Influence of repeated fertilization on forest ecosystems: relative habitat use by snowshoe hares (*Lepus americanus*)

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Abstract: This study was designed to test the hypothesis that large-scale precommercial thinning (PCT) and repeated fertilization of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) would enhance relative habitat use by snowshoe hares (*Lepus americanus* Erxleben) in managed stands. Study areas were located near Summerland, Kelowna, and Williams Lake in south-central British Columbia, Canada. Each study area had nine treatments: four pairs of stands thinned to densities of 250, 500, 1000, and 2000 stems/ha, with one stand of each pair fertilized five times at 2-year intervals, and an unthinned stand. Understory vegetation and relative habitat use by snowshoe hares were measured annually from 1999 to 2003, 6–10 years after the onset of treatments. Mean crown volume index of herbs was significantly higher in fertilized than unfertilized stands, but density had no effect. Shrub volume was not affected by either treatment. Mean crown volume index of trees was significantly greater in the fertilized and high-density stands. Mean total richness of vascular plants was significantly reduced by fertilization. Mean total structural diversity of vegetation was highest in the low-density stands but was not affected by fertilization. Relative habitat use by hares, based on fecal pellet counts, was highest in the 2000 stems/ha and unthinned stands in summer. This pattern also occurred in winter when hare use was higher in fertilized than unfertilized stands. Overall, fertilized 2000 stems/ha stands provided habitat for hares to a degree comparable with unthinned stands of lodgepole pine.

Résumé : Cette étude visait à tester l'hypothèse voulant que l'éclaircie précommerciale (ÉPC) à grande échelle et la fertilisation à répétition de jeunes peuplements de pin tordu latifolié (*Pinus concorta* Dougl. ex Loud. var. *latifolia* Engelm.) puissent faire augmenter l'utilisation relative de l'habitat par le lièvre d'Amérique (*Lepus americanus* Erxleben) dans des peuplements aménagés. Les aires d'étude étaient situées près de Summerland, Kelowna, et Williams Lake dans le centre-sud de la Colombie-Britannique, au Canada. Chaque aire d'étude comportait neuf traitements : un témoin et quatre paires de peuplements éclaircis à des densités de 250, 500, 1000 et 2000 tiges/ha, dont un peuplement de chaque paire fertilisé cinq fois à intervalle de 2 ans. La végétation de sous-bois et l'utilisation relative de l'habitat par le lièvre ont été mesurées chaque année de 1999 à 2003, soit 6 à 10 ans après le début des traitements. L'indice de volume moyen de la couronne des herbacées était significativement plus élevé dans les peuplements fertilisés par rapport aux peuplements non fertilisés, mais il ne variait pas selon la densité de tiges. Le volume des arbustes ne variait pas entre les traitements. L'indice moyen du volume de la cime des arbres était significativement plus élevé dans les peuplements fertilisés et à forte densité de tiges. La fertilisation a réduit de façon importante la richesse totale moyenne en plantes vasculaires. La diversité structurale totale moyenne de la végétation était plus élevée dans les peuplements à faible densité de tiges, mais n'était pas affectée par la fertilisation. En été, l'utilisation relative de l'habitat par le lièvre, évaluée par comptage de fèces, était plus élevée dans les peuplements de 2000 tiges/ha et les peuplements non éclaircis. Ce patron se produisait aussi en hiver alors que l'utilisation par le lièvre était plus élevée dans les peuplements fertilisés que les dans les peuplements non fertilisés. Dans l'ensemble, les peuplements de 2000 tiges/ha fertilisés fournissaient un habitat comparable aux peuplements non éclaircis de pin tordu latifolié.

[Traduit par la Rédaction]

Introduction

The snowshoe hare (*Lepus americanus* Erxleben) is considered a keystone species in the boreal forest of North America (Boutin et al. 2003). This leporid has a 9- to 11-year fluctuation in abundance (Keith 1963) and represents the main prey for many of the vertebrate predators in northern forests, such as Canada lynx (*Lynx canadensis* Kerr), coyotes (*Canis latrans* Say), and great horned owls (*Bubo virginianus* Gmelin). Loss of snowshoe hares from northern forest ecosystems would likely lead to elimination of these predators (Boutin et al. 2003). It is not clear if this keystone

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status of hares also occurs in the montane western coniferous forests of British Columbia and the northwestern United States. The limited information on population dynamics of hares in this southern part of their range suggests that hare numbers may continue to cycle but at densities less than half of those in northern regions (Keith 1990; Hodges 2000), or they are irruptive or largely stable (Murray 2000).

The importance of snowshoe hares to the conservation of lynx in the Pacific Northwest interior areas of North America has generated considerable recent interest (Ruggiero et al. 2000). Lynx are clearly dependent on snowshoe hares as principal prey species throughout their overlapping ranges (Brand et al. 1976; Koehler and Aubry 1994). Thus, silvicultural manipulation of snowshoe hare habitat will undoubtedly have direct implications for lynx management.

In boreal, subboreal, and western montane forests, hares are usually most abundant in dense stands of pine (*Pinus* spp.), spruce (*Picea* spp.), or deciduous species, which provide the necessary food and cover (Sullivan and Sullivan 1983; Koehler 1990*a*, 1990*b*). This pattern of habitat use is strongly correlated with understory cover, which includes stands with shrubs, stands that are densely stocked, and those stands with heavy cover of lateral branches (Pietz and Tester 1983; Litvaitis et al. 1985). These habitat attributes provide cover for predator avoidance but need to be interspersed as a mosaic, with early seral stages providing palatable, nutritious food (Koehler and Brittell 1990; Hodges 2000). Hares shift from relatively "open" habitats, which have abundant herbaceous vegetation in summer, to dense coniferous stands in autumn and winter (Wolff 1980).

There are several reports relating presence or absence of snowshoe hares to cover attributes in recently harvested forest sites (Ferron et al. 1998; de Bellefeuille et al. 2001). However, except for the studies by Sullivan and Sullivan (1988) and Sullivan et al. (2002), there are no published reports of the responses of understory vegetation and habitat use by snowshoe hares to stand-management treatments in young (15- to 30-year old) commercial forests. Stand thinning, with and without fertilization, is used to enhance tree growth in young forests, and these treatments also may promote development of complex vegetative understories (Thomas et al. 1999; Lindgren et al. 2006). Silvicultural treatments such as precommercial thinning (PCT) have been viewed as negative for snowshoe hares because the reduction in stand density reduces the cover component and, hence, increases the susceptibility to predation for hares (Koehler 1990*b*; Ausband and Baty 2005).

This study was designed to test the hypothesis that large-scale PCT and repeated fertilization up to 10 years after the onset of treatments would enhance relative habitat use by hares in managed stands. This process should help determine a range of suitable stand density and fertilization regimes to maintain snowshoe hare habitat.

Study areas and methods

Study areas

Three study areas in southern British Columbia were chosen on the basis of having candidate stands of young lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) that had relatively uniform tree cover and comparable diameter, height, and density of trees prior to stand treatments. Location, proximity (boundaries), and size of candidate stands were determined by a balance between adequate interspersion of experimental units (Hurlbert 1984) and the logistics and access for conducting the operational-scale treatments of PCT and fertilization.

The Summerland study area was located in the Bald Range 25 km west of Summerland in south-central British Columbia (49°40′N, 119°53′W). This area is within the Montane Spruce (MS_{dm}) biogeoclimatic zone (Meidinger and Pojar 1991) at an elevation range of 1450–1520 m with gently rolling topography and sandy loam soil. The MS has a cool, continental climate with cold winters and moderately short, warm summers. Mean annual temperature is 0.5–4.7°C and precipitation ranges from 380 to 900 mm.

Clearcut harvesting of lodgepole pine with some single and group seed-tree reserves of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) began in this area in 1978 in response to an outbreak of mountain pine beetle (*Dendroctonus ponderosae* Hopkins). Depending on the original composition of the harvested stands and the degree of windthrow after harvesting, the number of residual Douglas-fir ranged from none to one or two trees per hectare in our candidate stands. Lodgepole pine regenerated naturally after harvesting and was the dominant tree species in these young stands. Three harvested units with prethinning stand densities ranging from 9980 to 11 150 stems/ha were divided into eight treatment stands and one control stand as per the experimental design. Minor components of the stands included Douglas-fir, interior hybrid spruce (*Picea glauca* (Moench) Voss × *Picea engelmannii* Parry), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), willow (*Salix* sp.), Sitka alder (*Alnus sinuata* (Regel) Rydb.), and trembling aspen (*Populus tremuloides* Michx.).

In 1998 at 5 years after the start of treatments and at the initiation of this study, diameter at breast height (DBH, 1.3 m aboveground) ranged from 5.0 ± 0.2 cm (mean ± SE) to 9.5 ± 0.2 cm and stand height ranged from 4.1 ± 0.1 m to 5.1 ± 0.1 m, with a mean age of 17–19 years. Area of stands ranged from 4.4 to 11.3 ha.

The Kelowna study area was located 37 km northwest of Kelowna, B.C. (50°04′N, 119°34′W), in the MS_{dm} biogeoclimatic subzone. Topography of this area is also gently rolling to flat with sandy loam soil at 1220–1240 m elevation. This area was also clearcut harvested in 1979–1980 and regenerated naturally to lodgepole pine with the other coniferous species, including western larch (*Larix occidentalis* Nutt.), as minor components. One large unit (84.8 ha) with a prethinning density of 8686 stems/ha was shaped in a horseshoe with an unharvested riparian buffer zone separating the two arms. This riparian zone had a steep ravine and varied in width from 75 to 300 m. The overall unit was separated into eight treatment stands as per the experimental design. An additional unit (12.6 ha) 0.5 km away was used as the unthinned stand.

In 1998, the DBH ranged from 6.2 ± 0.2 cm to 10.8 ± 0.2 cm and stand height ranged from 5.3 ± 0.1 m to 6.4 ± 0.1 m with a mean stand age of 17 or 18 years. Area of stands ranged from 9.5 to 12.6 ha.

The Cariboo study area was located in the Alex Fraser Research Forest (University of British Columbia), 75 km northeast of Williams Lake, B.C. (52°29′N, 121°45′W), in the Sub-Boreal Spruce (SBS_{dm}) biogeoclimatic zone (Meidinger and Pojar 1991). The general topography is gently rolling to flat at 850–870 m elevation. In mature stands, interior hybrid spruce, subalpine fir, and some Douglas-fir are mixed with extensive stands of lodgepole pine, which regenerated after wildfires. This unit covered 80 ha and was clearcut harvested in 1976 followed by some natural regeneration and some planting of lodgepole pine in 1983. Prethinning stand density was 3333 stems/ha. Eight treatment stands were located on this unit. Paired stands were contiguous on one side only. A ninth treatment unit acted as the unthinned stand as per the experimental design.

In 1998, DBH ranged from 8.5 ± 0.2 cm to 12.7 ± 0.3 cm and stand height ranged from 6.1 ± 0.1 m to 7.6 ± 0.2 m, with a mean stand age of 18 years. Area of stands ranged from 1.5 to 4.5 ha. These stands were separated by 0.2–0.5 km.

Experimental design

The three study areas acted as regional replicates (blocks). Within each replicate, there were five experimental units that had lodgepole pine stands treated (PCT) with the following randomized block design: (*i*) very low density, target 250 stems/ha; (*ii*) low density, target 500 stems/ha; (*iii*) medium density, target 1000 stems/ha; (*iv*) high density, target 2000 stems/ha; and (*v*) unthinned >3000 stems/ha. Fertilization treatments were applied to one-half of each of the thinned stands, resulting in a total of nine experimental units per replicate as follows: stand A, 250 stems/ha; stand B, 250 stems/ha with fertilization (250F); stand C, 500 stems/ha; stand D, 500 stems/ha with fertilization (500F); stand E, 1000 stems/ha; stand F, 1000 stems/ha with fertilization (1000F); stand G, 2000 stems/ha; stand H, 2000 stems/ha with fertilization (2000F); and stand I, unthinned > 3000 stems/ha. The restriction on randomization for the allocation of fertilizer treatment resulted in an overall split-plot design, with the initial PCT treatment (density) as the main plot and fertilization as the split plot. A fertilized unthinned experimental unit was not included in this design, because this treatment combination would likely not be part of any management prescription.

PCT was carried out at an appropriate time to maximize the growth response potential before the stands experienced growth repression (i.e., stand age of 12–14 years). This thinning was done at an operational scale in the late summer – early fall 1993. The objective was to establish research areas at a real-world scale that allowed for rigorous measurements of the various response variables. Fertilization (optimum nutrition regime) was conducted in fall 1994, spring 1997, fall 1998, fall 2000, and spring 2003. Optimum nutrition studies are designed to approximate the concept of "steady-state" nutrition, whereby small, balanced supplies of nutrients in solution are provided at rates consistent with estimated demand (Ingestad 1987; Raison and Myers 1992). These field experiments are less tightly controlled than steady-state studies, with nutrients applied less frequently, usually in solid form, and in larger amounts per application. In addition, foliar nutrient levels are monitored so that the rates and frequency of nutrient additions can be adjusted to maintain elevated foliar nutrient levels over a prolonged period. Pruning of all crop trees in the 250, 500, and 1000 stems/ha stands at each of the study areas was conducted in September–October 1998.

Additional details regarding these study areas and treatments are provided in T.P. Sullivan, D.S. Sullivan, P.M.F. Lindgren, R.P. Brockley, and R. Winter (in preparation).

Understory vegetation

Three 25 m transects, consisting of five 5 m × 5 m plots were systematically located in each stand following the method of Stickney (1980). Each plot contained three sizes of nested subplots: a 5 m × 5 m plot for sampling trees; a 3 m × 3 m subplot for sampling shrubs; and a 1 m × 1 m subplot for sampling herbs. Tree, shrub, and herb layers were subdivided into six height classes: 0–0.25, 0.25–0.5, 0.5–1.0, 1.0–2.0, 2.0–3.0, and 3.0–5.0 m. A visual estimate of percent cover of the ground was made for each species – height class combination within the appropriate nested subplot. Herbs, shrubs, and trees were determined by species not the size of the plants. Total percent cover for each layer was also estimated. These data were then used to calculate crown volume index (m^3/0.01 ha) for each plant species (Stickney 1980). The product of percent cover and representative height gives the volume of a cylindroid, which represents the space occupied by the plant in the community. Crown volume index values were then averaged by species for each plot size and standardized to volumes per 0.01 ha to allow comparisons among species and layer (herbs, shrubs, and trees). Sampling was done annually in July–August 1999–2003 through the sixth to tenth years since PCT. Sampling was done by the same person in all years. Grasses were not identified to species. Plant species were identified in accordance with Hitchcock and Cronquist (1973), Parish et al. (1996), and MacKinnon et al. (1992).

Habitat diversity was measured by species richness and structural diversity of all vascular plants. Species richness was the total number of species sampled for the plant (herbs, shrubs, and trees) communities in each stand (Krebs 1999). Structural diversity utilized the Shannon–Wiener index with plant species represented by height classes and the amount (crown volume index) of vegetation in each class. This index is well represented in the ecological literature (Magurran 2004).

Pellet counts

Estimates of relative habitat use by snowshoe hares were measured for summer (May to September) and winter (October to April) periods 1999 to 2003 by counting all fecal pellets on permanent sample plots (Litvaitis et al. 1985; Koehler 1990*a*; Ferron et al. 1998). We used 5.0 m^2 circular plots that were larger than the typical circular plots of 1.0 m^2 recommended by McKelvey et al. (2002) and Murray et al. (2002). This plot size and configuration was chosen to accommodate concurrent sampling of fecal pellet groups of mule deer (*Odocoileus hemionus* Raf.) and moose (*Alces alces* L.) on these same study areas (Sullivan et al. 2006). Plots were located systematically in five-plot arrays installed at stations every 50 m throughout each stand at each of the three study areas. Numbers of sample plots per

stand ranged from 55 to 145 in the Summerland study area, from 60 to 140 in the Kelowna study area, and from 35 to 100 in the the Cariboo study area. Plots were permanently marked with a flagged aluminum "pig-tail" stake, and a small painted rock was placed at the plot centre. Counts of pellets used a rope of 1.26 m radius attached to the centre stake and rotated around the plot. Plots were cleared of all pellets in early October 1998 at the initial sampling time. Pellet counts commenced in the spring of 1999, when overwinter habitat use by hares was measured during the first 2 weeks of May, immediately following snowmelt. Similarly, relative habitat use in summer was measured by counting pellets in the first 2 weeks of October. This same procedure was followed for five summer and five winter periods, and all sample plots at a given study area were assessed by the same observers throughout the 5 years. Pellet degradation was not likely an issue, because only new pellets deposited during a given summer or winter period were counted. Pellets were not included if they were incorporated into the duff and litter layers. Such pellets were nearly always a darker colour with a lack of light brown or green material in the center of the pellets when broken open (Krebs et al. 1987). Pellets located near the plot circumference were included or not, depending on where the end of the rope passed as the plot was surveyed. Density of pellets was estimated per 5 m^2 plot and then converted to a per-hectare basis.

Statistical analysis

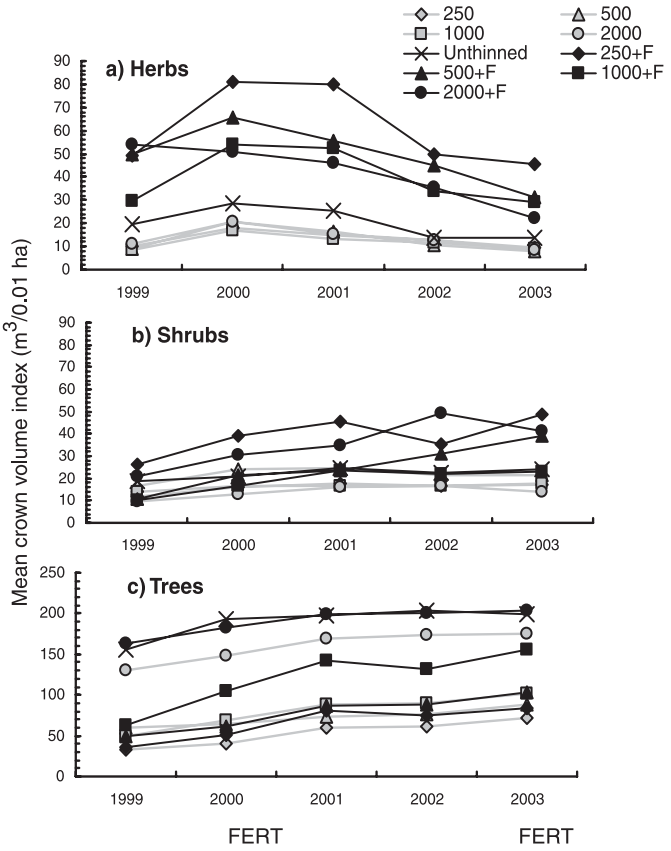
A split-split plot analysis of variance (ANOVA) was used to test for significant differences in mean crown volume index of herbs, shrubs, and trees; mean total species richness; and total structural diversity of all vascular plants. The density treatment was assigned as the main plot; fertilizer treatment, as the split plot; and time, as the split-split plot. Before performing any analyses, data not conforming to properties of normality and equal variance were subjected to various transformations to best approximate the assumptions required by any ANOVA (Zar 1999). Where significant density or fertilizer main effects were detected that also had significant time interactions, additional split-plot analyses were conducted within individual years.

The same split-split plot ANOVA was used to evaluate differences among treatments for numbers of pellets per hectare and, hence, relative habitat use by snowshoe hares. The five summers (1999–2003) and five winters (1998–1999 to 2002–2003) were analyzed independently.

Simple linear regression analyses were conducted to determine the relationships between relative habitat use by hares (mean number of pellets) and mean crown volume index, species richness, and structural diversity of vegetation components within the treatment stands. Regression of variables included 135 (3 replicates × 9 treatments × 5 years) data points for each relationship and the two seasons (summer and winter) of pellet counts were combined to yield one annual count of pellets per stand for each year.

Overall mean (n = 15; 3 replicates × 5 years) values and 95% confidence intervals were calculated for the number of pellets per hectare in the nine treatment stands during the summer and winter periods. In all analyses, the level of significance was at least P = 0.05.

Fig. 1. Mean (n = 3) crown volume index (m^3/0.01 ha) for (*a*) herbs, (*b*) shrubs, and (*c*) trees for the nine treatment stands (stems/ha) over the five-year (1999–2003) study. F and FERT, fertilized; Unth, unthinned.



Results

Understory vegetation

Mean crown volume index of herbs was significantly different among stands with respect to fertilization ($F_{[1,8]}$ = 15.24, P < 0.01) but not density ($F_{[4,8]}$ = 1.61, P = 0.26). The significant fertilizer × time interaction indicated that crown volume index of herbs increased with time in the fertilized stands but not in the unfertilized stands (Fig. 1*a*, Table 1). Crown volume indices of herbs, shrubs, and trees all increased significantly (P < 0.01) with time (Table 1). Mean crown volume index of shrubs was not affected by density or fertilization (Fig. 1*b*, Table 1). Mean crown volume index of deciduous and coniferous trees was significantly different among stands with respect to both density ($F_{[4,8]}$ = 12.08, P < 0.01) and fertilization ($F_{[1,8]}$ = 9.62, P = 0.01). With respect to stand density, the unthinned and 2000 stems/ha stands had significantly (Duncan's multiple range test (DMRT), P = 0.05) greater crown volume indices of trees than the other stands during this 1999–2003 period (Fig. 1*c*, Table 1). The lower three densities (250, 500, and 1000 stems/ha) had similar (DMRT, P = 0.05) mean tree crown volume indices. Fertilized stands had significantly greater tree crown volume index than unfertilized stands.

Mean total species richness of herbs, shrubs, and trees was significantly different among stands with respect to fer-

Table 1. Summary of split-split plot ANOVA results for vegetation data collected within three replicate blocks (n = 3) over 5 years (1999–2003).

	Density		Fertilizer		Density × fertilizer		Time		Density × time		Fertilizer × time	
	$F_{[4,8]}$	P	$F_{[1,8]}$	P	$F_{[3,8]}$	P	$F_{[4,72]}$	P	$F_{[16,72]}$	P	$F_{[4,72]}$	P
Volume												
Herb	1.61	0.26	15.24	<0.01	0.26	0.85	33.95	<0.01	0.84	0.64	3.42	0.01
Shrub	0.43	0.78	3.80	0.09	1.16	0.38	13.14	<0.01	0.47	0.95	2.77	0.03
Tree	12.08	<0.01	9.62	0.01	0.94	0.47	45.86	<0.01	0.79	0.69	1.21	0.32
Total richness	1.08	0.43	5.25	0.05	0.19	0.90	16.99	<0.01	0.60	0.88	7.93	<0.01
Total structural diversity	5.31	0.02	1.43	0.27	0.16	0.92	9.03	<0.01	1.06	0.41	3.50	0.01

Note: Density treatment is the main plot, fertilizer treatment is the split plot, and time is the split-split plot.

Fig. 2. Mean (n = 3) total species richness (a) and total structural diversity (b) of vascular plants, based on crown volume index, for the five-year (1999-2003) study. F and FERT, fertilized; Unth, unthinned.

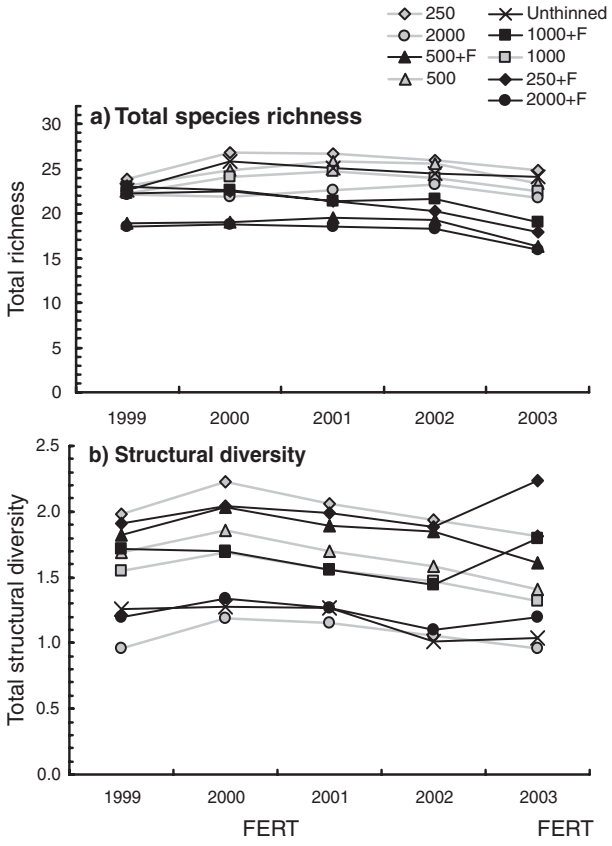
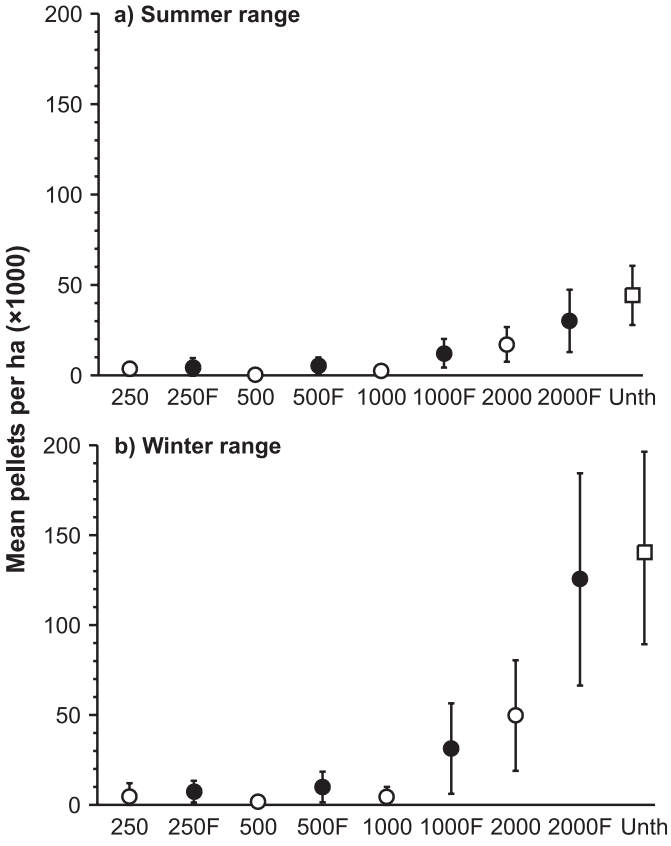


Fig. 3. Overall mean (n = 15) number (± 95% CI) of snowshoe hare pellets in the nine treatment stands (stems/ha) during (a) summer and (b) winter periods 1999–2003 at the three replicate study areas. F, fertilized; Unth, unthinned.



tilization ($F_{[1,8]}$ = 5.25, P = 0.05) but not density ($F_{[4,8]}$ = 1.08, P = 0.43). Total richness of vascular plants was significantly reduced by fertilization. The significant fertilizer × time interaction indicated that species richness of vascular plants declined with time in the fertilized stands but not in the unfertilized stands, at least during this 1999–2003 period (Fig. 2a, Table 1). Mean total structural diversity of vascular plants was significantly different among stands with respect to density ($F_{[4,8]}$ = 5.31, P = 0.02) but not fertilization ($F_{[1,8]}$ = 1.43, P = 0.27). In terms of density, structural diversity measurements of the 2000 stems/ha and unthinned stands were significantly (DMRT, P = 0.05) lower than those of the 500 and 250 stems/ha, whereas that of the 1000 stems/ha stand was intermediate (Fig. 2b, Table 1).

Additional details of plant community responses to thinning and fertilization are reported in T.P. Sullivan, D.S. Sullivan, P.M.F. Lindgren, R.P. Brockley, and R. Winter (in preparation).

Pellet counts

Density of hare pellets varied considerably across our treatment stands, with the vast majority of pellets (>90%) recorded in the 1000F, 2000, 2000F, and unthinned stands (Fig. 3). Pellets exhibited a clumped distribution in all

Fig. 4. Mean number (± 95% CI) of snowshoe hare pellets among the five density treatments (stems/ha) within each of the three replicate study areas (1, Summerland; 2, Kelowna; 3, Cariboo) during (*a*) summer and (*b*) winter periods. Means were averaged across fertilized and unfertilized stands and 5 years (n = 10 and 5 for PCT and unthinned stands, respectively). Density treatments with different uppercase letters had overall means (averaged across replicates; n = 3, not displayed) that were significantly different as determined by ANOVA and identified by Duncan's multiple range test (adjusted for multiple contrasts). Unth = unthinned.

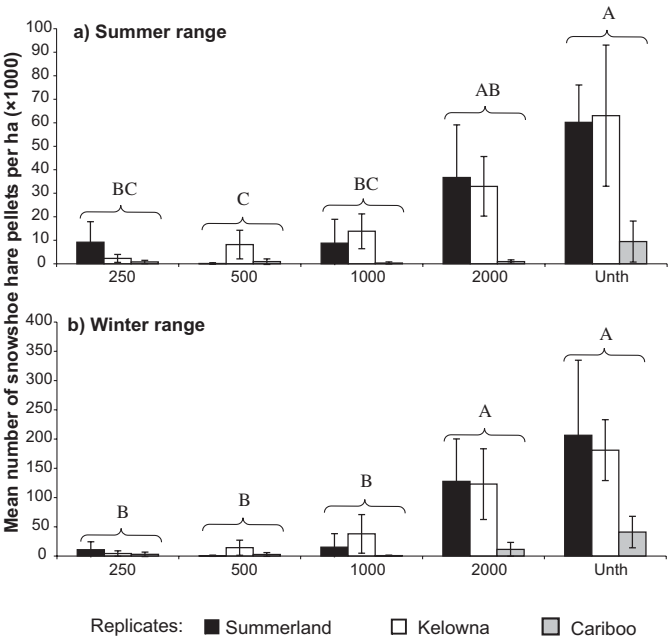
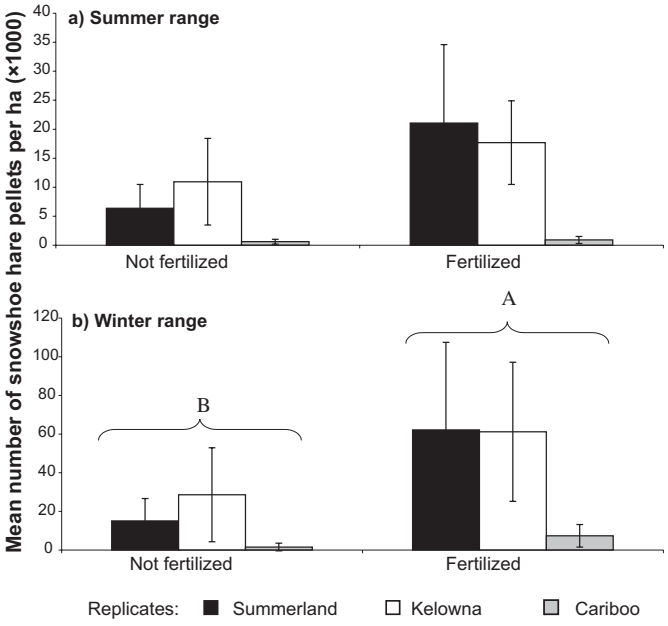


Fig. 5. Mean number (± 95% CI) of snowshoe hare pellets among unfertilized and fertilized stands within each of the three replicate study areas (1, Summerland; 2, Kelowna; 3, Cariboo) during (*a*) summer and (*b*) winter periods. Means were averaged across four thinning densities (250, 500, 1000, and 2000 stems/ha) and 5 years (n = 20). Treatments with different uppercase letters had overall means (averaged across replicates; n = 3, not shown) that were significantly different as determined by ANOVA and identified by Duncan's multiple range test (adjusted for multiple contrasts).



stands; variance was high at the plot level, and coefficients of variation exceeded the means in all stands. This pattern was particularly evident in those stands with fewer pellets.

Relative habitat use

During both summer and winter periods, relative habitat use by snowshoe hares in the nine treatment stands (based on counts of fecal pellets) followed a clear trend of higher use in the high- than low-density stands, as well as higher use in fertilized than unfertilized stands (Fig. 3). Relative habitat use was significantly different among stands with respect to density ($F_{[4,8]}$ = 4.92, P = 0.03; Fig. 4*a*) but not fertilization ($F_{[1,8]}$ = 3.07, P = 0.09; Fig. 5*a*) during summer periods 1999 to 2003 (Table 2). For density, the unthinned and 2000 stems/ha stands had similar pellet counts, with the unthinned stands significantly (DMRT, P = 0.05) higher than the other stands (250, 500, and 1000 stems/ha) (Table 2, Fig. 4*a*). The density × time and fertilization × time interactions were not significant for the summer periods.

This measure of relative habitat use was significantly different among stands with respect to density ($F_{[4,8]}$ = 11.07, P < 0.01; Fig. 4*b*) and fertilization ($F_{[1,8]}$ = 101.84, P < 0.01; Fig. 5*b*) during winter periods 1998–1999 to 2002–2003 (Table 2). The density × time and fertilizer × time interactions were both significant (Table 2); therefore, analyses were also conducted within individual years. For density, the overall analysis indicated that pellet counts in the unthinned and 2000 stems/ha stands were significantly (DMRT, P = 0.05) higher (on average, 11 times higher) than those in the other stands (Table 2). This pattern was maintained in the first two winters, with the addition of the 1000 stems/ha stands in the third and fourth winters (Table 2). There were no differences among densities in the fifth winter (2002–2003). Fertilized stands had significantly (DMRT, P = 0.05) more pellets than unfertilized stands in the first four winters, with no difference between these stand treatments in winter 2002–2003.

There was a significant (P < 0.01) increase in mean numbers of pellets over time in both summer and winter periods (Fig. 6, Table 2). In particular, hare use of the lower stand densities (250, 500, and 1000 stems/ha) increased in 2002 and 2003, in terms of annual changes in mean number of pellets (Fig. 6).

Habitat relationships

Linear regression analysis indicated that mean number of hare pellets was positively (r = 0.69, P < 0.01) related to crown volume index of trees (Fig. 7*a*). There was no relationship between numbers of hare pellets and crown volume index of herbs (r = 0.01, P = 0.87), and a very weak inverse relationship with volume of shrubs (r = –0.19, P = 0.03). Mean number of hare pellets was inversely (r = –0.57, P < 0.01) related to total structural diversity of vascular plants (Fig. 7*b*), and weakly inversely (r = 0.26, P < 0.01) related to total species richness of vascular plants.

Table 2. (A) Summary of split-split plot ANOVA results (density treatment is main plot, fertilizer treatment is split plot, and time is split-split plot) for hare fecal pellet data collected for five summers (1999–2003) and five winters (1998–1999 to 2002–2003) and (B) numbers of hare fecal pellets (×1000) in the nine treatment stands.

(A) ANOVA results

	Density		Fertilizer		Density × fertilizer		Time		Density × time		Fertilizer × time	
Season	$F_{[4,8]}$	P	$F_{[1,8]}$	P	$F_{[3,8]}$	P	$F_{[4,72]}$	P	$F_{[16,72]}$	P	$F_{[4,72]}$	P
Summer	4.92	0.03	3.70	0.09	0.86	0.50	14.64	<0.01	0.92	0.55	0.59	0.67
Winter	11.07	<0.01	101.84	<0.01	5.99	0.02	26.61	<0.01	3.92	<0.01	2.92	0.03

(B) Fecal pellet counts

Season	Tree density (stems/ha) and treatment								
and year	250	250F	500	500F	1000	1000F	2000	2000F	Unthinned
Summer									
1999	0.3±0.1	0.2±0.1	0.4±0.4	1.5±1.5	1.0±1.0	5.0±3.1	8.2±3.9	17.4±8.4	38.5±20.4
2000	0.5±0.4	0.4±.04	0.0±0.0	3.9±3.9	2.4±2.3	6.8±4.4	8.8±4.5	25.3±15.8	33.4±16.1
2001	0.5±0.3	0.9±0.1	0.4±0.4	6.4±4.5	2.9±2.9	7.0±4.7	19.6±10.2	28.5±14.3	42.2±15.6
2002	9.7±7.1	12.1±8.5	0.9±0.9	9.8±7.9	4.4±3.0	28.6±13.8	26.2±16.3	58.9±32.7	62.8±22.7
2003	7.4±3.8	9.2±7.4	1.2±1.2	6.3±5.0	4.7±2.8	13.6±6.8	20.1±13.1	22.5±12.5	44.2±19.0
Winter									
1998–1999	0.1±0.1	0.2±0.2	0.1±0.1	0.7±0.6	0.3±0.2	3.9±2.5	19.4±10.1	105.2±59.3	183.9±101.7
1999–2000	0.0±0.0	0.4±0.1	0.0±0.0	6.7±6.0	0.6±0.5	13.2±10.2	21.7±14.3	133.9±67.6	100.6±47.2
2000–2001	0.2±0.1	1.3±0.7	0.0±0.0	3.6±2.4	0.9±0.9	17.4±13.6	58.2±30.6	62.4±32.2	117.2±46.1
2001–2002	1.4±0.9	11.1±1.4	1.0±1.0	16.2±10.9	6.5±5.5	53.7±42.8	56.8±31.7	192.1±68.7	160.7±48.9
2002–2003	21.2±15.9	23.9±7.9	7.3±7.2	22.8±14.9	15.4±9.7	68.3±33.4	90.7±56.1	133.9±91.1	152.0±49.6

Note: Values are means ± SEs (n = 3). F, fertilized.

Discussion

Experimental design

Our study represents an ambitious experimental design that included a combined sampling area of 188 ha, of which 167 ha were thinned, 126 ha were pruned, and 84 ha were repeatedly fertilized (total of 63 000 kg of nitrogen). These stands are the most intensively managed young forests in British Columbia and likely all of Canada. The sizes of our experimental units were similar to what would be expected for operational applications of PCT and repeated fertilization treatments and, as such, were regarded as useful for studying the influences of these treatments on relative habitat use by snowshoe hares. Ideally, our experimental units would have been even larger to minimize edge effects and separated by larger distances to ensure independence among treatment units. However, limitations in resources and logistics did not allow for increasing the scale of this already extensive and replicated experimental design.

We understand the concern that the measurements of relative habitat use based on fecal pellet counts may have been influenced by habitats outside of a sample stand (i.e., edge effects and influence from neighbouring treatment stands). However, our data suggest that the experimental design was appropriate for studying the relative habitat use of snowshoe hares. If pellet densities in experimental units had been significantly influenced by the varied number of habitats that surrounded our stands, then there should have been different trends in relative habitat use among the three replicate study areas. Thus, it is reasonable to conclude that the observed pellet densities were not influenced by outside factors but rather were representative of the habitat use within a given treatment unit (see Figs. 4 and 5).

Pellet counts

Our sample plots for counting pellets of snowshoe hares were substantially larger than those used in other studies, particularly the 1.0 m^2 circular plots recommended by McKelvey et al. (2002) and Murray et al. (2002). We used intensive searching of plots for all new pellets during each spring and fall sampling period. This technique, the consistency of sampling personnel, and the relatively small edge to area ratio of our plots likely minimized the potential inclusion bias of pellets on the plot circumference, and also the missing of new pellets. It also assumes that the increased plot size (e.g., 5.0 m^2) did not become less efficient as search time increased and the confidence in actually detecting all pellets might have declined (Neff 1968).

Prugh and Krebs (2004) and Murray et al. (2005) have raised concerns about decomposition rates of hare pellets in different habitats and periods. However, we counted only "new" pellets on cleared plots for both summer and winter seasons over the 5-year period. Thus, it is unlikely that sufficient decomposition of pellets would have occurred over these relatively short 5-month (summer) and 7-month (winter) periods.

Relative habitat use

Our study is the first detailed investigation of relative habitat use by hares across a range of intensively managed (PCT and repeated fertilization) forest stands. Young (20–30 years) unmanaged lodgepole pine stands are preferred forest habitat

Fig. 6. Annual changes in the mean (n = 3) total number of snowshoe hare pellets in the nine treatment stands (stems/ha) during 1999–2003 at the three replicate study areas. F and FERT, fertilized; Unth, unthinned.

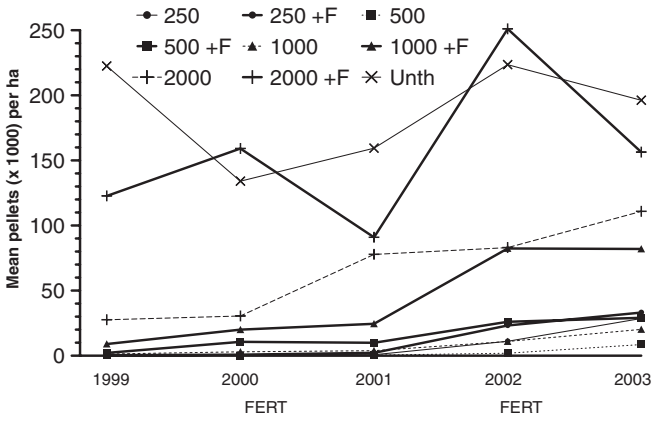
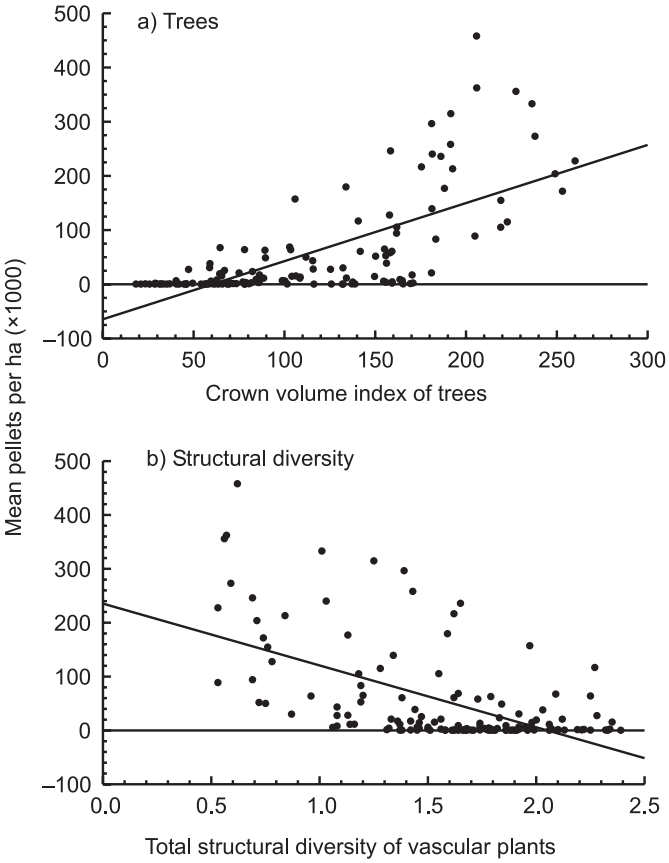


Fig. 7. Linear regression analysis relating mean number of snowshoe hare pellets to (*a*) crown volume index of trees ($y = -64.5 \times 10^3 + 1072.1x$) and (*b*) total structural diversity of vascular plants ($y = 235.4 \times 10^3 - 114.7 \times 10^3 x$).



for hares, providing both food and cover when interspersed with younger successional stages (Sullivan and Sullivan 1983; Koehler 1990*a*, 1990*b*). Our results concur with the findings in these studies that crown volume index of trees (primarily lodgepole pine) was the most important habitat variable affecting pellet counts of hares. Even the significantly higher structural diversity of vascular plants in the low-density stands was not sufficient cover to encourage habitat use by hares. A major concern with the onset of PCT in young pine stands is a decline in habitat suitability for hares. Clearly, heavy thinning to densities ≤1000 stems/ha reduced the carrying capacity of pine stands for hares, at least up to 10 years after the initiation of treatments. Thinning to 2000 stems/ha with repeated fertilization seemed to maintain habitat for hares in both summer and winter seasons. Stands thinned to 2000 stems/ha without fertilization and 1000 stems/ha with fertilization also began to develop habitat features attractive to hares in 2003, when annual pellet numbers reached ~50% of those in the 2000F and unthinned stands (see Fig. 6). Our results generally correspond to a period of relatively high numbers of hares, based on other B.C. studies documenting high hare populations near the start of a given decade, in 1980 (Sullivan and Sullivan 1988) and in 1990 (Sullivan 1994).

The significantly higher pellet counts in fertilized stands in winter was similar to the results reported by Krebs et al. (1995), Nams et al. (1996), and Ball et al. (2000) for *Lepus* species responding to nitrogen-supplemented vegetation. Herbivores seem to respond positively to the nitrogen content of their forage across a wide range of species (White 1993). Thus, our hypothesis that large-scale PCT and repeated fertilization up to 10 years after the onset of treatments would enhance relative habitat use by hares in managed stands is partially supported. The 2000F stands provided habitat for hares during both summer and winter periods to a degree comparable with the unthinned stands. This pattern is a major step towards integration of timber objectives and conservation goals for snowshoe hares and lynx across the southern ranges of these two species.

Forest management, particularly clearcut harvesting, has been documented as having a negative influence on snowshoe hare populations because of the loss of food and cover on harvested areas (Ferron et al. 1998; Potvin et al. 1999). Although subsequent vegetative succession on clearcut areas would likely benefit hares, particularly dense stands of regenerating lodgepole pine, "intensive management" of young stands would likely reduce understory cover for hares (Mowat and Slough 2003). This prediction was accurate for our low- to medium-density stands with or without fertilization and for the stands reported by Sullivan and Sullivan (1988). However, even the 1000 stems/ha fertilized and 2000 stems/ha unfertilized stands increased their habitat suitability for hares up to 10 years after the start of our intensive thinning and fertilization treatments.

Conclusions

As outlined by Wolff (1980), snowshoe hares will occupy most available habitats regardless of quality when populations are high but will retreat to "refugia" when populations are low. Refugia are likely high-quality habitats that start to develop 10–15 years after clearcutting or wildfire (Litvaitis et al. 1985; Potvin et al. 1999). Therefore, the goal of forest management should be to provide a mosaic of habitats that meet timber and conservation objectives through time. Clearly, some unmanaged coniferous stands are highly desirable for snowshoe hares (and lynx), but intensively managed

stands will also support hares if a high coniferous component is maintained. Our results suggest that a landscape that is comprised of a "matrix" of stands that include intensively managed and unmanaged stands, would support both conservation and utilitarian objectives (Pimentel et al. 1992; Franklin 1993).

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