

Research Article

Silviculture and Wildlife: Snowshoe Hare Abundance across a Successional Sequence of Natural and Intensively Managed Forests

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We tested the hypotheses H_1 that relative habitat use by snowshoe hares (*Lepus americanus*) would have a bimodal distribution with the highest abundance in young lodgepole pine (*Pinus contorta*) stands (both managed and unmanaged), minimal numbers in mature forests, and moderate abundance in old-growth forests and H_2 that habitat use would increase in response to enhanced stand attributes from PCT (precommercial thinning) and fertilization treatments. Habitat use was measured by counts of fecal pellets of hares from 1999 to 2003 in forest stands in south-central British Columbia, Canada. Our results did not support the bimodal distribution of hares among coniferous stands, such that old-growth stands, at least in our region, do not provide sufficient habitat for hare populations. High-density (5000 to 13000 stems/ha) unthinned young lodgepole pine stands provide optimum habitat for hares in terms of overstory and stand structure. Thinned and fertilized stands may also provide habitat, particularly at densities ≤ 1000 stems/ha, and over time as understory conifers develop. Managed stands provided habitat for hares at the same level as mature stands, at 6–10 years after PCT. Maintenance of a range of managed and unmanaged stands in a landscape mosaic would be ideal for integration of silvicultural and wildlife management goals.

1. Introduction

The snowshoe hare (*Lepus americanus*) is distributed across the boreal, subboreal, and western montane forests of North America [1]. This leporid has a 9- to 11-year fluctuation in abundance and is the main prey for many vertebrate predators in these forests, such as Canada lynx (*Lynx canadensis*), coyotes (*Canis latrans*), fisher (*Martes pennanti*), and great horned owls (*Bubo virginianus*) [2, 3]. As such, the snowshoe hare is considered to be a keystone species in these forest ecosystems [4, 5]. The importance of hares, as a principal prey species, for conservation of lynx in the Pacific Northwest (PNW) has generated considerable recent interest in managing forest habitats for them [6–8].

Densely stocked stands of pine (*Pinus* spp.), spruce (*Picea* spp.), or deciduous species, usually 15 to 30 years after

disturbance, provide the necessary food and cover that support hare populations [9, 10]. Heavy cover provided by understory herbs, shrubs, and lateral branches in or near dense stands is essential for predator avoidance [11, 12]. However, some early seral stages providing forage are required nearby and contribute to the shift in hares from relatively “open” habitats that have abundant herbaceous vegetation in summer to dense coniferous stands in autumn [4, 13, 14]. There would seem to be a plethora of potential hare habitat among the forested hectares in early seral stages (1 to 30 years old) across the interior lands of the PNW. In particular, lodgepole pine (*Pinus contorta* var. *latifolia*) is the dominant species comprising these young forests, having regenerated after both forest harvesting and wildfire [15].

Precommercial thinning (PCT) and fertilization are two practices that could help manage second-growth forests for

natural levels of biodiversity, through stimulation of understory vegetation and development of late successional structural features [16–18]. However, PCT has been viewed as negative for snowshoe hares because the reduction in stand density reduces the cover component, and hence susceptibility to predation [7, 19]. This pattern was also reported for the negative response of hares to cover attributes in recently harvested sites [19, 20], but with some use of riparian forest strips [21]. These studies were relatively short term (2–6 years), investigated recent PCT or harvesting treatments, and hence do not report on hare responses to development of understory vegetation and coniferous structure through time. Longer-term results, 10 to 20 years after the start of PCT and fertilization treatments in sapling to pole-size stands, concluded that relative habitat use by hares was highest in high-density stands (>3000 stems/ha and fertilized 2000 stems/ha), but also in lower-density (≤ 1000 stems/ha) stands where understory conifers provided essential cover [22, 23].

Most detailed research on population dynamics of hares has been conducted in the northern boreal forests of Canada and Alaska [4]. Populations of this leporid in southern parts of its range are less well studied but seem to have similar dynamics to northern populations with peak densities of only 1–2 hares/ha [24]. Because of the apparent differences in ecological relationships between hares in northern and southern parts of their range, [25] hypothesized that hares would have a bimodal distribution in mesic forests. This pattern would have the highest abundance in early successional stages, minimal numbers in mature forests, and moderate abundance in old-growth forests [25]. The patchy distribution of suitable hare habitats in the south, particularly if composed primarily of mature and old-growth forests, may explain low abundance of hares in population fluctuations [26]. Conversely, these older successional stages may provide habitat for hares at lower but more reliable numbers, particularly compared with low-productivity young forests on dry sites [25].

We know of no studies that have compared forest habitat variables and relative habitat use by snowshoe hares in intensively managed (PCT + fertilization) young (20–25 years) stands within a successional gradient of natural unmanaged stands. Our study areas in mesic montane forests in south-central British Columbia (BC), Canada, were in the southern range of snowshoe hares. We tested the hypotheses (H) that (H₁) relative habitat use by hares would have a bimodal distribution [25] with the highest abundance in young lodgepole pine stands (both managed and unmanaged), minimal numbers in mature forests, and moderate abundance in old-growth forests and (H₂) that habitat use would increase in response to enhanced abundance of herbs and shrubs, and abundance and structural diversity of conifers in these stands.

2. Study Areas and Methods

2.1. Experimental Design. Each mosaic block consisted of six habitats that represented the most common habitat types in these particular forest management areas: (1) young

plantation; (2) thinned stand; (3) thinned and fertilized stand; (4) unthinned stand; (5) mature stand; (6) old-growth stand (photographs in [27]). Three replicates were chosen in the south-central interior of BC, Canada, at the Kelowna (replicate (1) medium sites; replicate (2) wet sites) and Summerland (replicate (3)) study areas and hence constituted a randomized complete block experimental design [28, 29].

2.2. Study Areas. The Kelowna study area was located 37 km northwest of Kelowna, BC (50°04' N; 119°34' W), in the Montane Spruce (MS_{dm}) biogeoclimatic subzone [30]. Topography of this area is rolling to flat with sandy loam soil at 1240–1260 m elevation. 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. The MS landscape has extensive young and maturing seral stages of lodgepole pine, which have regenerated after wildfire. Hybrid interior spruce (*Picea glauca* × *P. engelmannii*) and subalpine fir (*Abies lasiocarpa*) are the dominant shade-tolerant climax trees. Douglas-fir (*Pseudotsuga menziesii*) is an important seral species in zonal ecosystems and is a climax species on warm south-facing slopes in the driest ecosystems. Trembling aspen (*Populus tremuloides*) is a common seral species and black cottonwood (*Populus trichocarpa*) occurs on some moist sites [30].

At Kelowna, the two plantations YP₁ and YP₂ were clear-cut harvested in 1995 and were 13.2 and 9.2 ha in area, respectively. These sites regenerated naturally to lodgepole pine. Previous forest cover was 99- to 101-year-old lodgepole pine with mean dbh of 19.5–20.0 cm and mean height of 20.0–20.5 m. The juvenile lodgepole pine stands were PCT thinned (1993) to 1,000 stems/ha (Th₁ and Th₂), thinned (1993) to 1,000 stems/ha and fertilized in fall 1994, spring 1997, fall periods of 1998, 2000, and spring 2003 (Th + F₁ and Th + F₂), and the unthinned stands (Unth₁ and Unth₂) were not treated. These sites were clearcut harvested in 1979 and 1982 and regenerated naturally to lodgepole pine with the other coniferous species, including western larch (*Larix occidentalis*), as minor components. Stand areas ranged from 9.5 to 12.6 ha at 17–18 years of age.

The mature forest stands (MF₁ and MF₂) were composed primarily of lodgepole pine with a minor component of Douglas-fir and interior spruce at 80–120 years of age. Each of these stands was located near the paired young plantation units (YP₁ and YP₂). The old-growth forest stands (OG₁ and OG₂) were in the 140–250 year age class. Stand OG₁ was dominated by Douglas-fir and stand OG₂ by subalpine fir, Douglas-fir, and interior spruce.

The Summerland study area was located 25 km west of Summerland (49°40' N; 119°53' W) in the MS_{dm} subzone at an elevation range of 1450–1520 m with gently rolling topography and sandy loam soil. The young plantation (YP₃) was clearcut harvested in winter 1995–1996 and was 12.8 ha in area. This unit was planted with lodgepole pine in spring 1997, and there was ingress of naturally regenerated lodgepole pine in subsequent years. Previous forest cover was 140- to 250-year-old lodgepole pine.

The juvenile lodgepole pine stands, unthinned (Unth₃), PCT (1993) to 1,000 stems/ha (Th₃), and PCT (1993) to 1,000 stems/ha and fertilized in fall 1994, spring 1997, fall periods of 1998, 2000, and spring 2003 (Th + F₃), were located on units clearcut harvested in 1978. Lodgepole pine regenerated naturally after harvesting and was the dominant tree species in these stands. Stand areas ranged from 4.4 to 11.3 ha at 17–19 years of age. Minor components of the stands included Douglas-fir, interior spruce, subalpine fir, Ponderosa pine (*Pinus ponderosa*), willow (*Salix* sp.), Sitka alder (*Alnus sinuata*), and trembling aspen.

The mature forest stand (MF₃) in this replicate was composed primarily of 80- to 120-year-old lodgepole pine with a minor component of Douglas-fir and subalpine fir. There were some veteran Douglas-fir (140–250 years old) dispersed through the stand. The old-growth forest stand (OG₃) had 120- to 140-year-old lodgepole pine and Douglas-fir with subalpine fir and spruce as minor components. Douglas-fir also occurred throughout the stand in the veteran age class of 251+ years. These stands covered several hundred ha.

2.3. Stand Treatments. The initial treatment was PCT of young stands of pine (Th₁₋₃ and Th + F₁₋₃) at an appropriate time to maximize growth response potential before they experience severe growth repression. Thinning to 1000 stems/ha was done at an operational scale at all study areas in the late summer-early fall of 1993. The fertilization treatments were designed as large-scale applications of previously established “optimum nutrition” fertilization field experiments in Sweden [31] and BC [32]. Fertilizer was applied at 2-year intervals for 10 years (total of 5 applications) starting in 1994, using multinutrient fertilizer formulations developed from annual nutrient diagnosis of lodgepole pine foliage samples. Additional details of the PCT and fertilization treatments are reported in [18]. Pruning of all pole-sized lodgepole pine and Douglas-fir crop trees in the thinned and thinned-fertilized stands at each study area, to a height of 3.0 m, was conducted in September to December 1998.

2.4. Coniferous Stand Structure. Sampling of coniferous tree species in layers in 0-1, 1-2, 2-3, and >3 m height classes was done in a 5.64 m radius circular plot (100 m²) located systematically at 50 m intervals throughout each stand in 2003. For all trees in a given plot, species, dbh (diameter at breast height, 1.3 m above soil surface), and total height were tallied. In the young plantation stands, only counts of trees in each height class were done because of the small average size (diameters <3 cm) of trees.

2.5. Understory Vegetation. Three 25 m transects, consisting of five 5 × 5 m plots, were systematically located in each habitat type following the method of [33]. Each plot contained three sizes of nested subplots: a 5 × 5 m plot for sampling trees, a 3 × 3 m subplot for sampling shrubs; and a 1 × 1 m subplot for sampling herbaceous species, mosses, and terrestrial lichens. Tree, shrub, and herb layers were subdivided into 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 percentage

cover of the ground was made for each species height class combination within the appropriate nested subplot. These data were summarized in terms of absolute crown volume (m³/0.01 ha) for each plant species. The product of percent cover and representative height gave the volume of a cylindroid, which represented the space occupied by the plant in the community. Volume values were averaged by species for each plot size and converted to a 0.01 ha base to produce a tabular value given for each species and life-form group. Sampling was done annually in July–August 1999 to 2003, through the sixth to tenth years, since PCT, by the same person. Plant species were identified in accordance with Hitchcock and Cronquist [34] and Parish et al. [35].

2.6. Diversity Measures. Diversity of vascular plant communities was measured by species richness and species diversity. Species richness was the total number of species sampled [36] for the plant (herbs, shrubs, and trees) communities in each stand. Species diversity was based on the Shannon-Wiener index [37]. Structural diversity was based on species richness and diversity with the height classes of the coniferous tree layers acting as “species” [38]. This measure of foliage height diversity used the Shannon-Wiener index with tree species represented by height classes and the number of conifers in each class.

2.7. Relative Habitat Use by Hares. 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 [9, 12, 20]. We used 5.0 m² circular plots that were larger than the typical circular plots of 1.0 m² recommended by McKelvey et al. [39] and Murray et al. [40]. This plot size and configuration was chosen to accommodate concurrent sampling of fecal pellet groups of mule deer (*Odocoileus hemionus*) and moose (*Alces alces*) on these same study areas [23, 41]. Plots were located systematically, in 5-plot arrays installed at stations every 50 m, throughout each stand at the three study areas. Numbers of sample plots ranged from 55 to 145 in the three areas. Plots were permanently marked with a flagged aluminum “pig-tail” stake and a small painted rock located in the plot center. Counts of pellets used a rope of 1.26 m radius attached to the center stake and rotated around the plot. Plots were cleared of all pellets in early May 1999 at the initial sampling time. Pellet counts commenced in the fall of 1999 when summer habitat use by hares was measured during the first two weeks of October. Similarly, relative habitat use in winter was measured by counting pellets in the first two weeks of May. This same procedure was followed for five summer and four winter periods and all sample plots at a given study area were assessed by the same observers throughout the five years. Pellet degradation was not an issue as only new pellets deposited during a given summer or winter period were counted. An attempt was made to count all pellets within a given plot and vegetation was moved if it obscured the ground. Pellets were not included if they were incorporated into the duff and litter layers. These 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 [42]. 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 m² plot and then converted to a per ha basis.

2.8. Statistical Analysis. A repeated measures analysis of variance (RM ANOVA) [43] was conducted to determine the effects of treatment and time (1999–2003) on mean crown volume index of herbs and shrubs, mean total species richness, and diversity of vascular plants across the six treatment stands, as well as mean number of fecal pellets of snowshoe hares during summer and winter periods. Where necessary, data were log-transformed to better approximate homogeneity of variance as measured by the Levene statistic [44]. Mauchly's *W* test statistic was used to test for sphericity (independence of data among repeated measures) [45, 46]. For data found to be correlated among years, the Huynh-Feldt correction was used to adjust the degrees of freedom of the within-subjects *F*-ratio [47].

A randomized block two-way ANOVA (Model III) [29] with factor stand treatment (six habitats) as a fixed effect and factor block as a random effect was used to evaluate differences in mean abundance, mean species diversity, and mean structural diversity of coniferous tree layers in 2003. This ANOVA was also used to compare mean diameter and height of overstory lodgepole pine and basal area (BA) of total overstory conifers. Analysis of overstory (>3 m height) trees did not include the young plantation treatment.

Regression analyses [29] were used to explore potential relationships between attributes of overstory conifers (BA, stand density, species and structural diversity) and several vegetation parameters (crown volume index of herbs and shrubs, total species richness and diversity) with relative habitat use by hares (abundance of pellets). Regression of variables included 15 (3 replicates × 5 treatments) data points for overall mean number of pellets and attributes of coniferous tree layers and 18 (3 replicates × 6 treatments) data points for overall mean pellets and attributes of vegetation.

Overall mean values and 95% confidence intervals (CIs) were calculated for crown volume index of herbs and shrubs ($n = 15$; 3 replicates × 5 years) and the number of snowshoe hare pellets on treatment sites during summer ($n = 15$; 3 replicates × 5 years) and winter ($n = 12$; 3 replicates × 4 years) periods. Duncan's multiple range test (DMRT), adjusted for multiple comparisons, was used to compare mean values [48], whenever a significant difference was found, based on ANOVA results. In all analyses, the level of significance was at least $P = 0.05$.

3. Results

3.1. Coniferous Stand Structure. The dominant tree species was lodgepole pine with a significant ($F_{4,8} = 45.63$; $P < 0.01$) difference in diameter among stands, ranging from 8 cm in the unthinned stands to 11–13 in the thinned and thinned-fertilized stands, 16–17 in the mature forest, and 19–23 in the old growth stands. Mean tree heights of pine were also

significantly ($F_{4,8} = 130.13$; $P < 0.01$) different among stands and ranged from 18–20 m in the mature and old-growth stands to 6–8 m in the three young pine stands. Other overstory coniferous species in the mature and old growth stands included Douglas-fir, interior spruce, and subalpine fir, with ranges of mean diameters from 11 to 33 cm and mean heights from 11 to 24 m. Mean BA of all overstory coniferous trees was significantly ($F_{4,8} = 30.81$; $P < 0.01$) different among stands with the highest (DMRT; $P = 0.05$) BA in the mature and old-growth stands (Figure 1(a)). Mean density of overstory trees was also significantly ($F_{4,8} = 6.65$; $P < 0.01$) different among stands and the highest (DMRT; $P = 0.05$) in the unthinned (6263 stems/ha) stands (Figure 1(a)).

Mean density of all coniferous trees was similar ($F_{4,8} = 2.60$; $P = 0.09$) and variable among stands, ranging from 2082 to 10673 stems/ha (Figure 1(b)). Mean species diversity of all conifers was significantly ($F_{5,10} = 5.47$; $P < 0.01$) different among stands with the thinned, thinned-fertilized, and mature forest stands having the highest (DMRT; $P = 0.05$) diversity, followed by the unthinned, old-growth, and young plantation stands. Mean structural diversity of all conifers was also significantly ($F_{5,10} = 3.60$; $P = 0.04$) different among stands with the thinned, thinned-fertilized, mature and old-growth forests similar in this measure of coniferous stand structure (Figure 1(b)).

3.2. Understory Vegetation. Mean crown volume index of herbs was significantly ($F_{5,10} = 5.31$; $P = 0.01$) different among stands (Figure 2(a)). The thinned-fertilized stands had the highest (DMRT; $P = 0.05$), albeit variable, volume of herbs with the unthinned stands similar in volume, but intermediate with the other four stands. Overall mean volume of herbs was 2.0 times higher in the thinned-fertilized than unthinned stands, and this range expanded from 3.9 to 177.9 times as much herb biomass in the thinned-fertilized than other four stands (Figure 2(a)). Mean crown volume index of shrubs was similar ($F_{5,10} = 1.50$; $P = 0.27$) among stands (Figure 2(b)). Overall mean volume of shrubs were higher (nonoverlapping 95% CIs) in all stands than the mature forest; the thinned and unthinned stands tended to be higher in mean volume than the old-growth stands (Figure 2(b)).

3.3. Relative Habitat Use by Hares. Relative habitat use by snowshoe hares during summer periods was significantly ($F_{5,10} = 8.20$; $P < 0.01$) different among stands, with the highest (DMRT; $P = 0.05$) mean number of pellets in the unthinned, thinned-fertilized, and mature forest stands (Table 1). The young plantations and old-growth stands had the lowest (DMRT; $P = 0.05$) number of pellets, with the thinned stands intermediate between them and the thinned-fertilized and mature stands. Relative habitat use by hares during winter periods was also significantly ($F_{5,10} = 23.04$; $P < 0.01$) different among stands (Table 2). Again, the mean number of pellets was the highest (DMRT; $P = 0.05$) in the thinned-fertilized, unthinned, and mature forest stands, followed by the old-growth stands (similar to the thinned-fertilized stands), and finally the young plantations. There

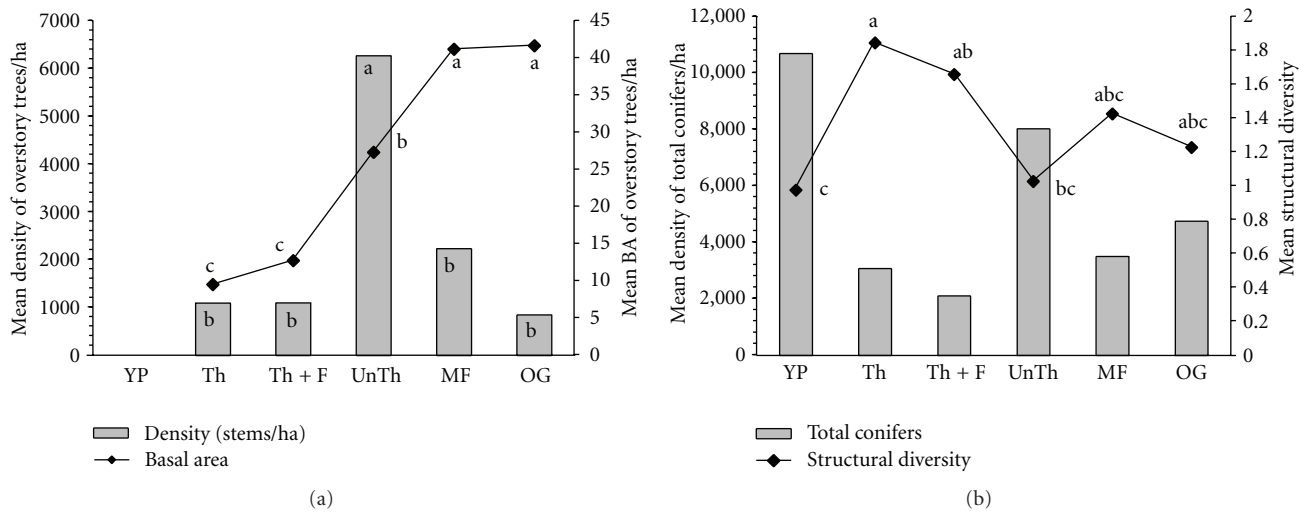


FIGURE 1: Mean ($n = 3$) (a) density and basal area (BA) of overstory coniferous trees per ha, and (b) density and structural diversity of total conifers, in the six treatment stands in 2003. YP: young plantation; Th: thinned; Th + F: thinned and fertilized; UnTh: unthinned; MF: mature forest; OG: old-growth forest. Mean values with different letters are significantly different by Duncan's multiple range test, adjusted for multiple contrasts.

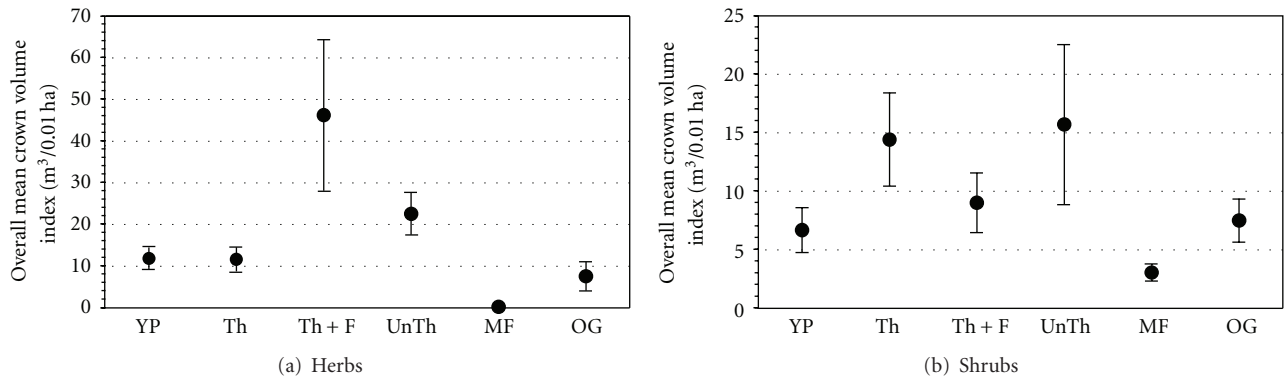


FIGURE 2: Overall mean ($n = 15$) \pm 95% CIs crown volume index of (a) herbs and (b) shrubs in the six treatment stands from 1999 to 2003. YP: young plantation; Th: thinned; Th + F: thinned and fertilized; UnTh: unthinned; MF: mature forest; OG: old-growth forest.

TABLE 1: Mean \pm SE ($n = 3$ replicate sites) number of fecal pellets per ha ($\times 1000$) for snowshoe hares for five summer periods, and results of repeated measures analysis of variance (RM-ANOVA). Columns of mean values with different letters are significantly different by Duncan's multiple range test (DMRT), adjusted for multiple contrasts. F -values identified by * were calculated using an H-F correction factor, which decreased the stated degrees of freedom due to correlation among repeated measures.

Year	Site						RM ANOVA results					
							Site	Time	Site \times time			
	YP	Th	Th + F	UnTh	MF	OG	$F_{5,10}$	P	$F_{4,48}$	P	$F_{20,48}$	P
	C	BC	AB	A	AB	C	8.20	<0.01	1.30*	0.29	0.37*	0.99
1999	0.09 \pm 0.03	1.63 \pm 1.15	6.47 \pm 1.86	42.86 \pm 16.93	3.55 \pm 0.36	0.77 \pm 0.57						
2000	0.15 \pm 0.10	3.73 \pm 2.00	9.49 \pm 3.37	43.58 \pm 6.50	11.72 \pm 1.38	2.93 \pm 2.77						
2001	1.93 \pm 1.86	4.88 \pm 3.53	12.05 \pm 3.51	53.37 \pm 6.70	12.56 \pm 2.71	2.64 \pm 1.24						
2002	0.67 \pm 0.29	6.40 \pm 3.32	35.94 \pm 4.21	76.55 \pm 10.46	26.20 \pm 0.62	1.29 \pm 1.08						
2003	0.90 \pm 0.69	7.74 \pm 1.83	17.21 \pm 3.57	60.79 \pm 6.26	5.45 \pm 0.08	0.98 \pm 0.57						

YP: young plantation; Th: thinned; Th + F: thinned and fertilized; UnTh: unthinned; MF: mature forest; OG: old-growth.

TABLE 2: Mean \pm SE ($n = 3$ replicate sites) number of fecal pellets per ha ($\times 1000$) for snowshoe hares in four winter periods, and results of repeated measures analysis of variance (RM ANOVA). Columns of mean values with different letters are significantly different by Duncan's multiple range test (DMRT), adjusted for multiple contrasts. Mauchly's test determined that these data were not correlated among repeated measures.

Year	Site						RM ANOVA results					
	YP	Th	Th + F	UnTh	MF	OG	Site		Time		Site \times time	
							$F_{5,10}$	P	$F_{3,36}$	P	$F_{15,36}$	P
	C	B	AB	A	A	B	23.04	<0.01	2.15	0.11	0.71	0.76
1999-2000	0.00 \pm 0.00	0.99 \pm 0.57	10.94 \pm 8.22	139.01 \pm 17.50	39.59 \pm 4.96	3.43 \pm 2.29						
2000-2001	0.23 \pm 0.22	1.92 \pm 0.92	21.88 \pm 10.95	152.75 \pm 10.92	49.29 \pm 5.51	7.12 \pm 3.42						
2001-2002	0.02 \pm 0.01	11.40 \pm 7.10	70.79 \pm 25.90	190.59 \pm 19.41	50.96 \pm 9.00	10.43 \pm 9.50						
2002-2003	0.27 \pm 0.14	23.16 \pm 6.25	85.48 \pm 10.98	173.27 \pm 29.76	46.46 \pm 3.73	4.22 \pm 2.69						

YP: young plantation; Th: thinned; Th + F: thinned and fertilized; UnTh: unthinned; MF: mature forest; OG: old-growth.

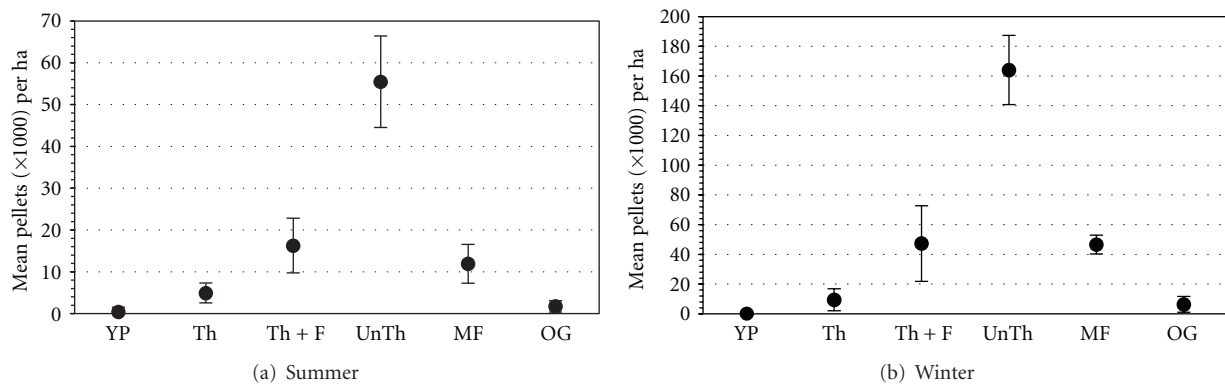


FIGURE 3: Overall mean (\pm 95% CI) number of fecal pellets per ha ($\times 10^3$) for snowshoe hares in the six treatment stands in (a) summer ($n = 15$) and (b) winter ($n = 12$) periods in 1999 to 2003. YP: young plantation; Th: thinned; Th + F: thinned and fertilized; UnTh: unthinned; MF: mature forest; OG: old growth-forest.

were no significant effects of time nor the site \times time interaction in either season.

The overall mean number of hare pellets was 3.4 to 4.7 times higher in the unthinned than the thinned-fertilized and mature forest stands during summer periods (Figure 3(a)). This range of difference was 3.5 times during winter periods (Figure 3(b)). Relative habitat use by hares was 6.9 to 7.4 times higher in the mature than in the old-growth forest over the summer and winter periods. Hare use of the thinned-fertilized and mature forest habitats was similar in both seasons.

3.4. Habitat Relationships. Regression analyses indicated that the overall mean number of hare pellets tended to show an initial increase with BA of overstory coniferous trees before declining with larger tree stature ($r = 0.54$; $P = 0.13$) (Figure 4(a)). There was a positive ($r = 0.89$; $P < 0.01$) relationship of hare pellets with density of overstory conifers, primarily lodgepole pine (Figure 4(b)). This pattern was also recorded for total conifers ($r = 0.54$; $P = 0.04$) (Figure 4(c)). The mean number of hare pellets was inversely related to species diversity of overstory conifers ($r = -0.54$; $P = 0.04$) and structural diversity of total conifers ($r = -0.48$; $P = 0.07$) (Figures 5(a) and 5(b)). There were no relationships

between numbers of hare pellets and crown volume index of herbs and shrubs, nor total species richness or diversity of vascular plants.

4. Discussion

This study is the first concurrent investigation of relative habitat use by snowshoe hares across a sequence of successional stages (young plantations to old-growth) of coniferous forests that included intensively managed and natural stands. Our results did not support H_1 that relative habitat use by hares would have a bimodal distribution with the highest abundance in young stands, minimal numbers in mature forest, and moderate abundance in old-growth forests. Clearly, habitat use by hares was the highest in the 20- to 25-year old lodgepole pine stands, particularly the unthinned high density stands, and this result was also reported by Koehler [9], Mowat and Slough [49], and Sullivan et al. [22]. However, we recorded significantly higher levels of habitat use by hares in mature forest than old-growth stands. Koehler [10] and Malloy [50] also reported the same pattern where more pellets were found in mature conifer stands than older stands in Washington and Montana, respectively. Conversely, Zahratka and Shenk [26] found higher densities

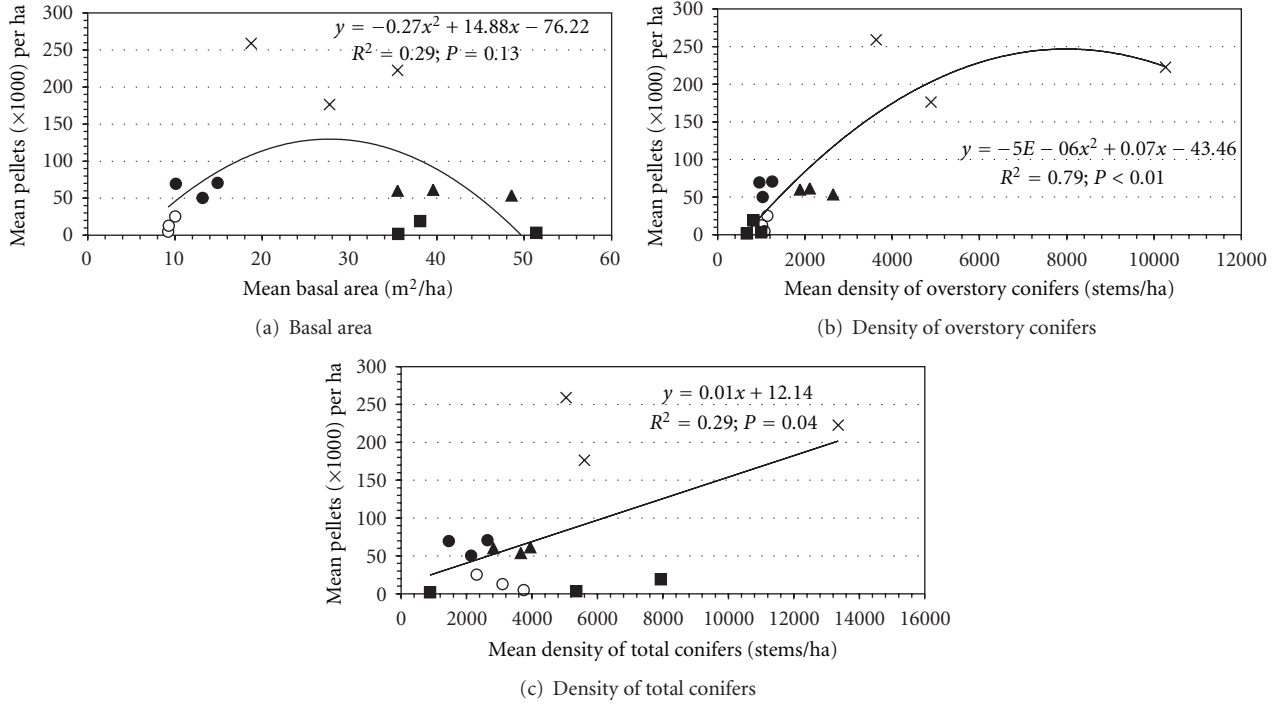


FIGURE 4: Regression relationships for overall mean number of hare pellets (x1000) per ha and (a) basal area and (b) density (stems/ha) of overstory conifers, and (c) density (stems/ha) of total conifers. ○: thinned; ●: thinned and fertilized; ×: unthinned; ▲: mature forest; ■: old-growth forest.

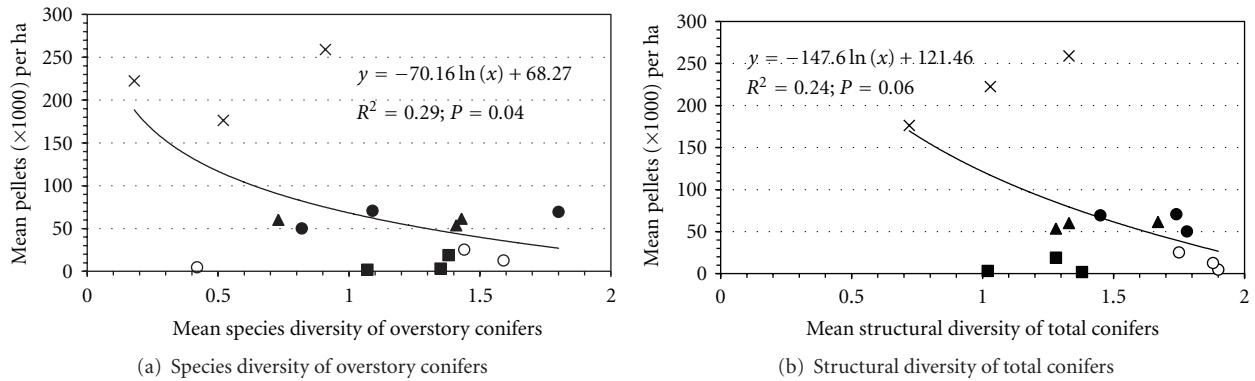


FIGURE 5: Regression relationships for overall mean number of hare pellets (x1000) per ha and (a) species diversity of overstory conifers, and (b) structural diversity of total conifers. ○: thinned; ●: thinned and fertilized; ×: unthinned; ▲: mature forest; ■: old-growth forest.

of snowshoe hares in mature Engelmann spruce-subalpine fir stands than in mature lodgepole pine stands in the southern Rocky Mountains in Colorado. Dolbeer and Clark [51] also reported that suitable hare habitat occurred in old-growth spruce-fir forests in Colorado, where canopy gaps provided openings for shrub development. Our mature and old-growth stands also had Douglas-fir, spruce, and subalpine fir tree species, but with a significantly more even distribution of species in the mature than old-growth stands.

The Buskirk et al. [25] hypothesis (H_1) suggested that gap-phase dynamics in old-growth forests would provide some openings for foraging opportunities for hares, thereby providing habitat for low to moderate numbers of hares

through time. Our old-growth forests had lower species diversity of total conifers than the thinned-fertilized and mature stands and a tendency towards relatively lower structural diversity of conifers, but not statistically so, than the thinned and thinned-fertilized stands. Similarly, our old-growth stands had the lowest mean (\pm SE) coefficient of variation for diameter of lodgepole pine (15.6 ± 2.2) compared with the highest value (40.1 ± 3.8) in the unthinned stands [27]. The mature stands were intermediate in this measure of stand diversity at 24.0 ± 2.1 . Thus, the high-density unthinned stands were able to support significantly more hares than the old-growth because of the cover provided by a combination of sufficient tree density and stand structure

to at least partially reduce predation pressure during winter seasons [52–54]. Although the amounts of herbs and shrubs were higher in the old-growth than mature forest stands, these elements of cover (and food) seemed to make little difference to hare habitat use in the older stands. Hodson et al. [55] concluded that food availability for hares was higher within gaps than under cover in old-growth forests, but their use of space during winter seemed influenced by a greater perception of predation risk within gaps. Although we have no data on incidence of mammalian carnivores or birds of prey in our study stands, susceptibility of hares to predation in old-growth stands seemed the most likely explanation for our results to refute the bimodal distribution hypothesis of Buskirk et al. [25].

Structural diversity of total conifers was as high in the thinned and thinned-fertilized stands as the mature and old-growth stands, and hence this supports part of H_2 . This pattern was predictable based on the accelerated development of understory conifer complexity in stands thinned to ≤ 1000 stems/ha [23]. The amount of herbaceous understory was the greatest in the thinned-fertilized stands, and herbs and shrubs generally do respond positively to PCT and fertilization [16, 56], but had little or no effect on relative habitat use in this study or other investigations [22, 57]. The second part of H_2 that habitat use by hares would increase with abundance of conifers was clearly supported, but in relation to structural diversity of conifers, was not. It was possible that because of the dominance of the high-density unthinned stands of young lodgepole pine, mean numbers of hare pellets declined significantly as species diversity of overstory conifers and structural diversity of total conifers increased. This latter pattern was also recorded for total structural diversity of vegetation across a range of stand densities and fertilization [22].

In conclusion, our results did not support the bimodal distribution of hares among coniferous stands, such that old-growth stands, at least in our region, do not provide sufficient habitat for hare populations. High-density (5000 to 13000 stems/ha) unthinned young lodgepole pine (and other coniferous species) stands provide optimum habitat for hares in terms of overstory and coniferous stand structure. Thinned and fertilized stands may also provide habitat, particularly at densities ≤ 1000 stems/ha, and over time as understory conifers develop [23]. These managed stands provided habitat for hares at the same level as mature stands, at 6–10 years after PCT. Maintenance of a range of successional stages (including old-growth), harvesting systems, PCT with a range of stand densities with and without fertilization, and unmanaged stands in a landscape mosaic would be ideal for integration of silvicultural and wildlife management goals.

In terms of study limitations, we counted and removed all pellets from each permanent plot in spring and autumn of each year from 1999 to 2003, yielding an annual and seasonal distribution of pellets among stands. Hodges and Mills [58] recommended 0.155 m^2 rectangles or 1 m^2 circles for optimum precision and efficiency of surveys of snowshoe hares. We acknowledge their concerns but needed a compromise in plot size (5 m^2 circles) and configuration to

sample concurrently for habitat use by hares, mule deer, and moose as components of related studies. This study was a multistand sampling regime (18 stands in two geographic locations) with number of sample plots ranging from 55 to 145 per stand, depending on area of stand. These plots had relatively high mean counts of hare pellets. Thus, we attempted to combine replication across stand treatments with a reasonably high per-stand accuracy and precision.

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References

- [1] A. W. F. Banfield, *The Mammals of Canada*, University of Toronto Press, Toronto, Canada, 1974.
- [2] L. B. Keith, *Wildlife's Ten-Year Cycle*, University of Wisconsin Press, Madison, Wis, USA, 1963.
- [3] C. J. Krebs, S. Boutin, R. Boonstra et al., "Impact of food and predation on the snowshoe hare cycle," *Science*, vol. 269, no. 5227, pp. 1112–1115, 1995.
- [4] K. E. Hodges, "Ecology of snowshoe hares in northern boreal forests," in *Ecology and Conservation of the Lynx in the United States*, L. F. Ruggiero, K. B. Aubry, S. W. Buskirk et al., Eds., pp. 117–161, University Press of Colorado, Boulder, Colorado, USA, 2000.
- [5] S. Boutin, C. J. Krebs, R. Boonstra, and A. R. E. Sinclair, "The role of the lynx-hare cycle in boreal forest community dynamics," in *Mammal Community Dynamics. Management and Conservation in the Coniferous Forests of Western North America*, C. J. Zabel and R. G. Anthony, Eds., pp. 487–509, Cambridge University Press, Cambridge, UK, 2003.
- [6] D. E. Ausband and G. R. Baty, "Effects of precommercial thinning on snowshoe hare habitat use during winter in low-elevation montane forests," *Canadian Journal of Forest Research*, vol. 35, no. 1, pp. 206–210, 2005.
- [7] P. C. Griffin and L. S. Mills, "Precommercial thinning reduces snowshoe hare abundance in the short term," *Journal of Wildlife Management*, vol. 71, no. 2, pp. 559–564, 2007.
- [8] J. R. Squires, N. J. Decesare, J. A. Kolbe, and L. F. Ruggiero, "Seasonal resource selection of Canada lynx in managed forests of the northern Rocky Mountains," *Journal of Wildlife Management*, vol. 74, no. 8, pp. 1648–1660, 2010.
- [9] G. M. Koehler, "Population and habitat characteristics of lynx and snowshoe hares in north central Washington," *Canadian Journal of Zoology*, vol. 68, no. 5, pp. 845–851, 1990.
- [10] G. M. Koehler, "Snowshoe hare, *Lepus americanus*, use of forest successional stages and population changes during 1985–1989 in North-central Washington," *Canadian Field-Naturalist*, vol. 105, no. 2, pp. 291–293, 1990.
- [11] P. J. Pietz and J. R. Tester, "Habitat selection by snowshoe hares in north central Minnesota," *Journal of Wildlife Management*,

- vol. 47, no. 3, pp. 686–696, 1983.
- [12] J. A. Litvaitis, J. A. Sherburne, and J. A. Bissonette, "Influence of understory characteristics on snowshoe hare habitat use and density," *Journal of Wildlife Management*, vol. 49, no. 4, pp. 866–873, 1985.
 - [13] J. O. Wolff, "The role of habitat patchiness in the population dynamics of snowshoe hares," *Ecological Monographs*, vol. 50, no. 1, pp. 111–130, 1980.
 - [14] G. M. Koehler and J. D. Brittell, "Managing spruce-fir habitat for lynx and snowshoe hares," *Journal of Forestry*, vol. 88, no. 10, pp. 10–14, 1990.
 - [15] P. Koch, *Lodgepole Pine in North America*, Forest Products Society, Madison, Wis, USA, 1996.
 - [16] S. C. Thomas, C. B. Halpern, D. A. Falk, D. A. Liguori, and K. A. Austin, "Plant diversity in managed forests: understory responses to thinning and fertilization," *Ecological Applications*, vol. 9, no. 3, pp. 864–879, 1999.
 - [17] C. L. VanderSchaaf, J. A. Moore, and J. L. Kingery, "The effect of multi-nutrient fertilization on understory plant diversity," *Northwest Science*, vol. 74, no. 4, pp. 316–324, 2000.
 - [18] P. M. F. Lindgren, T. P. Sullivan, D. S. Sullivan, R. P. Brockley, and R. Winter, "Growth response of young lodgepole pine to thinning and repeated fertilization treatments: 10-Year results," *Forestry*, vol. 80, no. 5, pp. 587–611, 2007.
 - [19] S. De Bellefeuille, L. Bélanger, J. Huot, and A. Cimon, "Clear-cutting and regeneration practices in Quebec boreal balsam fir forest: effects on snowshoe hare," *Canadian Journal of Forest Research*, vol. 31, no. 1, pp. 41–51, 2001.
 - [20] J. Ferron, F. Potvin, and C. Dussault, "Short-term effects of logging on snowshoe hares in the boreal forest," *Canadian Journal of Forest Research*, vol. 28, no. 9, pp. 1335–1343, 1998.
 - [21] M. Darveau, J. Huot, and L. Bélanger, "Riparian forest strips as habitat for snowshoe hare in a boreal balsam fir forest," *Canadian Journal of Forest Research*, vol. 28, no. 10, pp. 1494–1500, 1998.
 - [22] T. P. Sullivan, D. S. Sullivan, P. M. F. Lindgren, and D. B. Ransome, "Influence of repeated fertilization on forest ecosystems: relative habitat use by snowshoe hares (*Lepus americanus*)," *Canadian Journal of Forest Research*, vol. 36, no. 9, pp. 2080–2089, 2006.
 - [23] T. P. Sullivan, D. S. Sullivan, P. M. F. Lindgren, and D. B. Ransome, "Long-term responses of mammalian herbivores to stand thinning and fertilization in young lodgepole pine (*Pinus contorta* var. *latifolia*) forest," *Canadian Journal of Forest Research*, vol. 40, no. 12, pp. 2302–2312, 2010.
 - [24] K. E. Hodges, "Ecology of snowshoe hares in southern boreal and montane forests," in *Ecology and Conservation of the Lynx in the United States*, L. F. Ruggiero, K. B. Aubry, S. W. Buskirk et al., Eds., pp. 163–206, University Press of Colorado, Boulder, Colorado, USA, 2000.
 - [25] S. W. Buskirk, L. F. Ruggiero, K. B. Aubry, D. E. Pearson, J. R. Squires, and K. S. McKelvey, "Comparative ecology of lynx in North America," in *Ecology and Conservation of the Lynx in the United States*, L. F. Ruggiero, K. B. Aubry, S. W. Buskirk et al., Eds., pp. 397–418, University Press of Colorado, Boulder, Colorado, USA, 2000.
 - [26] J. L. Zahratka and T. M. Shenk, "Population estimates of snowshoe hares in the southern Rocky Mountains," *Journal of Wildlife Management*, vol. 72, no. 4, pp. 906–912, 2008.
 - [27] S. H. Hurlbert, "Pseudoreplication and the design of ecological field experiments," *Ecological Monographs*, vol. 54, no. 2, pp. 187–211, 1984.
 - [28] T. P. Sullivan, D. S. Sullivan, P. M. F. Lindgren, and D. B. Ransome, "Stand structure and the abundance and diversity of plants and small mammals in natural and intensively managed forests," *Forest Ecology and Management*, vol. 258, pp. S127–S141, 2009.
 - [29] J. H. Zar, *Biostatistical Analysis*, Prentice Hall, Englewood Cliffs, NJ, USA, 1999.
 - [30] D. Meidinger and J. Pojar, *Ecosystems of British Columbia*, Special Report Series, Research Branch, Ministry of Forests, Victoria, Canada, 1991.
 - [31] C. O. Tamm, A. Aronsson, B. Popovic, and J. Flower-Ellis, "Optimum nutrition and nitrogen saturation in Scots pine stands," *Studia Forestalia Suecica*, vol. 206, 126 pages, 1999.
 - [32] R. P. Brockley, "Effects of post-thinning density and repeated fertilization on the growth and development of young lodgepole pine," *Canadian Journal of Forest Research*, vol. 35, no. 8, pp. 1952–1964, 2005.
 - [33] P. F. Stickney, "Data base for post-fire succession, first 6 to 9 years, in Montana larch-fir forests," Tech. Rep. INT-62, USDA Forest Service Intermountain Research Station, 1980.
 - [34] C. L. Hitchcock and A. Cronquist, *Flora of the Pacific Northwest*, University of Washington Press, Seattle, Wash, USA, 1973.
 - [35] R. Parish, R. Coupe, and D. Lloyd, *Plants of Southern Interior British Columbia*, Lone Pine, Vancouver, Canada, 1996.
 - [36] C. J. Krebs, *Ecological Methodology*, Addison-Wesley, Reading, Mass, USA, 1999.
 - [37] A. E. Magurran, *Measuring Biological Diversity*, Blackwell, Oxford, UK, 2004.
 - [38] T. P. Sullivan, D. S. Sullivan, and P. M. F. Lindgren, "Stand structure and small mammals in young lodgepole pine forest: 10-year results after thinning," *Ecological Applications*, vol. 11, no. 4, pp. 1151–1173, 2001.
 - [39] K. S. McKelvey, G. W. McDaniel, L. S. Mills, and P. C. Griffin, "Effects of plot size and shape on pellet density estimates for snowshoe hares," *Wildlife Society Bulletin*, vol. 30, no. 3, pp. 751–755, 2002.
 - [40] D. L. Murray, J. D. Roth, E. Ellsworth, A. J. Wirsing, and T. D. Steury, "Estimating low-density snowshoe hare populations using fecal pellet counts," *Canadian Journal of Zoology*, vol. 80, no. 4, pp. 771–781, 2002.
 - [41] T. P. Sullivan, D. S. Sullivan, P. M. F. Lindgren, and D. B. Ransome, "Influence of repeated fertilization on forest ecosystems: relative habitat use by mule deer and moose," *Canadian Journal of Forest Research*, vol. 36, no. 6, pp. 1395–1406, 2006.
 - [42] C. J. Krebs, B. S. Gilbert, S. Boutin, and R. Boonstra, "Estimation of snowshoe hare population density from turd transects," *Canadian Journal of Zoology*, vol. 65, no. 3, pp. 565–567, 1987.
 - [43] SPSS Institute Inc., *Statistical Programs of the Social Sciences*, SPSS Institute Inc., Chicago, Ill, USA, 2007.
 - [44] J. Fowler, L. Cohen, and P. Jarvis, *Practical Statistics for Field Biology*, John Wiley & Sons, New York, NY, USA, 2nd edition, 1998.
 - [45] R. C. Littell, "Statistical analysis of experiments with repeated measures," *Hortscience*, vol. 24, no. 1, pp. 36–40, 1989.
 - [46] R. O. Kuehl, "Repeated measures designs," in *Statistical Principles of Research Design and Analysis*, pp. 499–528, Duxbury Press, Belmont, Calif, USA, 1994.
 - [47] H. Huynh and L. S. Feldt, "Estimation of the Box correction for degrees of freedom from sample data in the randomized block and split-plot designs," *Journal of Educational Statistics*, vol. 1, no. 1, pp. 69–82, 1976.
 - [48] D. J. Saville, "Multiple comparison procedures: the practical

- solution,” *American Statistician*, vol. 44, no. 2, pp. 174–180, 1990.
- [49] G. Mowat and B. Slough, “Habitat preference of Canada lynx through a cycle in snowshoe hare abundance,” *Canadian Journal of Zoology*, vol. 81, no. 10, pp. 1736–1745, 2003.
 - [50] J. C. Malloy, “Snowshoe Hare, *Lepus americanus*, fecal pellet fluctuations in western Montana,” *Canadian Field-Naturalist*, vol. 114, no. 3, pp. 409–412, 2000.
 - [51] R. A. Dolbeer and W. R. Clark, “Population ecology of snowshoe hares in the central Rocky Mountains,” *Journal of Wildlife Management*, vol. 39, no. 3, pp. 535–549, 1975.
 - [52] C. Beaudoin, M. Crête, J. Huot, P. Etcheverry, and S. D. Côté, “Does predation risk affect habitat use in snowshoe hares?” *Ecoscience*, vol. 11, no. 4, pp. 370–378, 2004.
 - [53] P. Etcheverry, J. P. Ouellet, and M. Crête, “Response of small mammals to clear-cutting and precommercial thinning in mixed forests of southeastern Quebec,” *Canadian Journal of Forest Research*, vol. 35, no. 12, pp. 2813–2822, 2005.
 - [54] J. A. Homyack, D. J. Harrison, and W. B. Krohn, “Effects of precommercial thinning on snowshoe hares in Maine,” *Journal of Wildlife Management*, vol. 71, no. 1, pp. 4–13, 2007.
 - [55] J. Hodson, D. Fortin, and L. Belanger, “Fine-scale disturbances shape space-use patterns of a boreal forest herbivore,” *Journal of Mammalogy*, vol. 91, no. 3, pp. 607–619, 2010.
 - [56] P. M. F. Lindgren, D. B. Ransome, D. S. Sullivan, and T. P. Sullivan, “Plant community attributes 12 to 14 years following precommercial thinning in a young lodgepole pine forest,” *Canadian Journal of Forest Research*, vol. 36, no. 1, pp. 48–61, 2006.
 - [57] T. P. Sullivan, D. S. Sullivan, P. M. F. Lindgren, and D. B. Ransome, “Long-term responses of ecosystem components to stand thinning in young lodgepole pine forest. IV. Relative habitat use by mammalian herbivores,” *Forest Ecology and Management*, vol. 240, no. 1–3, pp. 32–41, 2007.
 - [58] K. E. Hodges and L. S. Mills, “Designing fecal pellet surveys for snowshoe hares,” *Forest Ecology and Management*, vol. 256, no. 11, pp. 1918–1926, 2008.

