

1 The effects of clearcutting on Snowshoe Hare (*Lepus americanus*) relative
2 abundance in central Labrador.

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1 **Abstract**

2 To assess the effects of clearcutting on snowshoe hare (*Lepus*
3 *americanus*) relative abundance, we surveyed pellets in 1 m² circular plots and ,
4 vegetation and browse surveys in 4.5 m² circular plots among four different aged
5 clearcut (30, 20, 10, 5 years post-harvest) and mature forests (> 150 years old) in
6 central Labrador, Canada. Data were modeled at three grain sizes: transect
7 (4400 m²), plot (314 m²) and subplot scales (4.5 m²). *Betula papyrifera*, distance
8 from mature forest edge, tree and herb cover as well as remotely sensed forest
9 inventory data were used as predictors for hare pellets. We found pellet
10 abundance was 5 and 37 times greater (new and old pellets respectively) in
11 clearcut stands 30 years old than the next highest in 20 year old cuts. There
12 were few hare pellets in the remaining stand ages. *B. papyrifera* was the most
13 proportionately used browse species and most important of our fine-detailed
14 vegetation in predicting hare pellets. The coarse-detailed, forest inventory and
15 topographic data better predicted hare pellets than the fine-detailed vegetation
16 data.

17

18 **Key words:** browse, clearcut, Labrador, *Lepus americanus*, pellet counts,
19 relative abundance, snowshoe hare

1 **Introduction**

2 Major concerns of forest harvesting are the effects of altered forest
3 structure and successional patterns on biodiversity. In addition to removing the
4 overstory canopy, successional patterns are altered through disturbance to
5 understory vegetation and soil (Donnelly and Shane 1986; Greene *et al.* 1999;
6 Stone 2002; Simon and Schwab 2005). Since most terrestrial animals require
7 vegetation for food and cover, plant succession results in differing animal
8 communities through time. Edges between uncut forest and clearcuts often
9 produce a variety of plant species and structures over small areas (Yahner
10 1988). As a result, these edges often support diverse animal communities due to
11 the simultaneous availability of cover and forage (Yahner 1988). However,
12 edges may also support high predator densities (Dijak and Thompson 2000;
13 Forsey and Baggs 2001) suggesting reduced habitat quality for prey species
14 such as snowshoe hares, hereafter hares (Forsey and Baggs 2001).

15 The nature and magnitude of logging effects on hare requirements depend
16 upon time since harvesting (Telfer 1974; Monthey 1986; Ferron *et al.* 1998). The
17 immediate effect of clearcutting is that some hares relocate while home ranges
18 increased for hares that remained due to reduced habitat quality (Ferron *et al.*
19 1998). An important habitat attribute for hare survival is a dense understory
20 cover to escape predation (Litvaitis *et al.* 1985; Wolff 1982). Therefore, clearcut
21 avoidance continues until woody vegetation reaches protective cover heights of >
22 2 m (Sullivan and Moses 1986; Ferron *et al.* 1998; de Bellefeuille *et al.* 2001).
23 The dense understories in 10-30 year old regenerating conifer stands provide

1 prime hiding cover for hares (Wolff 1980; Fuller and Heisey 1986; Rogowitz
2 1988; Ferron and Ouellet 1992; Ferron *et al.* 1998).

3 Plant regeneration during the later stages of stand initiation after
4 harvesting provides abundant hare forage (Sullivan and Moses 1986; Rogowitz
5 1988). In winter, hares forage on bark, twigs and leaves of low growing trees
6 and shrubs, e.g., *Abies* spp., *Betula* spp., *Picea* spp., *Salix* spp., (Dodds 1960;
7 de Vos 1964; MacCracken *et al.* 1988; Ferron and Ouellet 1992). In spring and
8 summer, hares consume nutrient-rich new growth of woody plants, e.g., those
9 listed above, as well as *Ledum groenlandicum*, *Vaccinium* spp. and herbs, e.g.,
10 *Cornus canadensis*, *Equisetum* spp., *Trifolium* spp. (Dodds 1960; MacCracken *et*
11 *al.* 1988) in the order of emergence. Relative to other stand types, regenerating
12 clearcuts 11-30 years of age have abundant forage and therefore high hare
13 abundance (Parker 1984; Monthey 1986; Ferron *et al.* 1998). Hare abundance
14 may return to pre-disturbance levels in harvested sites over time (Ferron *et al.*
15 1998). Further, mature forest-clearcut edges provide hare with cover and food in
16 close proximity suggesting high quality habitat (Meslow and Keith 1968; Wolff
17 1980; Buehler and Keith 1982; Litvaitis *et al.* 1985; Radvanyi 1987; Forsey and
18 Baggs 2001). However, these benefits may be offset by increased predator
19 densities near edges (Dijak and Thompson 2000; Forsey and Baggs 2001).

20 Hares have considerable ecological, recreational, and economic values
21 throughout their range (de Bellefeuille *et al.* 2001). In Labrador, hares and their
22 predators provide recreation, subsistence food and economic benefit for
23 residents. Thus, there is interest in logging effects and increased access from

1 hunters and predators due to larger road networks, on hare densities (Forest
2 Management District 19A Planning Team 2003). Many studies report that
3 harvesting causes increased hare densities following sufficient regeneration, but
4 this time varies geographically, upwards to 30 years, likely due to different
5 successional patterns (Wolff 1980; Fuller and Heisey 1986; Rogowitz 1988;
6 Ferron and Ouellet 1992; Ferron *et al.* 1998). This may be a short time frame
7 relative to natural disturbances and hare population cycles but represents a
8 significant portion of a hunter's lifespan. Thus, forest managers must ensure
9 sufficient forest of the appropriate structure to support the traditional hunting
10 needs of local communities. This necessitates site specific understanding of
11 hare abundance relative to forest harvesting regimes.

12 To evaluate the effects of harvesting on hares, we assessed their relative
13 abundance in mature forests and regenerating clearcuts and related their
14 abundance to vegetation structure. Such models can be linked to forest
15 succession models to predict hare habitat quality under various management
16 scenarios. However, fine-detailed vegetation descriptions are difficult to collect
17 so we modeled hare abundance using coarse-detailed forest inventory and
18 topographic maps—data routinely available to forest managers. As ecological
19 patterns and processes change with scale (Wiens 1989; Legendre and Legendre
20 1998), modeling was conducted at three grain sizes: subplot (4.5 m²), plot (314
21 m²), and transect (4400 m²) and the efficacy of both the fine- and coarse-detailed
22 models were compared.

23

1 **Study Area**

2 We conducted pellet surveys from 28 June to 10 August 2004 within 40
3 km of Happy Valley - Goose Bay (53°19' N 60°25' W) Newfoundland and
4 Labrador, Canada (Figure 1). All transects were located in the High Boreal
5 Forest Ecoregion of Labrador (Meades 1990) which contains the most productive
6 forests for commercial timber in Labrador (Wilton 1959; Lopoukhine *et al.* 1975)
7 and is accessed by forest harvesting roads (Figure 1). The moderately rolling
8 terrain is dominated by *Picea mariana* / *Pleurozium schreberi* forest (Lopoukhine
9 *et al.* 1975) at the higher elevations and *Abies balsamea* / *P. mariana* / *Betula*
10 spp. forest at slightly lower elevations.

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

21 **Methods**

22 *Study design*

1 We established 20, 250m transects in different stands, with four transects
2 representing each of five stand ages: clearcut in the mid-1970's, mid-1980's,
3 mid-1990's, after 2000, or uncut mature (>150 years old) forest. Stands ranged
4 from 30 to 700 ha and those within the same age group were selected to be as
5 far apart as possible (= 700 m) while still being accessible. Prior to harvest,
6 stands were dominated by *P. mariana* and classified as commercial, i.e.,
7 supporting > 100 m³ of timber with canopy height ranging from 9.5-18.5 m tall
8 and crown closure ranging from 50-75% (Newfoundland and Labrador
9 Department of Natural Resources, unpublished data). Our mature forest plots
10 reflected this variation. All sites regenerated naturally and were free from any
11 post-harvest silvicultural treatments. Transects in harvested stands started at
12 commercial mature forest edges and were oriented to avoid all other stand
13 edges, roads and patches of remnant forest. Transects consisted of evenly
14 spaced plots at 50 m intervals. Each plot consisted of five, 1 m² circular
15 subplots: one central and the remaining four in the cardinal directions 10 m from
16 the centre point. We used pellet counts in each subplot as an index of hare
17 relative abundance (Murray *et al.* 2002). Pellets were classified new or old
18 according to Krebs *et al.* (1987). Pellets on the plot boundary were included in
19 the survey. Pellet counts are considered a reliable indicator of habitat use by
20 hare (Wolfe *et al.* 1982) and hare density (Krebs *et al.* 1987; Krebs *et al.* 2001).

21

22 *Vegetation surveys*

1 Centered around each subplot, tree species and the number of stems
2 were recorded in a 4.5 m² circle. Trees and taller shrubs were placed into height
3 classes: =50 cm, 51-100 cm, 101-200 cm, 201-300 cm, 301-400 cm, 401-500 cm
4 and >500 cm. The presence of hare browsing was recorded for each stem.
5 Ground vegetation, shrubs typically = 0.75 m, prostrate woody shrubs, forbs,
6 mosses, and lichens, were estimated using a system adapted from Daubenmire
7 (1968). At the centre of each subplot, the cover of ground vegetation within a 0.1
8 m² quadrat was recorded as one of 7 percentage classes: 0, 0-5, 5-25, 25-50,
9 50-75, 75-95, 95-100. The midpoints of these classes were the data used in
10 analyses.

11

12 *Data Analyses*

13 To assess the effect of forest management on hare abundance, we
14 compared mean pellet abundances between forest ages. Hare pellet –
15 vegetation relationships were analyzed at three different grain sizes: the subplot
16 grain (4.5 m², n = 500), the plot grain which combined all subplots within a plot
17 (314 m², n = 100) and the transect grain which combined all subplots within a
18 transect (4400 m², n = 20). Spatial dependence in observations violates the
19 assumption of independence, and can cause false correlations, i.e., no causal
20 effect, unless spatial pattern is accounted for in statistical models (Legendre and
21 Legendre 1998; Keitt *et al.* 2002; Lichstein *et al.* 2002). Count data like our pellet
22 counts, often violate assumptions required by Gaussian models and are typically
23 analyzed using generalized linear models with a Poisson distribution (McCullagh

1 and Nelder 1989). Unfortunately, autoregressive models with a Poisson
2 response distribution (auto-Poisson) are impractical because they can only have
3 negatively correlated errors (Cressie 1993). Therefore, we analyzed our log + 1
4 transformed pellet count data using Gaussian models. Similar to Lichstein *et al.*
5 (2002), we compared non-spatial Gaussian models with Poisson models and the
6 results were qualitatively similar. We followed the approach of Keitt *et al.* (2002)
7 and Lichstein *et al.* (2002) to incorporate spatial patterns in our analyses: 1) We
8 tested for spatial patterns in the residuals of non-spatial statistical models
9 (ordinary least-squared regression) using code in Ecological Archives M072-007-
10 S1 from Lichstein *et al.* (2002) to compute significance tests for correlograms,
11 $\alpha=0.05$, Bonferroni corrected. Correlogram lags were chosen as a compromise
12 between resolution, extent, and sample size within each lag. Our nested subplot
13 design did not permit equal lag distances thus lag distances and extents varied
14 within and between grains: at the subplot scale, 10 m lag followed by 30 m; 50 m
15 and 100 m; 200 m lags up to 3200 m; at the plot scale: 50 m lags up to 200 m
16 then 250 m lags up to 4200 m, at the transect scale: 1000 m lag followed by 500
17 m lags up to 5500 m. 2) If pattern was detected in the residuals, we reanalyzed
18 the data using autoregressive models. Space was accounted for in models up to
19 the maximum distance that autocorrelation appeared in the residuals. We then
20 re-examined the residuals of the spatial models for patterns. Relative
21 contributions of environment and space to particular models were assessed
22 through partial R^2 (Nagelkerke 1991) for the proportion of variance explained by
23 a) non-spatial model, b) space only, c) environment and space (autoregressive

1 models) (Borcard *et al.* 1992; Legendre and Legendre 1998; Lichstein *et al.*
2 2002).

3 Within the framework described above we constructed models to evaluate
4 the effects of vegetation on pellet counts. From the literature, variables were
5 chosen to represent cover and food of likely importance to hares in our region
6 (Dodds 1960; de Vos 1964; MacCracken *et al.* 1988; Ferron and Ouellet 1992):
7 distance to mature forest edge, *B. papyifera* stem densities, total tree density
8 (height = 3 m), herb cover, shrub cover, *P. mariana*, and *A. balsamea* stem
9 densities. To better assess which variables would likely influence hare
10 abundance in Labrador, we compared our study area with those of the above
11 reports and discussed variables with local hunters leading us to expect the first
12 four variables to be most important. Traditional knowledge such as that from
13 hunters is an underused but useful component in scientific research (Usher
14 2000). As Burnham and Anderson (2002) stress the importance of evaluating the
15 smallest possible set of models, we constructed global models using only the first
16 four variables. Goodness of fit was usually on the global models only. If
17 residuals of the global model were autocorrelated we proceeded with spatial
18 models (described above). We removed variables from the global model through
19 backward elimination; if the elimination of a variable reduced the Akaike's
20 Information Criterion (AIC), it was not included in further models. The strength of
21 evidence for each model was evaluated by the AIC weight (Burnham and
22 Anderson 2002). If the partial R^2 due to environmental factors < 0.15 , we felt the
23 explained variance was too low to be of biological relevance, therefore did not

1 investigate further models. For global models with a low R^2 we sequentially
2 added the remaining three variables (shrub cover, *P. mariana*, and *A. balsamea*
3 stem densities) to the best model and retained the variable if it reduced the AIC
4 and recalculated the R^2 .

5 We followed a similar approach to determine if coarse-detailed data could
6 sufficiently explain variation in pellet counts. Stand age is a strong indicator of
7 vegetation structure but this is influenced by slope and aspect (Fralish 1994). To
8 model the predicted parabolic relationship between pellet counts and stand age,
9 we included stand age + stand age². Also included were indices of northness
10 [$\cos(\text{aspect}) \times \tan(\text{slope})$] and northeastness [$\cos(\text{aspect}-45^\circ) \times \tan(\text{slope})$]
11 adapted from Beers *et al.* (1966). Stand age was determined from 1:12 500
12 forest inventory maps based on 1992 data (Department of Natural Resources,
13 unpublished data) while slope and aspects were derived from digital elevation
14 models based on 1:50 000 topographic maps.

15

16 **Results**

17 *Vegetation surveys*

18 *A. balsamea* and *P. mariana*, were the most abundant tree species, and
19 were found in all height classes and stand ages (Table 1). Tree and shrub
20 species richness were highest in 20 year old stands. *B. papyrifera* only occurred
21 > 50 cm and was most abundant in 30 year old stands in all height zones. Trees
22 and taller shrubs <50 cm were abundant in all stand ages but while those in
23 height zones between 50 and 300 cm were most abundant on 20 and 30 year old

1 stands. Trees and taller shrubs > 300 cm were most abundant on 30 and >180
2 year old stands. Smaller shrubs, herbs, mosses, lichens and liverworts showed
3 species-specific differences between stand ages but there was no consistent
4 pattern among vegetation groupings.

5

6 *Browse*

7 *B. papyrifera* was the most proportionately browsed species by hares with
8 55% of stems browsed compared with 25%, 16% and 15% of *Viburnum edule*,
9 *Vaccinium boreale*, and *Salix* spp., respectively. Although *A. balsamea* and *P.*
10 *mariana* were the dominant species, they were browsed minimally by hares
11 (=0.3%) (Table 2).

12

13 *Pellet abundance*

14 Pellet numbers were highest in 30 year old stands, with greater than 37
15 and 5 times the amount of pellets, new and old respectively, found in the next
16 closest counts (20 year old stands). The remaining stand ages had very few
17 pellets (Figure 2).

18

19 *Habitat variables analyses*

20 The R^2 values for environmental variables (distance to mature forest edge,
21 *B. papyrifera* stem densities, total tree density (height = 3 m) and herb cover)
22 were relatively low (0.09 – 0.37) thus substantial variation in pellet abundance
23 was not captured by our models. Adding spatial variables where residuals were

1 autocorrelated added an additional 13 – 24 % to the total R^2 . Pellet abundance
2 was positively related to *B. papyrifera* which was the most important variable. All
3 models with a ? AIC value <4 contained *B. papyrifera* and half of the best models
4 contained only this variable: old at plot grain; both new and old at transect grain
5 (Table 3). The association with distance to forest edge was consistently negative
6 but was less important as it only appeared in the best model for new pellets at
7 the plot grain. Herbs and tree density had inconsistent associations both within
8 and between grain sizes.

9 Adding shrub cover, *A. balsamea* and *P. mariana* densities to the best
10 models from the above procedure provided little extra explanation. For new
11 pellets at the subplot scale, adding these variables did not increase the R^2 above
12 0.15. Despite the reduction in the AIC of 8.67 by adding shrub cover and *P.*
13 *mariana* density for old pellets at the subplot grain, the R^2 was increased by only
14 0.02. The addition of other variables did not reduce the AIC for any other grain.

15 Coarse-detailed variables better explained pellet abundance than fine
16 detailed vegetation (Table 4). The R^2 values increased with grain and were 29%
17 to 86% higher than the corresponding fine-detail vegetation models. Pellet
18 counts followed the expected parabolic relationship with stand age as indicated
19 by the negative relationship with stand age² in all models. Stand age + stand
20 age² appeared to be the most important variables in the models but northness
21 and northeastness appeared important as well, particularly at smaller grain sizes.
22 When present in a model, the coefficient for northness was consistently negative
23 indicating greater pellet abundance on south-facing slopes. Slope and aspect

1 appeared less important at the transect grain as the best model for both new and
2 old pellets consisted only of stand age and stand age².

3

4 **Discussion**

5 Our finding that hare abundance was highest in the 30 year old stands
6 with lesser amounts in the 20 year old stands is similar to other studies. Parker
7 (1984) and Monthey (1986) found hare abundance to peak in regenerating
8 stands of 11-16 years in New Brunswick and Maine, respectively. The earlier
9 peak in hare abundance in those studies is likely due to faster regeneration
10 resulting from a more southern climate, differing growth rates of varying species
11 and manual planting which was present in the New Brunswick study. Our high
12 hare pellet counts in 30 year old stands is likely, in part, due to abundant *B.*
13 *papyrifera*. This species was of undoubted importance in our models for both old
14 and new pellets on all three grains. Support for *B. papyrifera* as hare preferred
15 forage was found in insular Newfoundland, Ontario, Alaska and Québec (Dodds
16 1960; de Vos 1964; MacCracken et al. 1988; Darveau et al. 1998). Compared
17 with those studies, *B. papyrifera* was used to a much greater degree in this
18 region. Those studies report high use of *Salix* spp. and *Picea* spp., but despite
19 their abundance in our study area, we found little proportional use for these
20 species.

21 Contrary to our expectations and that of several investigators, we did not
22 find consistent positive associations between pellet abundance and both tree
23 densities and herb cover. Hares selected stands with dense trees and

1 understories in insular Newfoundland (Dodds 1960) and Maine (Litvaitis *et*
2 *al.*1986). Hares in eastern Québec used herbaceous ground cover as forage
3 and dense vegetation closure as protection from predators (Ferron and Ouellet
4 1992). Prolonged snow cover in our study area may increase hare dependence
5 on areas with abundant woody browse, hence the weaker and inconsistent
6 relationship between pellet abundance and herb cover. Since many of the
7 predators in the above quoted studies occur in Labrador (though densities may
8 be different), the lack a consistent positive tree density relationship is
9 unexpected. Furthermore, understory cover, as winter thermal protection, should
10 be important for hares (Meslow and Keith 1968; Wolff 1980; Buehler and Keith
11 1982; Wolfe *et al.* 1982; Litvaitis *et al.* 1985). The mean daily minimum
12 temperatures are below the -8°C critical low temperature for hares (Irving *et al.*
13 1957), for four months of the year in Labrador (Environment Canada Climate
14 Normals: <http://www.msc-smc.ec.gc.ca>; viewed 27 September 2004), thus one
15 would expect a consistent positive tree density relationship for thermal cover in
16 our study area.

17 The negative relationship between pellet occurrence and distance to
18 mature forest edge was weak. However, the relative importance of mature forest
19 for hares is inconsistent among studies. Both Ferron *et al.* (1998) and de
20 Bellefeuille *et al.* (2001) found remnant mature forest to be important to hares
21 immediately following harvesting. We detected very little hare use of mature and
22 early regenerating stands in this area. Similar to other studies, we found greater

1 hare use of older regenerating stands than uncut forest (Parker 1984; Monthey
2 1986; Darveau *et al.* 1998).

3 Despite measuring features consistently identified in the literature as
4 important for hares, the low R^2 values in our fine-detailed vegetation analyses
5 suggest hares are selecting features not captured by our models. Interestingly,
6 our coarse-detailed vegetation analysis provided a significant improvement in
7 explaining variation in pellet counts. Using existing coarse vegetation data was
8 also effective in other studies. Seoane *et al.* (2003) found data from existing
9 general-purpose vegetation maps were as accurate as more detailed remotely
10 sensed data in predicting bird distributions. Similarly, Vernier *et al.* (2002) found
11 that existing forest inventory data was sufficient to model bird abundances.

12 The collection of vegetation data in the field is time consuming and costly.
13 Finding that existing data can equally or better predict relative hare abundance
14 makes forest management options easier to evaluate. It seems likely that stand
15 age is a surrogate for other vegetation features that we have not directly
16 measured. These stands may provide the prime combination of forage and
17 cover (both thermal and predator avoidance cover) habitat for hares (Koehler
18 1990). The younger successional stands and mature forests lack these specific
19 components that are found in the 30 year old stands that are conducive to higher
20 hare use. Open areas, such as recent clearcuts, are considered poor quality
21 habitat due to increased exposure to predation and less forage availability (Wolff
22 1980).

1 The subplot and plot grains at which our pellet-vegetation data were
2 analyzed were 4.5 m² and 314 m² respectively. This is small relative to hare
3 home range sizes, e.g. up to 10 ha (Banfield 1974) and likely do not characterize
4 habitat at an appropriate scale for this species. Further, it is possible that the
5 location of pellets within a home range may differ slightly from “preferred” areas
6 within the home range, adding noise to our data. As our grain size increased
7 there was a general increase in variance explained by environment in our
8 models, though this may be an artifact of varying sample size. Even our largest
9 grain of 4400 m² may not have been large enough to fully capture hare-
10 environment relationships. The increase in R²_e with grain was particularly strong
11 in our coarse-detailed variable models. This may be because the variables in
12 those models, particularly stand age, tend to vary at relatively large scales.

13 Despite what appears to be a clear association with 30 year old clearcuts
14 and a strong association with *B. papyrifera* there are possible sources of error
15 with this research. Because pellet decay rates differ among forest types, old
16 pellets are considered less accurate than new pellets in ascertaining hare
17 abundance (Prugh and Krebs 2004). Observer bias can be considerable in
18 distinguishing between new and old pellets (Prugh and Krebs 2004). To
19 minimize this bias, we evaluated new and old pellets separately and both
20 appeared to show similar patterns. The possibility exists that pellet detectability
21 differs between forest types, potentially biasing in our data. Although this
22 potential bias remains untested, it seems reasonable to assume that pellets
23 would be more difficult to detect where ground cover is highest. Our herbaceous

1 and shrub cover is lowest on the 5 year old sites, which has the fewest pellets,
2 and similar on all other age groups. Thus, we do not believe this potential bias
3 significantly affected our results. Dodds (1960) outlined several factors
4 potentially biasing browse observations: over-browsing on the same stems by
5 moose, re-browsing by hares, and missing browse after leaf-out. Voles may
6 browse in a similar manner as hares potentially adding error to our analyses.
7 Further, this study was conducted over one season (likely near a cycle peak) and
8 therefore may not adequately represent hare selection as organisms may occupy
9 sub-optimal environments during high densities (Van Horne 1983).

10

11 **Conclusion**

12 Forest harvesting may displace hare populations for a relatively short
13 period but hares use regenerating stands, once cover and forage needs,
14 particularly *B. papyrifera*, are provided, to a greater degree than mature forest in
15 this area. The coarse-detailed vegetation data better predicted hare pellet
16 abundance. This suggests that forest management scenarios may be more
17 feasible to evaluate because labor intensive, fine-detailed vegetation data may
18 not be required to describe patterns in hare abundance, particularly at larger
19 grain sizes. We suspect coarse-detailed vegetation could be sufficient to broadly
20 predict hare abundance throughout most of snowshoe hare's geographic range.
21 However, differences in hare peaks through succession will exist as forest
22 regeneration rates differ between areas.

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13 snowshoe hares. *Ecol. Monogr.* 50, 111-130.
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- 1 Table 1: Vegetation succession following clearcutting black spruce stands (*Picea*
 2 *mariana*). Abundance of trees and tall shrubs are expressed as mean number of
 3 stems. Remaining plants are expressed as mean percent cover.

Species	Approximate stand age (years)				
	5	10	20	30	>180
TREES/SHRUBS <50 cm					
<i>Abies balsamea</i>	228	158	550	271	259
<i>Alnus crispa</i>			25		
<i>Picea glauca</i>			91	46	11
<i>Picea mariana</i>	543	701	126	178	718
<i>Viburnum edule</i>	11				
TREES/TALL SHRUBS 51-100cm					
<i>Abies balsamea</i>	33	30	99	93	16
<i>Alnus crispa</i>			18		
<i>Betula papyrifera</i>				16	
<i>Picea glauca</i>			27		
<i>Picea mariana</i>	39	47	100	69	45
TREES/TALL SHRUBS 100-200 cm					
<i>Abies balsamea</i>	20	17	148	120	35
<i>Alnus crispa</i>	5	1	39	4	7
<i>Alnus rugosa</i>	1	4	15		8
<i>Betula papyrifera</i>			6	29	
<i>Picea glauca</i>		1	20	4	
<i>Picea mariana</i>	30	36	80	100	59
<i>Salix spp.</i>	3	2	18	2	
TREES/TALL SHRUBS 200-300 cm					
<i>Abies balsamea</i>	7	4	37	55	14
<i>Alnus crispa</i>	2		37	4	3
<i>Alnus rugosa</i>	2	3	1		
<i>Betula papyrifera</i>			8	77	
<i>Picea glauca</i>			3	1	
<i>Picea mariana</i>	4	5	34	47	12
<i>Salix spp.</i>			2	5	
TREES/TALL SHRUBS >300 cm					
<i>Abies balsamea</i>	2	6	16	59	20
<i>Alnus crispa</i>	1		10	8	2
<i>Alnus rugosa</i>	3		7		
<i>Betula papyrifera</i>	1	2	27	60	
<i>Picea glauca</i>			2	1	
<i>Picea mariana</i>	8	6	12	72	81
<i>Salix spp.</i>			3	9	
SHRUBS/HERBS					
<i>Amelanchier bartramiana</i>	0.2		0.2	0.1	
<i>Coptis groenlandica</i>	0.2		0.2	0.1	0.1
<i>Cornus Canadensis</i>	5.3	11.2	9.9	5.1	1.7
<i>Dryopteris disjuncta</i>	0.2		0.2	0.1	
<i>Equisetum sylvaticum</i>	0.2	0.2	1.3	0.4	0.1
<i>Gaultheria hispidula</i>	5.0	11.0	11.3	5.8	11.5
<i>Ledum groenlandicum</i>	1.5	3.5	2.5	1.8	4.5
<i>Linnaea borealis</i>	2.5	0.4	3.1	2.1	0.4
<i>Maianthemum canadensis</i>	0.1		0.1		0.2

<i>Rubus chamaemorus</i>	0.2	0.9	1.4	1.8	1.3
<i>Rubus pubescens</i>			0.6	0.2	
<i>Trientalis borealis</i>	0.2		0.1	0.1	
<i>Vaccinium boreale</i>	1.6	2.9	1.3	4.5	6.7
<i>Vaccinium ovalifolium</i>	0.4	0.2		0.5	
<i>Vaccinium vitis-idaea</i>	0.4	2.4	0.6	0.9	1.5
MOSESSES/LICHENS/LIVERWORTS					
<i>Bazzania trilobata</i>			0.1	0.7	
<i>Cladonia alpestris</i>			0.7	1.6	2.6
<i>Cladonia arbuscula</i>	0.8	1.0	1.5	2.6	3.6
<i>Cladonia chlorophaea</i>		0.6	1.0	0.7	0.1
<i>Dicranum majus</i>	1.9	3.1	1.5	2.3	1.1
<i>Hylocomium splendens</i>	0.8	0.6	1.2	5.4	
<i>Lycopodium annotinum</i>	0.5	0.7	4.2	1.0	2.3
<i>Lycopodium lucidulum</i>	0.2	0.7	0.1	0.2	0.9
<i>Peltigera lepidophora</i>	2.8	2.7	0.6	0.7	2.0
<i>Pleurozium schreberi</i>	14.3	17.5	15.4	35.9	27.6
<i>Ptilium crista-castrensis</i>	2.5	0.2	1.1	4.6	7.6
<i>Sphagnum spp.</i>	2.3	3.0	12.7	2.9	12.5

1

2

- 1 Table 2. Proportional browsing of woody vegetation by snowshoe hare (*Lepus*
- 2 *americana*) in regenerating clearcut and mature black spruce (*Picea mariana*)
- 3 stands. Numbers include all 4.5 m² sample units (n=500).

Species	number of stems	browsed stems	proportion	SE ^a
<i>Betula papyrifera</i>	259	142	0.548	0.031
<i>Viburnum edule</i>	20	5	0.250	0.099
<i>Vaccinium boreale</i>	111	18	0.162	0.035
<i>Salix spp.</i>	73	11	0.151	0.042
<i>Alnus rugosa</i>	74	7	0.095	0.033
<i>Alnus crispa</i>	189	8	0.042	0.014
<i>Ledum groenlandicum</i>	111	1	0.009	0.009
<i>Abies balsamea</i>	2336	6	0.003	0.001
<i>Picea mariana</i>	3205	6	0.002	0.001

- 4 ^aStandard error on the proportion of stems browsed.

1 Table 3: Goodness of fit statistics for global models of snowshoe hare (*Lepus*
2 *americana*) pellet abundance in relation to fine-detailed vegetation
3 characteristics. Least-squares regression was used were the residuals were not
4 autocorrelated; otherwise conditional autoregressive models were used and
5 partial R^2 values computed. The strength of evidence of all nested models was
6 assessed by differences in Akaike's Information Criterion (Δ AIC) and the AIC
7 weights. Only models with Δ AIC ≤ 4.00 are displayed.

Model ^a	Goodness of fit statistics ^b	Δ AIC	weight
Subplot (n=500 @ 1m²) - new pellets	$R^2_e=0.09$; $R^2_\gamma=0.21$; $R^2_i=0.22$; $N^b=1900$		
Subplot (n=500 @ 1m²) - old pellets	$R^2_e=0.24$; $R^2_\gamma=0.42$; $R^2_i=0.49$; $N =3000$		
0.171+0.079*Bp-0.010*H-0.020*TD		0.00	5.76x10 ⁻¹
0.193+0.080*Bp-0.010*H+0.021*TD-0.000*D		2.01	2.11x10 ⁻¹
0.155+0.078*Bp+0.021*TD		2.74	1.47x10 ⁻¹
Plot (n=100 @ 314 m²) - new pellets	$R^2_e=0.31$; $R^2_\gamma=0.29$; $R^2_i=0.49$; $N =1900$		
0.5034+0.079*Bp-0.002*D		0.00	2.35x10 ⁻¹
0.689+0.092*Bp-0.008*TD-0.002*D		0.06	2.28x10 ⁻¹
0.502+0.077*Bp+0.004*H-0.002*D		1.50	1.11x10 ⁻¹
0.657+0.090*Bp+0.005*H-0.008*TD-0.002*D		1.52	1.10x10 ⁻¹
0.0533+0.089*Bp-0.008*TD		1.60	1.05x10 ⁻¹
0.369+0.075*Bp		1.64	1.03x10 ⁻¹
0.503+0.087*Bp+0.005*H-0.008*TD		2.88	5.56x10 ⁻²
0.338+0.073*Bp+0.005*H		3.00	5.24x10 ⁻²
Plot (n=100 @ 314 m²) - old pellets	$R^2_e=0.37$; $R^2_\gamma=0.43$; $R^2_i=0.51$; $N=1900$		
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-0.002*D		0.58	0.15
0.702+0.062*Bp+0.006*H		1.58	0.09
0.499+0.045*Bp+0.005*H+0.011*TD		1.80	0.08
0.0417+0.019*TD		2.18	0.07
0.844+0.065*Bp+0.005*H-0.002*D		2.26	0.06
0.0641+0.048*Bp+0.005*H+0.011*TD-0.002*D		2.38	0.06
0.530+0.020*TD-0.002*D		3.18	0.04
0.382+0.007*H+0.018*TD		3.42	0.04
Transect (n=20 @ 4400m²) - new pellets	$R^2_e=0.36$		
0.707+0.0386*Bp		0.00	0.59
0.823+0.04*Bp-0.004*H		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 @ 4400m²) - old pellets	$R^2_e=0.37$		
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-0.004*H		3.01	0.11

- 1 ^a Bp=*Betula papyrifera*; TD= tree density; H=herbs; D=distance
- 2 ^b R_e^2 = Variation explained by environmental variables; R_p^2 = Variation explained
- 3 by spatial variables; R_t^2 = Variation explained by both environmental and spatial
- 4 variables; N=distance at which autocorrelation was incorporated.

1 Table 4: Goodness of fit statistics for global models of snowshoe hare (*Lepus*
2 *americana*) pellet abundance in relation to coarse-detailed variables. Least-
3 squares regression was used were the residuals were not autocorrelated;
4 otherwise conditional autoregressive models were used and partial R^2 values
5 computed. The strength of evidence of all nested models was assessed by
6 differences in Akaike's Information Criterion (Δ AIC) and the AIC weights. Only
7 models with Δ AIC ≤ 4.00 are displayed.

Model ^a	Goodness of fit statistics ^b	Δ AIC	weight
Subplot (n=500 @ 1m²) - new pellets	$R^2_e=0.17; R^2_s=0.21; R^2_t=0.25; N=1700$		
-0.073+0.023A-1.25x10 ⁻⁴ A ² -1.383N+1.640NE		0.00	0.710
-0.106+0.024A-1.28x10 ⁻⁴ A ² -0.510N		3.08	0.152
-0.096=0.023A-1.27x10 ⁻⁴ A ² +0.558NE		3.27	0.138
Subplot (n=500 @ 1m²) - old pellets	$R^2_e=0.31; R^2_s=0.43; R^2_t=0.45; N=3100$		
-0.133+0.042A-2.21x10 ⁻⁴ A ² -1.281N		0.00	0.519
-0.147=0.040A-2.19x10 ⁻⁴ A ²		1.17	0.289
-0.134+0.041A-2.21x10 ⁻⁴ A ² -1.154N-0.230NE		2.00	0.191
Plot (n= 100 @ 314 m²) - new pellets	$R^2_e=0.45$		
-0.264+0.074A-3.92x10 ⁻⁴ A ² -4.021N+3.915NE		0.00	0.944
-0.366+0.076A-4.03x10 ⁻⁴ A ² -1.749N		6.23	0.042
Plot (n=100 @ 314 m²) - old pellets	$R^2_e=0.48; R^2_s=0.43; R^2_t=0.54; N=1300$		
-0.205+0.103A-5.53x10 ⁻⁴ A ² -2.634N		0.00	0.484
-0.201+0.101A-5.53x10 ⁻⁴ A ²		0.69	0.343
-0.196+0.103A-5.54x10 ⁻⁴ A ² -3.053N+0.778NE		2.06	0.173
Transect (n=20 @ 4400m²) - new pellets	$R^2_e=0.67$		
-0.482+0.157A-8.47x10 ⁻⁴ A ²		0.00	0.703
-0.448+0.153A-8.14x10 ⁻⁴ A ² -2.504N		2.66	0.186
-0.257+0.146A-7.76x10 ⁻⁴ A ² -7.292N+7.554NE		3.70	0.111
Transect (n=20 @ 4400m²) - old pellets	$R^2_e=0.60$		
0.362+0.168A-9.31x10 ⁻⁴ A ²		0.00	0.810
0.377+0.166A-9.16x10 ⁻⁴ A ² -1.126N		3.49	0.142
0.580+0.159A-8.75x10 ⁻⁴ A ² -6.205N+8.014NE		5.65	0.048

8 ^a A= stand age; N= northness; NE=northeastness

9 ^b R^2_e = Variation explained by environmental variables; R^2_p = Variation explained
10 by spatial variables; R^2_t = Variation explained by both environmental and spatial
11 variables; N=distance at which autocorrelation was incorporated.

- 1 Figure 1: Study area showing transect locations, number refers to year of harvest
- 2 where 00=2000; 90=1990; 80=1980; 70=1970 and M=mature.
- 3
- 4 Figure 2: Mean and standard error of snowshoe hare (*Lepus americana*) pellet
- 5 numbers by stand age.