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Long-term responses of ecosystem components to stand thinning in young lodgepole pine forest
IV. Relative habitat use by mammalian herbivores

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Abstract

Pre-commercial thinning (PCT) is a silvicultural practice that can provide diverse understory and overstory vegetation conditions. We tested the hypothesis that relative habitat use by snowshoe hare (*Lepus americanus*), mule deer (*Odocoileus hemionus*), and moose (*Alces alces*) would increase in response to enhanced abundance of herbs and shrubs, and species diversity and structural diversity of conifers, in heavily thinned ($\leq$1000 stems/ha) stands, at 12–15 years post-thinning. Replicate study areas were located near Penticton, Kamloops, and Prince George in south-central British Columbia, Canada. Each study area had three young pine stands thinned to densities of ~500 stems/ha (low), ~1000 stems/ha (medium), and ~2000 stems/ha (high), with an unthinned young pine and old-growth pine stand for comparison.

Relative habitat use, based on counts of fecal pellets and pellet-groups, was similar among the five treatment stands for hares ($P = 0.24$), deer ($P = 0.23$), and moose ($P = 0.16$). However, low-density stands (~500 stems/ha) had ca. 3–20 times as many deer pellet-groups, and ca. 2–4 times as many moose pellet-groups, than other stands. Low-density stands had significantly greater canopy openness, volume of shrubs <2 m, and horizontal hiding cover <1.6 m than other treatments. Relative habitat use by deer and moose was positively related to understory characteristics such as enhanced abundance of forage and security cover. These results support our hypothesis that deer and moose responded positively to enhanced volume of herbs and shrubs as well as to species diversity and structural diversity of conifers and overall vegetation in heavily thinned ($\leq$1000 stems/ha) stands at 12–15 years post-thinning. Our results suggest that ungulate management would be enhanced if greater emphasis was placed on forage enhancement throughout the year, which differs from current management recommendations which tend to focus on winter range and snow-interception cover.

Keywords: *Alces alces*; *Lepus americanus*; *Odocoileus hemionus*; Lodgepole pine; Pre-commercial thinning; Relative habitat use

1. Introduction

Second-growth forests cover millions of ha of the temperate and boreal zones of North America. Managing these forests for natural levels of biodiversity requires a variety of tree species, successional stages, stand structures, stand densities, edges, and riparian zones in landscape mosaics (Hunter, 1999; Lindenmayer and Franklin, 2002). There are several forestry practices such as commercial and pre-commercial thinning (PCT), planting of multiple species, and vegetation management (conifer release) that provide a variety of understory and overstory vegetative composition and structure (Hayes et al., 1997; Busing and Garmen, 2002; Homyack et al., 2004).

Conventional PCT, that prescribes a single target density to an entire stand, generally increases the biomass of understory vegetation (Crouch, 1986; Klinka et al., 1996; Thomas et al., 1999). In addition, Sullivan et al. (2001, 2006) and Lindgren et al. (2006) reported that size and architecture of crop trees, coniferous stand structure, and abundance and diversity of vegetation were enhanced by heavy thinning of lodgepole pine (*Pinus contorta*) stands to $\leq$1000 trees/ha at 10–15 years after PCT.

The structural attributes of crown architecture have considerable relevance to nesting, foraging, and cover (both hiding and thermal) requirements of a wide variety of wildlife species (Hayes et al., 1997; Suzuki and Hayes, 2003). Similarly,

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understory vegetation provides foraging, nesting, and roosting opportunities for birds (Woodcock et al., 1997; Sallabanks et al., 2002) and hiding and thermal cover for small herbivores (e.g., snowshoe hare, *Lepus americanus*) (Wolff, 1980; Litvaitis et al., 1985) and their predators (Thompson and Harestad, 1994). In particular, the snowshoe hare is a keystone species in the boreal forest of North America (Boutin et al., 2003), as it is the main prey for vertebrate predators such as Canada lynx (*Lynx canadensis*) and fisher (*Martes pennanti*). In addition, ungulates such as mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) need these early successional understory (herbs and shrubs) conditions to provide not only forage, but also thermal and hiding cover (Lyon, 1987; Nyberg, 1990). In areas and years of relatively high snowpacks, both mule deer and moose (*Alces alces*) appear to require mature and old-growth forest with high levels of crown closure for snow interception during winter months (Armleder et al., 1994; Pierce and Peek, 1984). Old forests often provide the best winter range conditions because of overstory snow interception and provision of forage via herbs, shrubs, and arboreal lichen litterfall (Bunnell, 1985; Nyberg, 1990).

Mule deer, moose, and snowshoe hares are all commonly found in temperate and boreal forests, including lodgepole pine stands, throughout inland areas of the Pacific Northwest of North America (Banfield, 1974; Koch, 1996; Hodges, 2000). To date, there have been few studies that have investigated responses of these mammals to silvicultural management of lodgepole pine stands. Increases in forage production from stand thinning appeared to result in increased habitat use by mule deer, elk, and snowshoe hares in lodgepole pine stands in certain seasons (Blair and Enghardt, 1976; Crouch, 1986; Lyon, 1987; Sullivan and Sullivan, 1988). It is possible that these herbivores were also responding to the cover provided by increased species and structural diversity commonly observed following thinning (Thomas et al., 1999; Thysell and Carey, 2000; Lindgren et al., 2006). However, responses of these species to a wide range of stand densities from PCT in young lodgepole pine stands have not been investigated. Thus, this study was designed to test the hypothesis that relative habitat use by snowshoe hares, mule deer, and moose would increase in response to enhanced abundance of herbs and shrubs, and species diversity and structural diversity of conifers, in heavily thinned ($\leq$1000 stems/ha) stands at 12–15 years post-thinning.

2. Materials and methods

2.1. Study areas

Five lodgepole pine stands were located at each of three replicate study areas in south-central British Columbia, Canada: Penticton Creek, Kamloops, and Prince George. These areas were selected on the basis of having several thousand hectares of young lodgepole pine forest having arisen from wildfire or large-scale harvesting activities (Sullivan et al., 2001). Stands within these tracts of young forest had relatively uniform tree cover and comparable diameter, height, and density of lodgepole pine trees prior to PCT. Each replicate had four second-growth lodgepole pine stands (age range of 17–27 years); three of which were PCT to low ($\sim$500 stems/ha), medium ($\sim$1000 stems/ha) or high ($\sim$2000 stems/ha) density. Second-growth stands had very few remnant trees and snags remaining from previous stands. In addition, an old-growth lodgepole pine stand (age range 160–250 years) was included in the set of treatment stands at each replicate study area (Sullivan et al., 2001).

The Penticton Creek treatment stands (the thinned stands ranged in area from 20 ha each to the unthinned stand at 100+ ha) were situated within ca. 5000 ha of similar-aged stands originating from a wildfire in 1971 (Sullivan et al., 1996). The vast majority of the area was unthinned young pine stands with densities of several thousand stems/ha. Similarly, at the Kamloops study area, the treatment stands (the thinned stands ranged in area from 15 to 22 ha and the unthinned stand was 100+ ha) were embedded within 15,000 ha of young pine stands from a fire in 1961. There were virtually no mature stands of timber, other than single trees and small patches (<1 ha) in this landscape. Again, this very large area was primarily dense (>3000 stems/ha) stands of unthinned pine. The Prince George study area occurred within ca. 1000 ha of extensive harvesting (1966–1972) that regenerated naturally to young stands of lodgepole pine ranging from a density of 2700 to 4700 stems/ha. The treatment stands ranged in area from 30 to 39 ha (thinned stands) and 41 ha (unthinned stand).

Additional details of these study areas are described in Sullivan et al. (2006).

2.2. Study design

Low-, medium-, and high-density stands of young lodgepole pine forest were examined in our experimental design. Unthinned young and old-growth lodgepole pine stands were also included at each study area in the following design: Stand A is low density, target 500 stems/ha; Stand B is medium density, target 1000 stems/ha; Stand C is high density, 2000 stands/ha; Stand D is unthinned >2000 stems/ha; stand E is old growth. Treatments were assigned to stands in a randomized complete block design. Each of the three study areas was considered a regional replicate (block).

Operational thinning was conducted after the growing season in fall of 1988 at the Penticton and Prince George study areas, and in fall of 1989 at the Kamloops study area. There was no treatment of slash, from the PCT, in these stands, which is standard practice in BC. Trees in low-density stands were pruned to a 2.8-m lift (above ground level) at Penticton (October 1992), Kamloops (September 1992), and Prince George (November 1991). Densities of pine (stems/ha) in unthinned stands were 5000 at Penticton, 6000 at Kamloops, and 4700 at Prince George in 1988. These densities were 5730, 6620, and 4065, respectively, in 2003 (Sullivan et al., 2006).

2.3. Stand structure and vegetation attributes

Sampling of coniferous stand structure was conducted in 2003 within 5.64-m radius circular plots (100 m^2) that recorded the total number of stems, by species, within four height classes; 0–1, 1–2, 2–3, and >3 m. Twenty stand structure plots were systematically located within each of the thinned pine stands (Sullivan et al., 2006). Ten stand structure plots were located every 50 or 100 m in a grid pattern throughout the unthinned and old-growth stands.

Understory vegetation was sampled according to Lindgren et al. (2006). Three 25-m transects, consisting of five contiguous 5 m × 5 m plots, were randomly located in each of the five stands at each of the study areas. Each plot contained three sizes of nested plots: the 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 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 then used to calculate a crown volume index (m^3/0.01 ha) for each plant species. The product of percent cover and corresponding height yields 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 converted to a 0.01-ha base to produce values for species and layer. Sampling was carried out during July–August 2000, 2001, and 2002. Plant species were identified in accordance with Hitchcock and Cronquist (1973), Parish et al. (1996), and MacKinnon et al. (1992).

Plant communities were described by species richness, species diversity, and structural diversity. All diversity measures were calculated separately for herb, shrub, and tree layers, as well as a combined total layer, which included all species. Species richness was the total number of species sampled (Krebs, 1999). Species diversity was described using the Shannon–Wiener index, which is sensitive to changes in rare species, has good discriminant ability, and is well represented in the ecological literature (Burton et al., 1992; Magurran, 2004). Species diversity was calculated using the crown volume index for each plant species averaged across the three transects, each of which was an average of five subplots, in a given stand. Species diversity was calculated separately for herbs, shrubs and trees, as well as a combined total layer. Structural diversity (height classes acting as "species") was also described using the Shannon–Wiener index. Structural richness was the total number of height classes occupied by the various vegetative layers.

Hiding cover was determined by visually estimating the percentage of a 1.6-m pole that was concealed by herbs and shrubs. The cover pole was observed from a standing position at a distance of 10 m and was oriented vertically with one end touching the ground. The cover pole was painted with 16 alternating 0.1-m red and white bands. The total number of bands concealed by various forms of vegetation was recorded. This number was divided by 16 and multiplied by 100% to get an estimate of horizontal hiding cover similar to that described by Griffith and Youtie (1988). Three randomly located plots (based on the three transects used for detailed vegetation sampling, see Lindgren et al., 2006) were used to sample horizontal cover. Four cover pole measurements were made at each plot, where the observer remained stationary at the plot centre for each of the four measurements. The cover pole was initially positioned 10 m away following a random bearing, the other three positions rotated around the observer at 90°, 180°, and 270° from the initial bearing. All 12 (4 per plot × 3 plots per stand) measurements were averaged for stand-level estimates of horizontal hiding cover.

Canopy openness, an index of both the amount of light to reach the understory and vertical hiding cover, was estimated using a spherical densiometer (Lemmon, 1956; D'Eon, 2001). Four densiometer readings were made at each of the three randomly located vegetation transects (see Lindgren et al., 2006) resulting in a total of 12 measurements per stand. The four plots were systematically located 5 m apart and corresponded with the corner of four of the five herb plots used for sampling vegetation. All 12 measurements were averaged for a stand-level estimate of canopy openness.

A mean ($n = 3$) value (2000–2002) was calculated for each of the vegetation attributes (see Lindgren et al., 2006). Herb, shrub, and tree volume <2 m, canopy openness, and horizontal hiding cover were measured in 2002 and coniferous stand structure data were collected in 2003 (Sullivan et al., 2006). The measurements for vegetation volumes <2 m, and horizontal hiding cover <1.6 m, were chosen because forage in this height range should be available to deer and moose year-round.

2.4. Mammalian herbivores

Relative habitat use by the three herbivore species was measured for the 12–15 years post-PCT period by counting and removing all fecal pellets of snowshoe hares (Litvaitis et al., 1985; Koehler, 1990; Ferron et al., 1998), and fecal pellet-groups of mule deer and moose (Neff, 1968; Loft and Kie, 1988; Edge and Marcum, 1989) within permanent sample plots. We used 5.0 m^2 circular plots that were larger than the typical circular plots of 1.0 m^2 recommended for snowshoe hares by McKelvey et al. (2002) and Murray et al. (2002). This plot size and configuration were chosen to accommodate concurrent sampling of fecal pellets and pellet-groups of the three-herbivore species. One hundred plots were located systematically, in 5-plot arrays installed at each of 20 stations located every 50 m, throughout each stand at the three study areas. Plot boundaries were delineated using a 1.26 m rope attached to and rotated around the center stake. Plots were cleared of all pellets at the initial sampling time in early October 2000, and pellet counts were conducted again in the spring of 2004, representing a period of four winters and three summers. New pellet-groups had to have a minimum of 20 pellets per group. All sample plots at a given study area were assessed by the same observers at each sampling time. Pellet-groups located on the edge of a sample plot had to have 50% or more of the group within the plot to be counted. Hare pellets located near the plot circumference were included or not, depending on where the end of the rope passed, on the circumference, as the plot was surveyed. Pellets were not included if they were incorporated into the duff and litter layers as these pellets were likely deposited prior to the initial plot clearing. Such pellets from hares were nearly always a darker color with a lack of light brown or green material in the center of the pellets when broken open (Krebs et al., 1987). Pellet degradation was likely not an issue as only new pellets deposited during the 3-year period were counted (although see Sullivan et al., 2002 and Murray et al., 2005). Density of pellets was estimated per 5 m^2 plot and then converted to a per-ha basis. Descriptive statistics were calculated on a per-plot basis and were averaged and presented on a stand basis.

2.5. Statistical analysis

For those data with repeated measurements each year, a repeated measures analysis of variance (RM-ANOVA) (SPSS Institute Inc., 1997) was conducted to determine the effects of PCT (12–14 years post-thinning) on mean crown volume index of the herb, shrub, and tree layers, mean total species diversity, and mean total structural diversity of the combined layers (Lindgren et al., 2006). 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). Mauchly's W test statistic was used to test for sphericity (independence of data among repeated measures) (Littel, 1989; Kuehl, 1994). For data found to be correlated among years, the Huynh–Feldt correction (Huynh and Feldt, 1976) was used to adjust the degrees of freedom of the within-subjects F-ratio.

For those data with single measurements only, a randomized block two-way ANOVA-Model III (Zar, 1999), with stand (five stand treatments) as a fixed effect and block as a random effect, was used to evaluate differences in mean pellet and pellet-group densities per ha. This same analysis was used to evaluate differences in abundance, species diversity, and structural diversity of coniferous tree layers (Sullivan et al., 2006). It was also used to detect differences in crown volume index of shrubs <2 m height, canopy openness, and horizontal cover <1.6 m height.

Simple linear regression analyses (Zar, 1999) were used to determine the relationships between relative habitat use (as indicated by pellet and pellet-group densities per ha) and several vegetation attributes. These attributes included measures of volume of herbs, shrubs, and trees, total species diversity, and total structural diversity, total density of trees (>3 m height), canopy openness, and horizontal hiding cover. To remove the block effect from the regression analyses, both the pellet and vegetation attributes being compared were standardized within each block by converting each value to a proportion of the largest measurement for that attribute within that block. Duncan's multiple range test (DMRT) was used to compare mean values. In all analyses, the level of significance was at least $P = 0.05$.

3. Results

3.1. Relative habitat use

Relative habitat use, based on mean density of hare pellets, was similar ($F_{4,8} = 1.72$; $P = 0.24$) among the five treatment stands despite the apparent magnitude of differences observed in Fig. 1a. At the stand level, it was clear that more hare pellets were recorded at Penticton Creek than at either Kamloops or Prince George (Table 1) and this was verified by a significant ($F_{2,8} = 9.14$; $P < 0.01$) block effect. In addition, variability of hare pellets among plots was high with coefficients of variation exceeding the means for all treatment stands, thereby indicating a clumped distribution of pellets (Table 1).

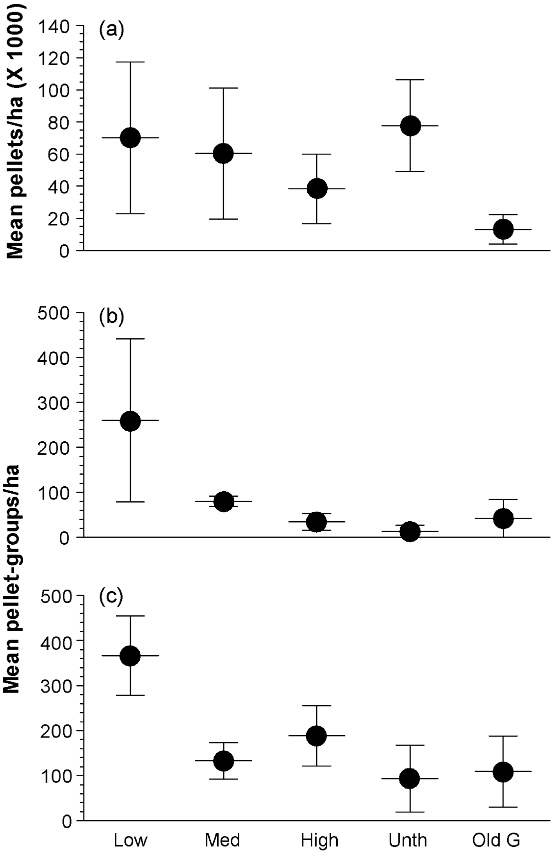

Fig. 1. Mean ($n = 3$) number ± S.E. per ha of (a) snowshoe hare pellets, (b) mule deer pellet-groups, and (c) moose pellet-groups in five treatment stands. Low: low density; Med: medium density; High: high density; Unth: unthinned; Old G: old growth.

Mean density of fecal pellet-groups of mule deer was similar ($F_{4,8} = 1.77$; $P = 0.23$) among treatment stands and among blocks ($F_{2,8} = 2.21$; $P = 0.17$). Again, although not statistically significant, relative habitat use by deer appeared highest in low-density stands, which had 3.3–19.5 times as many pellet-groups as the other stands (Fig. 1b). This apparent trend was largely attributed to high use of the low-density stand at Penticton (Table 1). Deer pellet-groups were also distributed in a clumped pattern as indicated by the high coefficients of variation (Table 1). In addition, deer did not use the unthinned or old-growth stands at Kamloops or at Prince George, nor the high-density stand at this latter study area (Table 1).

Relative habitat use by moose was also similar ($F_{4,8} = 2.22$; $P = 0.16$) among treatment stands and among blocks ($F_{2,8} = 0.60$; $P = 0.57$). There were moose pellet-groups in all stands but the unthinned stand at Kamloops, and coefficients of variation were again substantially higher than the means

Table 1
Descriptive statistics for pellet and pellet-group density (per 5 m^2) of snowshoe hares, deer, and moose for the 12–15 years post-thinning period in the five stand treatments

	Low	Medium	High	Unthinned	Old growth
Snowshoe hare					
Penticton					
Maximum	364.00	421.00	143.00	372.00	127.00
Mean	81.36	70.21	39.77	58.17	15.72
CV	87.97	92.69	74.73	109.14	139.62
Kamloops					
Maximum	52.00	38.00	73.00	590.00	13.00
Mean	3.76	3.18	3.11	47.50	0.87
CV	228.10	215.86	317.55	142.35	242.28
Prince George					
Maximum	255.00	107.00	103.00	67.00	52.00
Mean	20.18	17.10	14.66	10.91	3.22
CV	197.67	128.60	117.25	135.87	256.38
Deer					
Penticton Creek					
Maximum	3.00	1.00	1.00	1.00	1.00
Mean	0.31	0.04	0.03	0.02	0.06
CV	192.87	492.37	559.70	703.53	387.18
Kamloops					
Maximum	1.00	1.00	1.00	0.00	0.00
Mean	0.06	0.03	0.02	0.00	0.00
CV	397.81	571.49	703.53	0.00	0.00
Prince George					
Maximum	1.00	1.00	0.00	0.00	0.00
Mean	0.02	0.05	0.00	0.00	0.00
CV	703.53	438.09	0.00	0.00	0.00
Moose					
Penticton Creek					
Maximum	2.00	1.00	1.00	2.00	1.00
Mean	0.25	0.10	0.07	0.12	0.01
CV	198.75	301.51	358.44	296.82	974.68
Kamloops					
Maximum	2.00	1.00	1.00	0.00	2.00
Mean	0.20	0.07	0.05	0.00	0.13
CV	213.20	366.33	438.09	0.00	301.68
Prince George					
Maximum	1.00	1.00	2.00	1.00	1.00
Mean	0.10	0.03	0.16	0.02	0.02
CV	301.51	571.49	262.32	703.53	703.53

(Table 1). As a trend that might be biologically significant, low-density stands had 1.9–3.9 times as many moose pellet-groups than the other treatment stands (Fig. 1c).

3.2. Herbivores and vegetation variables

Herb volume <2 m (total herbs) was significantly ($F_{4,8} = 10.23$; $P < 0.01$) greater in the thinned stands (DMRT; $P = 0.05$) than unthinned and old-growth stands (Table 2). Shrub volume <2 m ($F_{4,8} = 4.87$; $P = 0.03$) and canopy openness ($F_{4,8} = 6.62$; $P = 0.01$) were significantly greater in the low-density stands (DMRT; $P = 0.05$) than in the other stands. Species and structural diversity of conifers were also significantly different among stands, being highest (DMRT; $P = 0.05$) in the low-density stands (Table 2). Horizontal cover was significantly ($F_{4,8} = 3.70$; $P = 0.05$) different among stands with the low-density stand higher (DMRT; $P = 0.05$) than the old-growth stand.

For the relationships of relative habitat use to vegetation variables, only those relationships found to be at least marginally significant ($P < 0.10$) are presented. There was a trend between snowshoe hare habitat use and total shrub volume and horizontal cover (Table 3). Otherwise, there were no other relationships between relative habitat use by hares and vegetation variables.

There was a positive relationship between density of pellet-groups for deer and species diversity and structural diversity of coniferous trees (Table 3). However, there was a negative relationship between pellet-group density and total tree density, as well as volume of trees (Fig. 2a). Density of pellet-groups for deer was also positively related to volume of shrubs <2 m, total species diversity and total structural diversity of vegetation (Fig. 2b); canopy openness (Fig. 2c), and horizontal hiding cover provided by herbs and shrubs <1.6 m.

There was a positive relationship between density of pellet-groups for moose and volume of total herbs, total shrubs, and shrubs <2 m; as well as a negative relationship with the volume of trees (Table 3; Fig. 3a). This measure of relative habitat use for moose was also positively related to total species diversity and total structural diversity of vegetation, canopy openness (Fig. 3b), and horizontal hiding cover <1.6 m (Fig. 3c).

4. Discussion

4.1. Snowshoe hares

From a biological perspective, pellet counts for snowshoe hares appeared to be highest in the heavily thinned stands at Penticton and Prince George with far fewer pellets, and hence hares, recorded at the Kamloops stands where most activity occurred in the unthinned stand (see Table 1). Snowshoe hares are distributed throughout the montane and sub-boreal forests of the Pacific Northwest of North America and have relatively similar population fluctuations as their counterparts in the northern boreal forests (Hodges, 2000). Hare populations appeared to peak in abundance at the end or start of a decade with recorded peaks in central Alberta in 1960 (Keith, 1963) and 1970 (Keith, 1990), the Yukon in 1980 (Krebs et al., 1986) and 1990 (Krebs et al., 1995) and Prince George in 1980 (Sullivan and Sullivan, 1988) and 1990 (Sullivan, 1994). Thus, hares may have started to decline in abundance during our first winter (2000–2001) and been at relatively low numbers by spring 2004. Unfortunately, we do not have an independent measure (e.g., live trapping) of hare population fluctuations during this period.

The lack of relationships between hare pellet counts and all vegetation variables, whether it was overall density of conifers or structural diversity of understory vegetation, seemed perplexing. This study was conducted during the initial part of the decline phase of the hare cycle, a period when the risk of

Table 2
Mean ($n = 3$ replicate stands) crown volume index (m^3/0.01 ha) of herbs, shrubs, and trees <2 m, percent canopy openness, and horizontal hiding cover <1.6 m for the 12–15 years post-thinning period in the five stand treatments

Habitat attributes	Treatment					Significance	
	Low	Medium	High	Unthinned	Old growth	$F_{4,8}$	P
Volume							
Total herbs	10.12 a	10.14 a	12.32 a	4.36 b	3.91 b	10.23	**<0.01**
Shrubs <2 m	33.21 a	18.14 b	14.23 b	12.92 b	8.06 b	4.87	**0.03**
Total shrubs	55.91	61.73	55.70	43.28	11.16	1.60	0.26
Trees <2 m	3.19	0.86	2.14	1.70	3.67	0.84	0.54
Total trees	122.65	136.83	136.89	185.86	185.28	3.14	0.08
Density of trees >3 m	665.0 b	1068.3 b	1631.7 b	5525.0 a	1626.7 b	28.93	**<0.01**
Diversity							
Conifer species diversity	1.58 a	1.30 a	0.77 b	0.46 b	0.73 b	13.89	**<0.01**
Conifer structural diversity	1.79 a	1.51 ab	0.85 cd	0.50 d	1.12 bc	8.68	**<0.01**
Total species diversity	2.22	1.71	1.86	1.42	1.56	2.80	0.10
Total structural diversity	1.70	1.17	1.08	0.87	0.95	3.61	0.06
Canopy openness	43.25 a	24.25 b	26.53 b	21.42 b	21.28 b	6.62	**0.01**
Horizontal cover <1.6 m	50.87 a	28.47 ab	34.98 ab	33.49 ab	10.59 b	3.70	**0.05**

Column of mean values with different letters were significantly different by Duncan's multiple range test (DMRT), adjusted for multiple contrasts. P is the level of significance; bold values were those significant at $P = 0.05$.

predation is highest. Snowshoe hares born during this period adopt a safe-feeding strategy (predator-sensitive foraging), and restrict their activities to relatively safe environments to reduce the risk of predation (Gilbert and Boutin, 1991; Krebs, 1996). Thus, abundance of food may have been adequate in open areas, but was not accessible to hares. Consequently, the scale at which we measured stand structure and habitat attributes may not have been sufficient to distinguish between high-risk and low-risk foraging sites within each stand (Murray et al., 2005). This may have resulted in the poor correlations between density of hare pellets and vegetation attributes. However, we documented a nearly significant ($P \leq 0.07$), albeit weak, relationship ($r < 0.50$) of density of hare pellets with both the volume of shrubs and horizontal hiding cover provided by herbs and shrubs <1.6 m (Table 3).

Table 3
Results of linear regression analyses of pellet and pellet-group density per ha of snowshoe hares, deer, and moose with measured vegetation variables for the 12–15 years post-thinning period in the five stand treatments

Species	Vegetation variable	r	P
Hares	Total shrub volume	0.49	0.06
	Horizontal cover <1.6 m	0.49	0.07
Deer	Shrub volume <2 m	0.62	**0.01**
	Total tree volume	−0.55	**0.04**
	Density of trees >3 m	−0.55	**0.03**
	Conifer species diversity	0.75	**<0.01**
	Conifer structural diversity	0.73	**<0.01**
	Total species diversity	0.55	**0.03**
	Total structural diversity	0.66	**<0.01**
	Canopy openness	0.69	**<0.01**
	Horizontal cover <1.6 m	0.53	**0.04**
Moose	Total herb volume	0.49	0.07
	Total shrub volume	0.49	0.07
	Shrub volume <2 m	0.65	**<0.01**
	Total tree volume	−0.55	**0.03**
	Total species diversity	0.57	**0.03**
	Total structural diversity	0.57	**0.03**
	Canopy openness	0.70	**0.01**
	Horizontal cover <1.6 m	0.65	**<0.01**

r represents the linear regression relationship; negative values represent an inverse relationship. P is the level of significance; bold values were those significant at $P = 0.05$.

Presumably, heavily thinned stands, with a significantly enhanced herb and shrub layer, provided low-risk foraging sites for snowshoe hares. This pattern fits where young (20–30 years since harvesting or wildfire) unmanaged lodgepole pine stands were preferred forest habitat for hares, providing both cover and food when interspersed with young successional stages (Sullivan and Sullivan, 1983; Koehler, 1990). Correlating density of pellets with more detailed measurements of habitat attributes (e.g., measurements of hiding and escape cover near ground-level) may have revealed the vegetation attributes characteristic of low-risk foraging sites for snowshoe hares. This information could then be used to enhance habitat for this keystone species and the predators that rely on them, particularly during periods of low hare abundance.

It is likely that large areas of heavy PCT in young pine stands could enhance habitat values for hares over time, but within a mosaic of unmanaged stands to provide a diversity of stand types and food and cover attributes for these leporids. It is also important to note that our thinned stands ranged in area from 15 to 39 ha, and were interspersed within much larger (1000s of ha) landscapes of unmanaged young pine forest. Thus, our results may not necessarily be extrapolated to those areas of thinned lodgepole pine that cover 100s or 1000s of ha, without interspersion of unthinned stands.

4.2. Mule deer and moose

A pattern consistent in all replicates was that the highest relative use by deer and moose occurred in either low- or

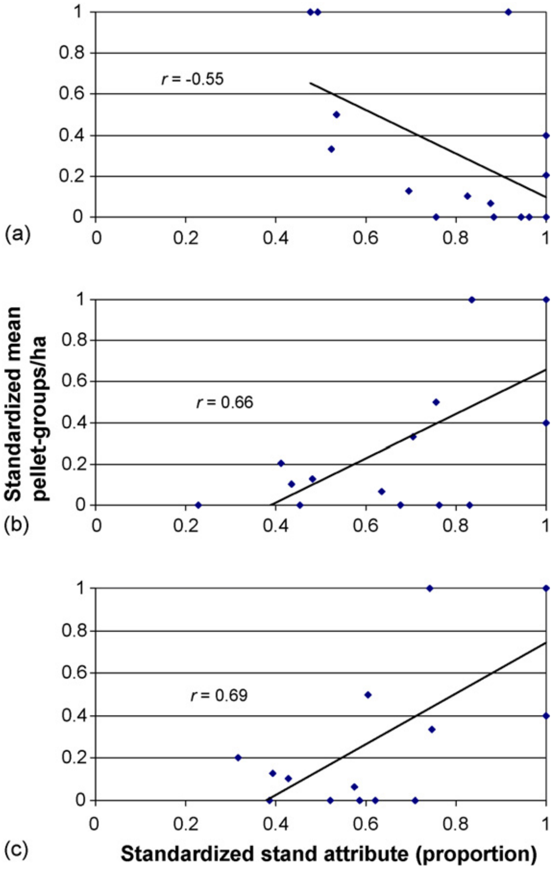

Fig. 2. Linear regression analyses relating mean pellet-groups per ha (standardized to a proportion of the highest density within each block) for mule deer to stand attributes (standardized to a proportion of the highest value within a block): (a) volume of trees, (b) total structural diversity, and (c) canopy openness.

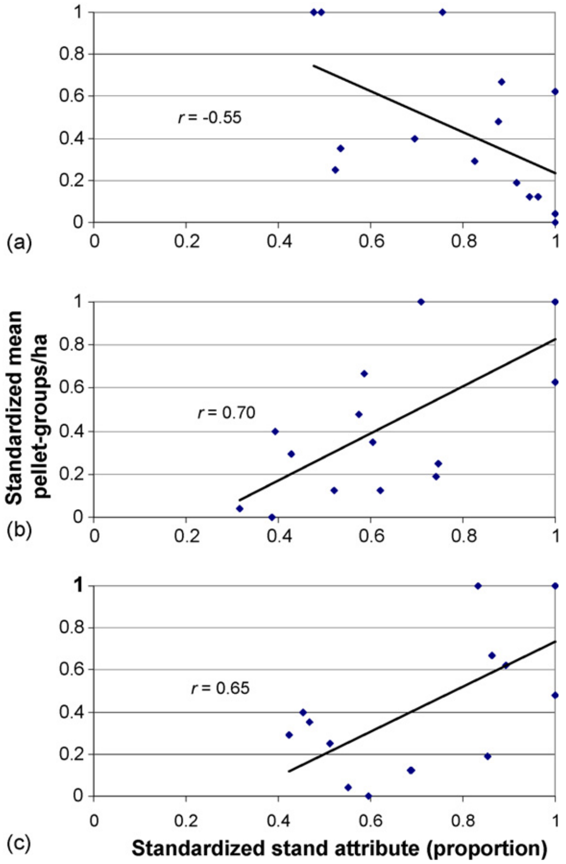

Fig. 3. Linear regression analyses relating mean pellet-groups per ha (standardized to a proportion of the highest density within each block) for moose to stand attributes (standardized to a proportion of the highest value within a block): (a) volume of trees, (b) canopy openness, and (c) horizontal hiding cover.

medium-density stands, while the lowest use occurred in either the unthinned or old-growth stands. In fact, old-growth and unthinned stands in Kamloops and Prince George received little use by deer during this 3-year study. Species diversity and structural diversity of conifers and total vegetation (herbs, shrubs, and trees) were significantly related to pellet-group density of mule deer. However, conifers appeared unimportant for moose where total species diversity and total structural diversity of vegetation were significantly related to density of moose pellet-groups. There was a significant positive relationship between density of deer and moose pellet-groups and volume of shrubs (<2 m), canopy openness, and horizontal hiding cover provided by herbs and shrubs <1.6 m. In contrast, there was a significant negative relationship between density of trees >3 m (deer) and volume of trees (deer and moose). Mule deer and moose appeared to have selected stands with more open canopies and well developed herb and shrub layers, especially below 2 m. This conclusion was further supported by the trend for a greater abundance of pellet groups in low-density stands than in other stands.

Habitat requirements of deer have been studied extensively. Forest canopies seem to reduce convectional energy loss (Bunnell et al., 1986), reduce snow depth (Harestad and Bunnell, 1981) thereby reducing energy expended during locomotion (Parker et al., 1984), and trap long-wave radiation that elevates ambient temperatures in stands in winter relative to more open forest stands. Consequently, it has been suggested that cover characteristics of these mature and old-growth stands provide ideal winter range for ungulates and are critical for their survival. Presumably, old-growth stands, as thermal cover, would minimize energy loss by ungulates in winter while providing snow interception, food, and security cover (Nyberg, 1990; Armleder et al., 1994). Consequently, the key management objective for ungulates has primarily focused on establishment and maintenance of mature and old-growth stands as winter range.

The primary support for the hypothesis that ungulates require thermal cover to survive is derived from observational studies of habitat selection (Peek et al., 1982; Mysterud and Ostbye, 1999). However, only three studies, to date, have examined the energetic benefits of thermal cover on ungulates: Robinson (1960); Gilbert and Bateman (1983), and Cook et al. (1998). These studies concluded that presence of thermal cover, during severe winters, did not significantly enhance survival, reproduction, or body condition of ungulates, the key indicators of a population's health (Cook et al., 1998). However, in years of heavy snow accumulation, ungulates require late-seral forests that provide snow interception and forage (Armleder et al., 1989; Nyberg, 1990). Consequently, establishing and maintaining closed-canopy forests for ungulates may primarily benefit ungulates only during years of heavy snow accumulation. In contrast, effects of quality and quantity of forage on survival, body condition, and reproduction of ungulates have been well established through scientific experiments (Cook et al., 1998). Population size of deer may be limited by spring forage condition, which significantly influences fawn production and survival (Peek et al., 2002). Similarly, energy gained in summer, coupled with energy lost in winter, had the greatest impact on body condition of deer (Parker, 1988). Presumably, enhancing body condition of ungulates prior to winter will significantly enhance their chances of survival during severe winters (Hanley and McKendrick, 1985; Parker, 1988). Peek et al. (2002) concluded that there was a general correlation between deteriorating forage condition and declining deer populations since the 1930s. The deteriorating forage condition (and deer populations) was attributed to increased fire suppression, forest maturation and canopy closure, and succession towards mature forests (Peek et al., 2001, 2002).

Establishment and maintenance of foraging habitat for ungulates has received little attention from wildlife and forest managers. However, enhancing foraging habitat may have a significantly greater impact, on an annual basis, on ungulate populations than only managing for winter range conditions in mature closed-canopy forests. The greatest potential to enhance foraging habitat for ungulates, with minimal impacts to the forest resource, is by thinning young second-growth stands. The inverse relationship between canopy cover and abundance of understory vegetation has been well documented (Thomas et al., 1999; Thysell and Carey, 2000; Lindgren et al., 2006).

The significant positive relationship between pellet-group density and both well-developed understory characteristics and canopy openness in our study indicated that deer and moose primarily selected stands with enhanced abundance and availability of forage. Further support for this inference was the significant negative relationships with tree cover attributes (density and volume), which indicated that deer and moose avoided habitats with dense tree cover, presumably because of the limited forage availability within the shaded understories of these stands. This positive relationship between relative habitat use by deer and moose and forage availability has been well documented (Peek et al., 1976; Crete, 1977; Lyon and Jensen, 1980; Eschholz et al., 1996). Lautenschlager et al. (1999) also demonstrated that quality of forage may be significantly enhanced following release from overstory competition.

In general, conventional PCT within the Pacific Northwest reduces stand densities to approximately 1600 stems per ha. Our results indicated that thinning to lower levels will significantly enhance foraging habitat for ungulates. Enhanced forage opportunities resulting from decreased canopy closure may last more than 20 years compared to stands that are not thinned (Newton et al., 1989). Thus, heavily thinned stands with abundant forage could help reverse the apparent decline in deer numbers noted by Peek et al. (2001, 2002). In addition, high-quality forage on summer range will enhance body condition, and hence annual survival of ungulates during winter (Hanley and McKendrick, 1985; Parker, 1988). Furthermore, heavily thinned stands develop those features associated with old-growth forests faster than unthinned stands (Busing and Garmen, 2002; Lindgren et al., 2006; Sullivan et al., 2006). Thus, PCT stands, in the long-term, will promote habitat for species associated with old-growth forests, including enhanced development of stand attributes that provide winter range for ungulates. However, as noted earlier, the juxtaposition of thinned and unthinned stands needs to be carefully managed, since our inferences are from relatively small units of thinned stands within much larger unmanaged landscapes.

5. Conclusions

Our hypothesis that relative habitat use by snowshoe hares, mule deer, and moose would increase in response to enhanced abundance of herbs and shrubs, and species diversity and structural diversity of conifers, in heavily thinned ($\leq$1000 stems/ha) stands of lodgepole pine, was partly supported. Habitat use by snowshoe hares did not fit this pattern, possibly because the scale at which vegetation attributes were measured may not have been sufficient to distinguish between low- and high-risk foraging sites. Relative habitat use by mule deer and moose appeared to increase in response to the enhanced species diversity and structural diversity of conifers (deer), and overall diversity of vegetation (deer and moose), in heavily thinned ($\leq$1000 stems/ha) stands at 12–15 years post-thinning.

During our investigation, snow accumulation on the study areas was average, or slightly below average, when compared to historic snow-depth data for the regions. Our findings suggest that deer and moose selected stands with enhanced forage abundance rather than stands with thermal or snow-interception cover. Presumably, during periods of average or mild winters, ungulates select foraging habitat rather than thermal or snow-interception cover. However, current management of ungulates primarily emphasizes ungulate winter range (i.e., cover) with little effort to enhancing foraging habitat. Although winter range would be critical to ungulates during periods of heavy snow accumulation, enhancing forage production as a primary management objective would contribute more to maintaining ungulate populations on an annual basis than primarily focusing management on severe winter habitat. Thinning stands to lower densities than currently conducted will enhance foraging habitat for deer and moose, possibly increasing carrying capacity of local habitats.

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