature (>180 years old) forest. Stands ranged from 30 to 700 ha and those within the same age group were selected to be as far apart as possible (≥700 m) while still being accessible. Prior to harvest, stands were dominated by *P. mariana* and classified as commercial, i.e., supporting >100 m^3 of timber with canopy height ranging from 9.5 to 18.5 m tall and crown closure ranging from 50 to 75% (Newfoundland and Labrador Department of Natural Resources, unpublished data). Our mature forest plots reflected this variation. All sites regenerated naturally and were free from any post-harvest silvicultural treatments. Transects in harvested stands started at commercial mature forest edges and were oriented to avoid all other stand edges, roads and patches of remnant forest. Transects consisted of evenly spaced plots at 50 m intervals. Each plot consisted of five, 1 m^2 circular subplots: one central and the remaining four in the cardinal directions 10 m from the center point. We used pellet counts in each subplot as an index of hare relative abundance (Murray et al., 2002). Pellets were classified new or old according to Krebs et al. (1987). Pellets on the plot boundary were included in the survey. Pellet counts are considered a reliable indicator of habitat use by hare (Wolfe et al., 1982) and hare density (Krebs et al., 1987, 2001).

3.2. Vegetation surveys

Centered around each subplot, tree species and the number of stems were recorded in a 4.5 m^2 circle. Trees and taller shrubs were placed into height classes: ≤50, 51–100, 101–200, 201–300, 301–400, 401–500 and >500 cm. The presence of hare browsing was recorded for each stem. Ground vegetation, shrubs typically ≤0.75 m, prostrate woody shrubs, forbs, mosses, and lichens, were estimated using a system adapted from Daubenmire (1968). At the center of each subplot, the cover of ground vegetation within a 0.1 m^2 quadrat was recorded as one of 7% classes: 0, 0–5, 5–25, 25–50, 50–75, 75–95, 95–100. The midpoints of these classes were the data used in analyses.

3.3. Data analyses

To assess the effect of forest management on hare abundance, we compared mean pellet abundances between forest ages. Hare pellet–vegetation relationships were analysed at three different grain sizes: the subplot grain (4.5 m^2, $n = 500$), the plot grain which combined all subplots within a plot (314 m^2, $n = 100$) and the transect grain which combined all subplots within a transect (4400 m^2, $n = 20$). Spatial dependence in observations violates the assumption of independence, and can cause false correlations, i.e., no causal effect, unless spatial pattern is accounted for in statistical models (Legendre and Legendre, 1998; Keitt et al., 2002; Lichstein et al., 2002). Count data like our pellet counts, often violate assumptions required by Gaussian models and are typically analysed using generalized linear models with a Poisson distribution (McCullagh and Nelder, 1989). Unfortunately, autoregressive models with a Poisson response distribution (auto-Poisson) are impractical because they can only have negatively correlated errors (Cressie, 1993). Therefore, we analysed our log + 1 transformed pellet count data using Gaussian models. Similar to Lichstein et al. (2002), we compared non-spatial Gaussian models with Poisson models and the results were qualitatively similar. We followed the approach of Keitt et al. (2002) and Lichstein et al. (2002) to incorporate spatial patterns in our analyses: (1) We tested for spatial patterns in the residuals of non-spatial statistical models (ordinary least-squared regression) using code in Ecological Archives M072-007-S1 from Lichstein et al. (2002) to compute significance tests for correlograms, $\alpha = 0.05$, Bonferroni corrected. Correlogram lags were chosen as a compromise between resolution, extent, and sample size within each lag. Our nested subplot design did not permit equal lag distances thus lag distances and extents varied within and between grains: at the subplot scale, 10 m lag followed by 30 m; 50 and 100 m; 200 m lags up to 3200 m; at the plot scale: 50 m lags up to 200 m then 250 m lags up to 4200 m, at the transect scale: 1000 m lag followed by 500 m lags up to 5500 m. (2) If pattern was detected in the residuals, we reanalysed the data using autoregressive models. Space was accounted for in models up to the maximum distance that autocorrelation appeared in the residuals. We then re-examined the residuals of the spatial models for patterns. Relative contributions of environment and space to particular models were assessed through partial R^2 (Nagelkerke, 1991) for the proportion of variance explained by (a) non-spatial model, (b) space only, (c) environment and space (autoregressive models) (Borcard et al., 1992; Legendre and Legendre, 1998; Lichstein et al., 2002).

Within the framework described above we constructed models to evaluate the effects of vegetation on pellet counts. From the literature, variables were chosen to represent cover and food of likely importance to hares in our region (Dodds, 1960; de Vos, 1964; MacCracken et al., 1988; Ferron and Ouellet, 1992): distance to mature forest edge, *B. papyiferia* stem densities, total tree density (height $\geq$3 m), herb cover, shrub cover, *P. mariana*, and *A. balsamea* stem densities. To better assess which variables would likely influence hare abundance in Labrador, we compared our study area with those of the above reports and discussed variables with local hunters leading us to expect the first four variables to be most important. Traditional knowledge such as that from hunters is an underused but useful component in scientific research (Usher, 2000). As Burhnam and Anderson (2002) stress the importance of evaluating the smallest possible set of models, we constructed global models using only the first four variables. Goodness of fit was usually on the global models only. If residuals of the global model were autocorrelated we proceeded with spatial models (described above). We removed variables from the global model through backward elimination; if the elimination of a variable reduced the Akaike's information criterion (AIC), it was not included in further models. The strength of evidence for each model was evaluated by the AIC weight (Burhnam and Anderson, 2002). If the partial R^2 due to environmental factors <0.15, we felt the explained variance was too low to be of biological relevance, therefore did not investigate further models. For global models with a low R^2 we sequentially added the remaining three variables (shrub cover, *P. mariana*, and *A. balsamea* stem densities) to the best model and retained the variable if it reduced the AIC and recalculated the R^2.

We followed a similar approach to determine if coarse-detailed data could sufficiently explain variation in pellet counts. Stand age is a strong indicator of vegetation structure but this is influenced by slope and aspect (Fralish, 1994). To model the predicted parabolic relationship between pellet counts and stand age, we included stand age + stand age^2. Also included were indices of northness [cos(aspect) × tan(slope)] and northeastness [cos(aspect − 45°) × tan(slope)] adapted from Beers et al. (1966). Stand age was determined from 1:12 500 forest inventory maps based on 1992 data (Department of Natural Resources, unpublished data) while slope and aspects were derived from digital elevation models based on 1:50 000 topographic maps.

4. Results

4.1. Vegetation surveys

A. balsamea and *P. mariana,* were the most abundant tree species, and were found in all height classes and stand ages (Table 1). Tree and shrub species richness were highest in 20-year-old stands.

Table 1
Vegetation succession following clearcutting black spruce stands (*P. mariana*)

Species	Approximate stand age (years)				
	5	10	20	30	>180
Trees/shrubs (<50 cm)					
A. balsamea	228	158	550	271	259
Alnus crispa			25		
Picea glauca			91	46	11
P. mariana	543	701	126	178	718
V. edule	11				
Trees/tall shrubs (51–100 cm)					
A. balsamea	33	30	99	93	16
A. crispa			18		
Betula papyrifera				16	
P. glauca			27		
P. mariana	39	47	100	69	45
Trees/tall shrubs (100–200 cm)					
A. balsamea	20	17	148	120	35
A. crispa	5	1	39	4	7
Alnus rugosa	1	4	15		8
B. papyrifera			6	29	
P. glauca		1	20	4	
P. mariana	30	36	80	100	59
Salix spp.	3	2	18	2	
Trees/tall shrubs (200–300 cm)					
A. balsamea	7	4	37	55	14
A. crispa	2		37	4	3
A. rugosa	2	3	1		
B. papyrifera			8	77	
P. glauca			3	1	
P. mariana	4	5	34	47	12
Salix spp.			2	5	
Trees/tall shrubs (>300 cm)					
A. balsamea	2	6	16	59	20
A. crispa	1		10	8	2
A. rugosa	3		7		
B. papyrifera	1	2	27	60	
P. glauca			2	1	
P. mariana	8	6	12	72	81
Salix spp.			3	9	
Shrubs/herbs					
Amelanchier bartramiana	0.2		0.2	0.1	
Coptis groenlandica	0.2		0.2	0.1	0.1
C. Canadensis	5.3	11.2	9.9	5.1	1.7
Dryopteris disjuncta	0.2		0.2	0.1	
Equisetum sylvaticum	0.2	0.2	1.3	0.4	0.1
Gaultheria hispidula	5.0	11.0	11.3	5.8	11.5
L. groenlandicum	1.5	3.5	2.5	1.8	4.5
Linnaea borealis	2.5	0.4	3.1	2.1	0.4
Maianthemum canadensis	0.1		0.1		0.2
Rubus chamaemorus	0.2	0.9	1.4	1.8	1.3
Rubus pubescens			0.6	0.2	
Trientalis borealis	0.2		0.1	0.1	
V. boreale	1.6	2.9	1.3	4.5	6.7
Vaccinium ovalfolium	0.4	0.2		0.5	
Vaccinium vitis-idaea	0.4	2.4	0.6	0.9	1.5
Mosses/lichens/liverworts					
Bazzania trilobata			0.1	0.7	
Cladonia alpestris			0.7	1.6	2.6
Cladonia arbuscula	0.8	1.0	1.5	2.6	3.6
Cladonia chlorophae		0.6	1.0	0.7	0.1
Dicranum majus	1.9	3.1	1.5	2.3	1.1
Hylocomium splendens	0.8	0.6	1.2	5.4	
Lycopodium annotinum	0.5	0.7	4.2	1.0	2.3
Lycopodium lucidulum	0.2	0.7	0.1	0.2	0.9
Peltigera lepidophora	2.8	2.7	0.6	0.7	2.0
P. schreberi	14.3	17.5	15.4	35.9	27.6
Ptilium crista-castrensis	2.5	0.2	1.1	4.6	7.6
Sphagnum spp.	2.3	3.0	12.7	2.9	12.5

Abundance of trees and tall shrubs are expressed as mean number of stems. Remaining plants are expressed as mean percent cover.

B. papyrifera only occurred >50 cm and was most abundant in 30-year-old stands in all height zones. Trees and taller shrubs <50 cm were abundant in all stand ages but while those in height zones between 50 and 300 cm were most abundant on 20- and 30-year-old stands. Trees and taller shrubs >300 cm were most abundant on 30- and >180-year-old stands. Smaller shrubs, herbs, mosses, lichens and liverworts showed species-specific differences between stand ages but there was no consistent pattern among vegetation groupings.

4.2. Browse

B. papyrifera was the most proportionately browsed species by hares with 55% of stems browsed compared with 25, 16 and 15% of *Viburnum edule*, *Vaccinium boreale*, and *Salix* spp., respectively. Although *A. balsamea* and *P. mariana* were the dominant species, they were browsed minimally by hares (≤0.3%) (Table 2).

4.3. Pellet abundance

Pellet numbers were highest in 30-year-old stands, with greater than 37 and 5 times the amount of pellets, new and old, respectively, found in the next closest

Table 2
Proportional browsing of woody vegetation by snowshoe hare (*L. americana*) in regenerating clearcut and mature black spruce (*P. mariana*) stands

Species	Number of stems	Browsed stems	Proportion	S.E.[a]
B. papyrifera	259	142	0.548	0.031
V. edule	20	5	0.250	0.099
V. boreale	111	18	0.162	0.035
Salix spp.	73	11	0.151	0.042
A. rugosa	74	7	0.095	0.033
A. crispa	189	8	0.042	0.014
L. groenlandicum	111	1	0.009	0.009
A. balsamea	2336	6	0.003	0.001
P. mariana	3205	6	0.002	0.001

Numbers include all 4.5 m^2 sample units ($n = 500$).

[a] Standard error on the proportion of stems browsed.

counts (20-year-old stands). The remaining stand ages had very few pellets (Fig. 2).

4.4. Habitat variables analyses

The R^2 values for environmental variables (distance to mature forest edge, *B. papyiferia* stem densities, total tree density (height $\geq$3 m) and herb cover) were relatively low (0.09–0.37) thus substantial variation in pellet abundance was not captured by our models. Adding spatial variables where residuals were autocorrelated added an additional 13–24% to the total R^2.

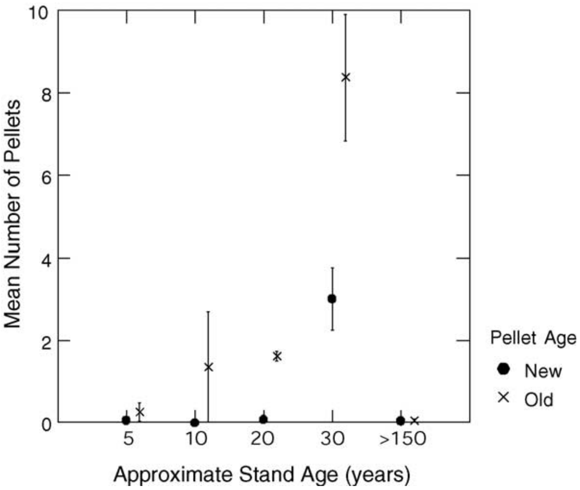

Fig. 2. Mean and standard error of snowshoe hare (*Lepus americana*) pellet numbers by stand age.

Pellet abundance was positively related to *B. papyrifera* which was the most important variable. All models with a ΔAIC value <4 contained *B. papyrifera* and half of the best models contained only this variable: old at plot grain; both new and old at transect grain (Table 3). The association with distance to forest edge was consistently negative but was less important as it only appeared in the best model for new pellets at the plot grain. Herbs and tree density had inconsistent associations both within and between grain sizes.

Adding shrub cover, *A. balsamea* and *P. mariana* densities to the best models from the above procedure provided little extra explanation. For new pellets at the subplot scale, adding these variables did not increase the R^2 above 0.15. Despite the reduction in the AIC of 8.67 by adding shrub cover and *P. mariana* density for old pellets at the subplot grain, the R^2 was increased by only 0.02. The addition of other variables did not reduce the AIC for any other grain.

Coarse-detailed variables better explained pellet abundance than fine-detailed vegetation (Table 4). The R^2 values increased with grain and were 29–86% higher than the corresponding fine-detail vegetation models. Pellet counts followed the expected parabolic relationship with stand age as indicated by the negative relationship with stand age^2 in all models. Stand age + stand age^2 appeared to be the most important variables in the models but northness and northeastness appeared important as well, particularly at smaller grain sizes. When present in a model, the coefficient for northness was consistently negative indicating greater pellet abundance on south-facing slopes. Slope and aspect appeared less important at the transect grain as the best model for both new and old pellets consisted only of stand age and stand age^2.

5. Discussion

Our finding that hare abundance was highest in the 30-year-old stands with lesser amounts in the 20-year-old stands is similar to other studies. Parker (1984) and Monthey (1986) found hare abundance to peak in regenerating stands of 11–16 years in New Brunswick and Maine, respectively. The earlier peak in hare abundance in those studies is likely due to faster regeneration resulting from a more southern climate,

Table 3
Goodness of fit statistics for global models of snowshoe hare (*L. americana*) pellet abundance in relation to fine-detailed vegetation characteristics

Model[a]	Goodness of fit statistics[b]	ΔAIC	Weight
Subplot ($n = 500$ at 1 m^2), new pellets	$R_e^2 = 0.09$; $R_p^2 = 0.21$; $R_t^2 = 0.22$; $N = 1900$		
Subplot ($n = 500$ at 1 m^2), old pellets	$R_e^2 = 0.24$; $R_p^2 = 0.42$; $R_t^2 = 0.49$; $N = 3000$		
0.171 + 0.079 Bp − 0.010H − 0.020 TD		0.00	5.76×10^{-1}
0.193 + 0.080 Bp − 0.010H + 0.021 TD − 0.000D		2.01	2.11×10^{-1}
0.155 + 0.078 Bp + 0.021 TD		2.74	1.47×10^{-1}
Plot ($n = 100$ at 314 m^2), new pellets	$R_e^2 = 0.31$; $R_p^2 = 0.29$; $R_t^2 = 0.49$; $N = 1900$		
0.5034 + 0.079 Bp − 0.002D		0.00	2.35×10^{-1}
0.689 + 0.092 Bp − 0.008 TD − 0.002D		0.06	2.28×10^{-1}
0.502 + 0.077 Bp + 0.004H − 0.002D		1.50	1.11×10^{-1}
0.657 + 0.090 Bp + 0.005H − 0.008 TD − 0.002D		1.52	1.10×10^{-1}
0.0533 + 0.089 Bp − 0.008 TD		1.60	1.05×10^{-1}
0.369 + 0.075 Bp		1.64	1.03×10^{-1}
0.503 + 0.087 Bp + 0.005H − 0.008 TD		2.88	5.56×10^{-2}
0.338 + 0.073 Bp + 0.005H		3.00	5.24×10^{-2}
Plot ($n = 100$ at 314 m^2), old pellets	$R_e^2 = 0.37$; $R_p^2 = 0.43$; $R_t^2 = 0.51$; $N = 1900$		
0.074 + 0.064 Bp		0.00	0.20
0.529 + 0.047 Bp + 0.011 TD		0.12	0.19
0.673 + 0.050 Bp + 0.011 TD − 0.002D		0.58	0.15
0.702 + 0.062 Bp + 0.006H		1.58	0.09
0.499 + 0.045 Bp + 0.005H + 0.011 TD		1.80	0.08
0.0417 + 0.019 TD		2.18	0.07
0.844 + 0.065 Bp + 0.005H − 0.002D		2.26	0.06
0.0641 + 0.048 Bp + 0.005H + 0.011 TD − 0.002D		2.38	0.06
0.530 + 0.020 TD − 0.002D		3.18	0.04
0.382 + 0.007H + 0.018 TD		3.42	0.04
Transect ($n = 20$ at 4400 m^2), new pellets	$R_e^2 = 0.36$		
0.707 + 0.0386 Bp		0.00	0.59
0.823 + 0.04 Bp − 0.004H		2.95	0.14
0.757 + 0.040 Bp − 0.00062 TD		3.16	0.12
0.153 + 0.009 TD		3.75	0.09
Transect ($n = 20$ at 4400 m^2), old pellets	$R_e^2 = 0.37$		
1.388 + 0.046 Bp		0.00	0.51
0.577 + 0.012 TD		2.15	0.17
1.15 + 0.038 Bp + 0.003 TD		3.00	0.11
1.511 + 0.476 Bp − 0.004H		3.01	0.11

Least-squares regression was used were the residuals were not autocorrelated; otherwise conditional autoregressive models were used and partial R^2 values computed. The strength of evidence of all nested models was assessed by differences in Akaike's information criterion (ΔAIC) and the AIC weights. Only models with $\Delta AIC \leq 4.00$ are displayed.

[a] Bp: *B. papyrifera*; TD: tree density; H: herbs; D: distance.

[b] R_e^2: variation explained by environmental variables; R_p^2: variation explained by spatial variables; R_t^2: variation explained by both environmental and spatial variables; N: distance at which autocorrelation was incorporated.

differing growth rates of varying species and manual planting which was present in the New Brunswick study. Our high hare pellet counts in 30-year-old stands is likely, in part, due to abundant *B. papyrifera*. This species was of undoubted importance in our models for both old and new pellets on all three grains. Support for *B. papyrifera* as hare preferred forage was found in insular Newfoundland, Ontario, Alaska and Québec (Dodds, 1960; de Vos, 1964; MacCracken et al., 1988; Darveau et al., 1998). Compared with

Table 4
Goodness of fit statistics for global models of snowshoe hare (*L. americana*) pellet abundance in relation to coarse-detailed variables

Model[a]	Goodness of fit statistics[b]	ΔAIC	Weight
Subplot ($n = 500$ at 1 m^2), new pellets	$R^2_e = 0.17$; $R^2_p = 0.21$; $R^2_t = 0.25$; $N = 1700$		
$-0.073 + 0.023A - 1.25 \times 10^{-4}A^2 - 1.383\mathrm{N} + 1.640\ \mathrm{NE}$		0.00	0.710
$-0.106 + 0.024A - 1.28 \times 10^{-4}A^2 - 0.510\mathrm{N}$		3.08	0.152
$-0.096 = 0.023A - 1.27 \times 10^{-4}A^2 + 0.558\ \mathrm{NE}$		3.27	0.138
Subplot ($n = 500$ at 1 m^2), old pellets	$R^2_e = 0.31$; $R^2_p = 0.43$; $R^2_t = 0.45$; $N = 3100$		
$-0.133 + 0.042A - 2.21 \times 10^{-4}A^2 - 1.281\mathrm{N}$		0.00	0.519
$-0.147 = 0.040A - 2.19 \times 10^{-4}A^2$		1.17	0.289
$-0.134 + 0.041A - 2.21 \times 10^{-4}A^2 - 1.154\mathrm{N} - 0.230\ \mathrm{NE}$		2.00	0.191
Plot ($n = 100$ at 314 m^2), new pellets	$R^2_e = 0.45$		
$-0.264 + 0.074A - 3.92 \times 10^{-4}A^2 - 4.021\mathrm{N} + 3.915\ \mathrm{NE}$		0.00	0.944
$-0.366 + 0.076A - 4.03 \times 10^{-4}A^2 - 1.749\mathrm{N}$		6.23	0.042
Plot ($n = 100$ at 314 m^2), old pellets	$R^2_e = 0.48$; $R^2_p = 0.43$; $R^2_t = 0.54$; $N = 1300$		
$-0.205 + 0.103A - 5.53 \times 10^{-4}A^2 - 2.634\mathrm{N}$		0.00	0.484
$-0.201 + 0.101A - 5.53 \times 10^{-4}A^2$		0.69	0.343
$-0.196 + 0.103A - 5.54 \times 10^{-4}A^2 - 3.053\mathrm{N} + 0.778\ \mathrm{NE}$		2.06	0.173
Transect ($n = 20$ at 4400 m^2), new pellets	$R^2_e = 0.67$		
$-0.482 + 0.157A - 8.47 \times 10^{-4}A^2$		0.00	0.703
$-0.448 + 0.153A - 8.14 \times 10^{-4}A^2 - 2.504\mathrm{N}$		2.66	0.186
$-0.257 + 0.146A - 7.76 \times 10^{-4}A^2 - 7.292\mathrm{N} + 7.554\ \mathrm{NE}$		3.70	0.111
Transect ($n = 20$ at 4400 m^2), old pellets	$R^2_e = 0.60$		
$0.362 + 0.168A - 9.31 \times 10^{-4}A^2$		0.00	0.810
$0.377 + 0.166A - 9.16 \times 10^{-4}A^2 - 1.126\mathrm{N}$		3.49	0.142
$0.580 + 0.159A - 8.75 \times 10^{-4}A^2 - 6.205\mathrm{N} + 8.014\ \mathrm{NE}$		5.65	0.048

Least-squares regression was used were the residuals were not autocorrelated; otherwise conditional autoregressive models were used and partial R^2 values computed. The strength of evidence of all nested models was assessed by differences in Akaike's information criterion (ΔAIC) and the AIC weights. Only models with $\Delta\mathrm{AIC} \leq 4.00$ are displayed.

[a] *A*: stand age; N: northness; NE: northeastness.

[b] R^2_e: variation explained by environmental variables; R^2_p: variation explained by spatial variables; R^2_t: variation explained by both environmental and spatial variables; *N*: distance at which autocorrelation was incorporated.

those studies, *B. papyrifera* was used to a much greater degree in this region. Those studies report high use of *Salix* spp. and *Picea* spp., but despite their abundance in our study area, we found little proportional use for these species.

Contrary to our expectations and that of several investigators, we did not find consistent positive associations between pellet abundance and both tree densities and herb cover. Hares selected stands with dense trees and understories in insular Newfoundland (Dodds, 1960) and Maine (Litvaitis et al., 1985). Hares in eastern Québec used herbaceous ground cover as forage and dense vegetation closure as protection from predators (Ferron and Ouellet, 1992). Prolonged snow cover in our study area may increase hare dependence on areas with abundant woody browse, hence the weaker and inconsistent relationship between pellet abundance and herb cover. Since many of the predators in the above quoted studies occur in Labrador (though densities may be different), the lack a consistent positive tree density relationship is unexpected. Furthermore, understory cover, as winter thermal protection, should be important for hares (Meslow and Keith, 1968; Wolff, 1980; Buehler and Keith, 1982; Wolfe et al., 1982; Litvaitis et al., 1985). The mean daily minimum temperatures are below the −8 °C critical low temperature for hares (Irving et al., 1957), for 4 months of the year in Labrador (Environment Canada Climate Normals: http://www.msc-smc.ec.gc.ca; viewed 27 September 2004), thus one would expect a consistent positive tree density relationship for thermal cover in our study area.

The negative relationship between pellet occurrence and distance to mature forest edge was weak. However, the relative importance of mature forest for hares is inconsistent among studies. Both Ferron et al. (1998) and de Bellefeuille et al. (2001) found remnant mature forest to be important to hares immediately following harvesting. We detected very little hare use of mature and early regenerating stands in this area. Similar to other studies, we found greater hare use of older regenerating stands than uncut forest (Parker, 1984; Monthey, 1986; Darveau et al., 1998).

Despite measuring features consistently identified in the literature as important for hares, the low R^2 values in our fine-detailed vegetation analyses suggest hares are selecting features not captured by our models. Interestingly, our coarse-detailed vegetation analysis provided a significant improvement in explaining variation in pellet counts. Using existing coarse vegetation data was also effective in other studies. Seoane et al. (2004) found data from existing general-purpose vegetation maps were as accurate as more detailed remotely sensed data in predicting bird distributions. Similarly, Vernier et al. (2002) found that existing forest inventory data was sufficient to model bird abundances.

The collection of vegetation data in the field is time consuming and costly. Finding that existing data can equally or better predict relative hare abundance makes forest management options easier to evaluate. It seems likely that stand age is a surrogate for other vegetation features that we have not directly measured. These stands may provide the prime combination of forage and cover (both thermal and predator avoidance cover) habitat for hares (Koehler, 1990). The younger successional stands and mature forests lack these specific components that are found in the 30-year-old stands that are conducive to higher hare use. Open areas, such as recent clearcuts, are considered poor quality habitat due to increased exposure to predation and less forage availability (Wolff, 1980).

The subplot and plot grains at which our pellet–vegetation data were analysed were 4.5 and 314 m^2, respectively. This is small relative to hare home range sizes, e.g. up to 10 ha (Banfield, 1974) and likely do not characterize habitat at an appropriate scale for this species. Further, it is possible that the location of pellets within a home range may differ slightly from "preferred" areas within the home range, adding noise to our data. As our grain size increased there was a general increase in variance explained by environment in our models, though this may be an artifact of varying sample size. Even our largest grain of 4400 m^2 may not have been large enough to fully capture hare–environment relationships. The increase in R_e^2 with grain was particularly strong in our coarse-detailed variable models. This may be because the variables in those models, particularly stand age, tend to vary at relatively large scales.

Despite what appears to be a clear association with 30-year-old clearcuts and a strong association with *B. papyrifera* there are possible sources of error with this research. Because pellet decay rates differ among forest types, old pellets are considered less accurate than new pellets in ascertaining hare abundance (Prugh and Krebs, 2004). Observer bias can be considerable in distinguishing between new and old pellets (Prugh and Krebs, 2004). To minimize this bias, we evaluated new and old pellets separately and both appeared to show similar patterns. The possibility exists that pellet detectability differs between forest types, potentially biasing in our data. Although this potential bias remains untested, it seems reasonable to assume that pellets would be more difficult to detect where ground cover is highest. Our herbaceous and shrub cover is lowest on the 5-year-old sites, which has the fewest pellets, and similar on all other age groups. Thus, we do not believe this potential bias significantly affected our results. Dodds (1960) outlined several factors potentially biasing browse observations: over-browsing on the same stems by moose, re-browsing by hares, and missing browse after leaf-out. Voles may browse in a similar manner as hares potentially adding error to our analyses. Further, this study was conducted over one season (likely near a cycle peak) and therefore may not adequately represent hare selection as organisms may occupy sub-optimal environments during high densities (Van Horne, 1983).

6. Conclusion

Forest harvesting may displace hare populations for a relatively short period but hares use regenerating stands, once cover and forage needs, particularly *B.*

papyrifera, are provided, to a greater degree than mature forest in this area. The coarse-detailed vegetation data better predicted hare pellet abundance. This suggests that forest management scenarios may be more feasible to evaluate because labor intensive, fine-detailed vegetation data may not be required to describe patterns in hare abundance, particularly at larger grain sizes. We suspect coarse-detailed vegetation could be sufficient to broadly predict hare abundance throughout most of snowshoe hare's geographic range. However, differences in hare peaks through succession will exist as forest regeneration rates differ between areas.

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