Long-term responses of mammalian herbivores to stand thinning and fertilization in young lodgepole pine (*Pinus contorta* var. *latifolia*) forest

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Abstract: Snowshoe hares (*Lepus americanus* Exrleben, 1777), mule deer (*Odocoileus hemionus* (Rafinesque, 1817)), and moose (*Alces alces* (L., 1758)) commonly occur in young coniferous forests. This study was designed to test the hypothesis that large-scale pre-commercial thinning (PCT) and repeated fertilization 15–20 years after the onset of treatments in young lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Wats.) stands would enhance relative habitat use by hares, deer, and moose compared with unmanaged stands. Study areas were located in south-central British Columbia, Canada. Habitat use was measured by fecal pellet and pellet-group counts. Understory vegetation and coniferous stand structure were measured in all stands. Habitat use by deer and moose was highest in heavily thinned stands, probably due to the higher levels of forage and cover provided by understory shrubs and conifers in thinned stands. Habitat use by snowshoe hares was highest in high-density stands, but also in lower-density (≤1000 stems·ha^{-1}) stands where an increase in understory conifers provided essential cover for hares. Managers should consider the long-term nature of understory development in young stands managed for timber production. Heavy thinning (≤1000 stems·ha^{-1}) will generate suitable understory habitat for these herbivores sooner than conventional PCT at higher stand densities.

Résumé : Le lièvre d'Amérique (*Lepus americanus* Exrleben, 1777), le cerf mulet (*Odocoileus hemionus* (Rafinesque, 1817)) et l'orignal (*Alces alces* (L., 1758)) occupent généralement les jeunes forêts de conifères. Cette étude visait à tester l'hypothèse que l'éclaircie précommerciale (ÉPC) et des fertilisations répétées, 10–15 ans après le début des traitements dans de jeunes peuplements de pin tordu latifolié (*Pinus contorta* var. *latifolia* Engelm. ex S. Wats.), devraient faire augmenter l'utilisation de l'habitat par le lièvre, le cerf et l'orignal comparativement aux peuplements non aménagés. Les aires d'études étaient localisées dans le centre-sud de la Colombie-Britannique, au Canada. L'utilisation de l'habitat a été mesurée par comptage de fèces et de groupes de fèces. La végétation du sous-bois et la structure des peuplements de conifères ont été mesurées dans tous les peuplements. L'utilisation de l'habitat par le cerf et l'orignal était maximale dans les peuplements fortement éclaircis, probablement en réponse à des quantités plus élevées de brout et de couvert fournis par les arbustes de sous-bois et les conifères dans les peuplements éclaircis. L'utilisation de l'habitat par le lièvre était à son plus fort dans les peuplements denses, mais aussi dans les peuplements de faible densité (≤1000 tiges·ha^{-1}) où une augmentation des conifères en sous-bois procurait le couvert essentiel au lièvre. Les aménagistes devraient prendre en compte le développement à long terme du sous-bois dans les jeunes peuplements aménagés pour la production ligneuse. Une éclaircie sévère ramenant la densité du peuplement à ≤1000 tiges·ha^{-1} produira un habitat de sous-bois de qualité pour ces herbivores plus rapidement que l'ÉPC conventionnelle à des densités de peuplement plus élevées.

[Traduit par la Rédaction]

Introduction

There are several silvicultural practices designed to accelerate the growth of timber that also generate a variety of understory vegetative compositions and overstory stand structures in second-growth forests (Homyack et al. 2004). These practices include pre-commercial (PCT) and commercial thinning, fertilization, and conifer release. When combined with a variety of tree species, stand development stages, stand structures, edges, and riparian zones, these practices should help manage second-growth forests for natural levels of biodiversity (Carey et al. 1999; Hunter 1999).

PCT and fertilization have perhaps the greatest potential to enhance forest understory vegetation. PCT contributes to both volume and quality increases in wood fibre on those crop trees selected for superior growth and form during stand thinning (Johnstone 1985), and fertilization, particularly with nitrogen, may enhance this effect (Brockley et al.

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1992). Young lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Wats.) forests cover up to 20 million ha in the Pacific Northwest (PNW) of North America and are amenable to these silvicultural treatments (Koch 1996). In general, both cover and volume of understory vegetation tend to increase in response to stand thinning (Sullivan et al. 2001; Lindgren et al. 2006) and fertilization (Thomas et al. 1999; Sullivan et al. 2006*a*). These silvicultural tools could also be used to accelerate late stand development structural features in young managed stands (Sullivan et al. 2001; Homyack et al. 2004). Such structural attributes would be suitable for wildlife populations inhabiting mature forests.

Snowshoe hares (*Lepus americanus* Exrleben, 1777), mule deer (*Odocoileus hemionus* (Rafinesque, 1817)), and moose (*Alces alces* (L., 1758)) are three mammalian herbivores that commonly occur in temperate and boreal forests, including lodgepole pine stands, throughout inland areas of the PNW (Koch1996; Hodges 2000). The snowshoe hare is considered a keystone species in boreal forests of North America (Boutin et al. 2003) and potentially in the montane western coniferous forests of the PNW (Hodges 2000). Hares have a 9- to 11-year fluctuation in abundance (Keith 1990) and represent the main prey for many vertebrate predators in coniferous forests such as Canada lynx (*Lynx canadensis* Kerr, 1792), coyotes (*Canis latrans* Say, 1823), fisher (*Martes pennanti* (Erxleben, 1777)), and Great-Horned Owls (*Bubo virginianus* (Gmelin, 1788)). Population dynamics of hares in the southern part of their range are poorly known but suggest that hare numbers may cycle at densities less than half of those in northern regions (Keith 1990; Hodges 2000).

In PNW forests, hares are usually most abundant in dense stands of pine (*Pinus* spp.), spruce (*Picea* spp.), or deciduous species, which provide both food and cover (Koehler 1990). Understory cover is the critical factor and a heavy cover provided by shrubs, dense tree stocking, and lateral branches are essential (Pietz and Tester 1983; Litvaitis et al. 1985). These habitat attributes provide cover for predator avoidance but need to be interspersed with early stand development stages that provide forage (Koehler 1990; Hodges 2000). Hares shift from relatively “open” habitats with abundant herbaceous vegetation in summer to dense coniferous stands in autumn (Wolff 1980).

Silvicultural treatments such as PCT have been viewed as negative for snowshoe hares because the reduction in stand density reduces the cover component and hence increases susceptibility to predation and overall habitat use (Koehler 1990; Ausband and Baty 2005; Griffin and Mills 2007). A negative response of hares to decreased cover has also been observed in recently harvested sites (Ferron et al. 1998; de Bellefeuille et al. 2001). However, these were short-term studies (2–3 years after treatment) and hence do not report on hare responses to development of understory vegetation in these managed stands through time. In a 5-year period, 6 to 10 years after the start of PCT and fertilization treatments, fertilized stands of 2000 stems·ha^{-1} provided habitat for hares to a degree comparable with unthinned stands of lodgepole pine (Sullivan et al. 2006*a*).

Mule deer and moose also need understory herbs and shrubs from early stand development to provide forage and thermal and hiding cover (Nyberg 1990). In areas and years of relatively high snowpacks, both ungulates appear to require mature and old-growth forest with high levels of crown closure for snow interception during winter months (Pierce and Peek 1984; Armleder et al. 1994). These old forests often provide the best winter range conditions because of characteristics that intercept snow and supply forage via herbs, shrubs, and arboreal lichen and Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) litterfall (Dawson et al. 1990; Nyberg 1990).

Nyberg (1990) discussed the use of thinning and fertilization to enhance summer and winter ranges of black-tailed deer (*Odocoileus hemionus columbianus* Richardson 1829) in coastal coniferous forests. Several authors reported generally on the positive responses of mule deer and elk (*Cervus canadensis* (Erxleben, 1777)) to thinning of lodgepole pine stands (Crouch 1986; Sullivan et al. 2006*b*, 2007). These ungulates likely responded to the enhanced structural diversity in the understory that provided forage and cover.

There are no studies investigating the long-term (several decades) responses of understory vegetation and relative habitat use by these three mammalian herbivores to a range of post-PCT stand densities and fertilization. Thus, this study was designed to test the hypothesis that large-scale PCT and repeated fertilization, at 15–20 years after the onset of treatments, would enhance relative habitat use by hares, mule deer, and moose in managed stands compared with unmanaged stands. Habitat use was predicted to increase in response to enhanced abundance of herbs and shrubs and abundance, species diversity, and structural diversity of conifers in these managed stands.

Materials and methods

Experimental design

Results are reported from two studies: (*i*) PCT and (*ii*) PCT + fertilization. The PCT study had four naturally regenerated young lodgepole pine stands, representing a wide range of stem densities, and an old-growth pine stand replicated at each of four study areas (n = 4 replicate blocks). The young stands were PCT to target densities of 500 (low), 1000 (medium), and 2000 (high) stems·ha^{-1} and unmanaged stands with densities >3000 stems·ha^{-1} (unthinned). The PCT + fertilization study had four densities: 250 (very low), 500 (low), 1000 (medium), and 2000 (high) stems·ha^{-1} with and without a repeated fertilization treatment at each of two study areas (n = 2 replicate blocks). Typical rotation times for intensively managed stands such as these would be 40–50 years. Unfortunately, the severe epidemic of mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins, 1902) in lodgepole pine stands throughout the central and southern interior of British Columbia (BC), Canada, resulted in the loss of our third replicate block. Treatments were assigned to stands in a randomized complete block design. Each of the four (PCT) and two (PCT + fertilization) study areas was considered a regional replicate (block).

Study areas

The PCT study was located at four replicate study areas in south-central BC: Penticton Creek, Kamloops, Summerland, and Kelowna. Penticton was in the Interior Douglas-fir (IDF_{dk}) biogeoclimatic zone, and the other three areas were in the Montane Spruce (MS_{dm}) biogeoclimatic zone (Meidinger and Pojar 1991). The PCT + fertilization study was located at the Summerland and Kelowna study areas. Characteristics of the stands at each area are listed in Table 1.

Minor components of the stands included Douglas-fir, interior hybrid spruce (*Picea glauca* (Moench) Voss × *Picea engelmannii* Parry ex Engelm.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), ponderosa pine (*Pinus ponderosa* P. & C. Lawson), willows (*Salix* sp.), Sitka alder (*Alnus sinuata* (Regel) Rydb.), and trembling aspen (*Populus tremuloides* Michx.). Dominant ground cover included willow, Sitka alder, grouseberry (*Vaccinium scoparium* Leib. ex Coville), twinflower (*Linnaea borealis* L.), fireweed (*Epilobium angustifolium* ssp. *angustifolium* L.), grasses, and Arctic lupine (*Lupinus arcticus* S. Wats.).

Treatments

At the PCT study areas, thinning using chainsaws was conducted during the fall in 1988 at Penticton, in 1989 at Kamloops, and in 1993 at each of Summerland and Kelowna (for further details, see Sullivan et al. (2001) and Lindgren et al. (2007)). Slash from the PCT was left onsite, which is currently standard practice in BC. However, removal of this biomass for energy production may occur in the foreseeable future.

At the PCT + fertilization study areas, the initial treatment was PCT conducted during the late summer – early fall of 1993. Fertilization treatments were designed as large-scale applications of previously established “optimum nutrition” fertilization field experiments in Sweden (Tamm et al.1999) and BC (Kishchuk et al. 2002; Brockley 2007). Our aim was to maintain elevated foliar nitrogen (N) levels (~1.3%), with levels of all other nutrients in proportional balance with N (Linder 1995).

Fertilization treatments were initiated in November 1994 using a blended fertilizer formulated to provide 100 kg $N{\cdot}ha^{-1}$ (100 N) (urea), 100 kg $phosphorus{\cdot}ha^{-1}$ (100 P), 100 kg $potassium{\cdot}ha^{-1}$ (100 K), 50 kg $sulfur{\cdot}ha^{-1}$ (50 S), 25 kg $magnesium{\cdot}ha^{-1}$ (25 Mg), and 1.5 kg $boron{\cdot}ha^{-1}$ (1.5 B). The blended product (11–25–13–5.5S–2.7Mg–0.17B) was applied by helicopter at a rate of 906 $kg{\cdot}ha^{-1}$ to each of the four fertilized stands at the two study areas. Foliar sampling was conducted in the year after fertilization to monitor the nutrient status of the crop trees and to develop appropriate multinutrient formulations for subsequent fertilizer applications (for details, see Lindgren et al. (2007)).

Findings from foliar analyses were used to develop appropriate blends and application rates for subsequent treatments. In May of 1997, two growing seasons after initial application, stands were refertilized with an N + S blended fertilizer (36–0–0–9S) at an application rate of 547 $kg{\cdot}ha^{-1}$ (200 N and 50 S). In October of 1998, two growing seasons after the second application, stands were refertilized with a blended product (37–0–0–6.1S–0.7B) at an application rate of 404 $kg{\cdot}ha^{-1}$ (150 N, 25 S, and 3 B). During the fall of 2000, two growing seasons after the third application, stands were refertilized with a blended product (31.1–0–0–11.3S) at an application rate of 439.4 $kg{\cdot}ha^{-1}$ (150 N and 50 S). Finally, during the spring of 2003, two growing seasons after the fourth application, stands were refertilized with a blended product (44.6–0–0–0.45B) at an application rate of 336.1 $kg{\cdot}ha^{-1}$ (150 N and 1.5 B).

Coniferous stand structure

Sampling of coniferous tree species was done at 5-year intervals (1993, 1998, 2003, and 2008) after the initiation of respective treatments in 1988 and 1993. Permanent circular plots (5.64 m radius; 100 m^2) at 20 grid points were systematically located at 50 m intervals throughout each managed stand. Ten plots were sampled in each of the unthinned and old-growth stands. All trees in a given plot were tallied by species and height class. Understory (<3 m) and overstory (>3 m) tree layers were each divided into three height classes, resulting in a total of six classes. Understory trees were seedlings (0–1 m), small saplings (1–2 m), or large saplings (2–3 m). Overstory trees were either part of the main canopy (dominant layer), suppressed layer (large sapling or pole-sized trees > 3 m but part of a distinct layer below the main canopy), or veteran trees. These veteran (legacy) or “emergent” trees have survived previous wildfire disturbance (old-growth stands). Within managed stands, crop trees (those trees selected to be retained during PCT) were identified so that the contribution of this cohort to the stand density 15 and 20 years post-PCT could be determined. Immediately following PCT, very few trees other than crop trees occupied these stands. As a result, all noncrop trees sampled likely became established post-PCT, arising from conifer seed from cones in the slash, natural seed bank in the soil, surrounding forest, or small seedlings present during PCT. These non-crop trees were collectively referred to as ingress. All tree sampling was done in the fall of 2008. Coniferous stand structure was represented by species diversity and structural diversity of these layers of coniferous trees. Both diversity measurements utilized the Shannon–Wiener index (Magurran 2004).

Understory vegetation

Understory vascular plants were sampled on three 25 m transects, consisting of five 5 m × 5 m plots 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 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 crown volume index ($m^3{\cdot}0.01\ ha^{-1}$) for each plant species. The product of percentage cover and representative height gives the volume of a cylindroid representing 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 for each species and layer (herbs, shrubs, and trees). Sampling was done in July of 2008. Grasses were not identified to species. Plant species were identified in accordance with Hitchcock and Cronquist (1973) and Parish et al. (1996).

Habitat diversity was measured by species richness and species diversity of all vascular plants. Species richness was

Table 1. Experimental design and characteristics of lodgepole pine (*Pinus contorta*) stands for pre-commercial thinning (PCT) and PCT + fertilization studies.

	Density (stems·ha^{-1})							
	Overstory (>3 m height)			Attributes of dominant tree layer (mean ± SE)				
Study area and stand	Crop trees[a]	All conifers	Understory (<3 m height)	DBH (cm)	Height (m)	Age (years)	Area (ha)	Latitude and longitude
PCT								
Penticton								49°34′N; 119°27′W
Low	485	875	815	19.7±0.3	12.1±0.2	37	20.0	
Medium	1050	1405	415	17.4±0.2	13.5±0.1	37	20.0	
High	1345	1415	285	15.7±0.2	12.8±0.1	37	20.0	
Unthinned	—	5380	770	10.9±0.5	10.2±0.2	37	100+	
Old growth	—	1500	8 310	26.6±1.3	25.3±0.7	140–250	100+	
Kamloops								50°28′N; 120°32′W
Low	385	960	1 935	18.3±4.4	14.1±1.8	47	22.0	
Medium	860	955	835	15.8±2.4	15.1±1.8	47	15.0	
High	1575	1685	380	13.6±1.8	12.9±0.9	47	19.0	
Unthinned	—	4920	80	13.1±0.4	14.0±0.5	47	100+	
Old growth	—	1610	22 930	25.7±1.8	20.7±0.8	140–250	100+	
Summerland								49°40′N; 119°53′W
Low	555	1275	2 065	14.1±0.2	8.1±0.1	28	7.6	
Medium	890	1431	1 555	13.3±0.1	7.9±0.1	28	4.5	
High	1471	1629	1 053	12.5±0.2	8.0±0.1	28	4.4	
Unthinned	—	9000	1 010	11.0±0.9	6.7±0.1	28	5.0	
Old growth	—	1110	700	34.7±3.5	23.1±0.7	140–250	10.0	
Kelowna								50°04′N; 119°34′W
Low	415	930	1 795	16.9±0.3	10.3±0.1	28	11.0	
Medium	1021	1275	988	13.7±0.2	9.9±0.1	28	9.5	
High	1290	1637	1 280	13.4±0.2	10.3±0.1	28	11.9	
Unthinned	—	3365	805	10.1±0.3	8.8±0.1	28	12.6	
Old growth	—	590	180	35.7±2.7	—	140–250	10.0	
PCT + fertilization								
Summerland								49°40′N; 119°53′W
Very low	275	930	545	16.8±0.2	7.6±0.1	28	11.3	
Low	495	1295	485	16.0±0.2	7.7±0.1	28	7.6	
Medium	818	1064	391	16.2±0.3	8.6±0.1	28	4.5	
High	1691	1809	343	14.2±0.9	7.9±0.1	28	4.4	
Kelowna								50°04′N; 119°34′W
Very low	236	679	371	18.6±0.2	9.5±0.1	28	10.0	
Low	560	965	460	19.2±0.3	10.9±0.1	28	11.0	
Medium	950	1294	519	15.6±0.3	10.4±0.1	28	9.5	
High	1610	1705	165	13.4±0.3	9.9±0.1	28	11.9	

[a] Crop trees were those trees selected to be retained during the PCT treatment.

the total number of species sampled for the plant (herbs, shrubs, and trees) communities in each stand (Krebs 1999). Species diversity utilized the Shannon–Wiener index with amount (crown volume index) of vegetation for each plant species.

Mammalian herbivores

Relative habitat use by the three herbivore species was measured by counting and removing all fecal pellets of snowshoe hares (Litvaitis et al. 1985) and fecal pellet-groups of mule deer and moose (Loft and Kie 1988) 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). This plot size and configuration were chosen to accommodate concurrent sampling of fecal pellets and pellet-groups of the three herbivore species. Plots were located systematically in five-plot arrays installed at stations every 50 m throughout each stand at all study areas. Numbers of sample plots per stand ranged from 55 to 145 at Summerland and from 60 to 140 at Kelowna. One-hundred plots were located throughout each stand at the Penticton and Kamloops study areas. Plots were cleared of all counted pellets at the last sampling time in fall of 2003. Pellet counts were conducted again in the spring of 2008. Ungulate pellet-groups had to have a minimum of 20 pellets per group. Groups located on the edge of a sample plot had to have 50% or more of the group within the plot. Individual hare pellets were counted, and those 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. All sample plots at a given study area were assessed by the same observers at each sampling time. 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 5-year period since the fall of 2003 clearing were present. Density of pellets was estimated per 5 m^2 plot and then converted to a per-hectare basis.

Statistical analysis

A randomized-block one- or two-way ANOVA model III (Zar 1999), with stand treatment(s) as a fixed effect(s) and block as a random effect (SPSS Institute Inc. 2007), was used to evaluate differences in mean pellet and pellet-group densities per hectare with respect to the five stand treatments in the PCT study and the four density and two fertilization treatments in the PCT + fertilization study. This same analysis was also used to evaluate differences in abundance, species diversity, and structural diversity of understory vegetation and coniferous tree layers. Where necessary, data were log-transformed to better approximate homogeneity of variance as measured by the Levene statistic (Fowler et al. 1998).

Regression analyses (Zar 1999) were used to explore potential relationships between attributes of overstory and understory trees, relative habitat use (as indicated by abundance of pellets and pellet-groups), and several vegetation parameters. These attributes included measures of crown volume index of herbs and shrubs, total species richness, total species diversity, density of trees, and coniferous stand structure. Regression analyses were performed for the managed stands only (i.e., did not include the unthinned or old-growth stands from the PCT study). In addition, relationships were explored within stands grouped by time since PCT (i.e., 15 or 20 years post-PCT) and whether or not the stands had received fertilization treatments.

Simple linear, logarithmic, quadratic, power, and exponential relationships were explored for all datasets (Fowler et al. 1998). Duncan's multiple range test (DMRT) was used to compare mean values (Saville 1990). In all analyses, the level of significance was at least $P = 0.05$.

Results

Relative habitat use — PCT

Relative habitat use by snowshoe hares, based on mean abundance of pellets, was significantly ($F_{[4,12]} = 4.78$, $P = 0.02$) different among stands when comparing the low, medium, high, unthinned, and old-growth stands (Fig. 1*a*). Mean number of pellets was higher (DMRT; $P = 0.05$) in the four young stands of lodgepole pine than in the old-growth stands. Mean abundance of fecal pellet-groups of mule deer ($F_{[4,12]} = 1.60$, $P = 0.24$) and moose ($F_{[4,12]} = 2.34$, $P = 0.11$) were similar among stands (Figs. 1*b* and 1*c*).

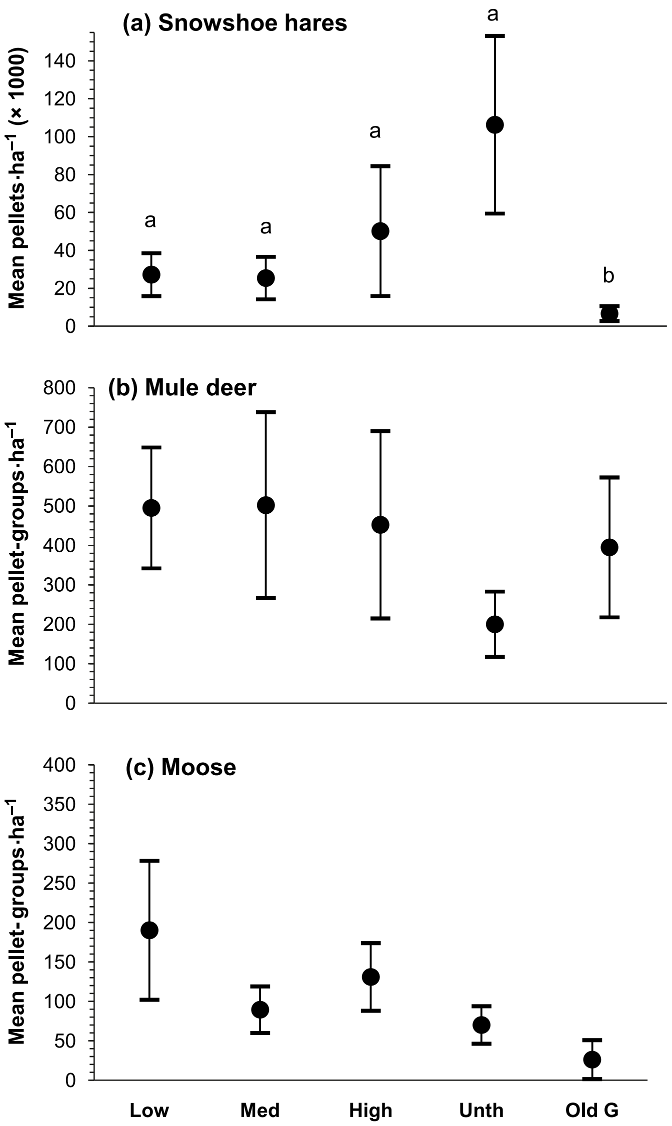
Relative habitat use — PCT + fertilization

Mean abundance of hare pellets was similar among stands with respect to density ($F_{[3,3]} = 2.79$, $P = 0.21$) and fertilization ($F_{[1,1]} = 0.03$, $P = 0.89$). Mule deer also followed this pattern for density ($F_{[3,3]} = 3.11$, $P = 0.19$) and fertilization ($F_{[1,1]} = 0.03$, $P = 0.90$), as did moose for density ($F_{[3,3]} = 2.07$, $P = 0.28$) and fertilization ($F_{[1,1]} = 6.93$, $P = 0.23$). There were no significant interactions between density and fertilization in these analyses.

Herbivores and stand structure

In the PCT study, mean crown volume index of herbs was similar ($F_{[4,12]} = 0.59$, $P = 0.68$) among the three thinning densities, unthinned, and old-growth stands (Table 2). Mean shrub volume also followed this pattern ($F_{[4,12]} = 2.90$, $P = 0.07$). However, it may be biologically significant that shrub volume in the low-density stands ranged from 1.9 to 4.2 times higher than volumes of shrubs in the other young pine stands (Table 2). Mean density of overstory trees was significantly ($F_{[4,12]} = 14.00$, $P < 0.01$) different among stands, with the unthinned stands having the highest (DMRT; $P = 0.05$) density of conifers at 5666 stems·ha^{-1} (Table 2). Mean density of understory trees was similar ($F_{[4,12]} = 1.70$, $P = 0.22$) among stands, with high variability in number of understory conifers in the old-growth stands (Table 2). Mean species diversity of conifers was similar among stands ($F_{[4,12]} = 2.22$, $P = 0.13$). Mean structural diversity was significantly ($F_{[4,12]} = 29.09$, $P < 0.01$) different, with the three thinned stands having greater (DMRT; $P = 0.05$) levels of diversity than the old-growth stands, and the low-density stands having a greater level of diversity than the unthinned stands (Table 2). Mean total species richness

Fig. 1. Mean number (± SE; $n = 4$ replicate sites) of (*a*) snowshoe hare (*Lepus americanus*) pellets, (*b*) mule deer (*Odocoileus hemionus*) pellet-groups, and (*c*) moose (*Alces alces*) pellet-groups in the five treatment stands. Low, low density (range, 500 stems·ha^{-1}); Med, medium density (range, 1000 stems·ha^{-1}); High, high density (range, 2000 stems·ha^{-1}); Unth, unthinned (range, >3000 stems·ha^{-1}); Old G, old-growth (range, 590–1610 stems·ha^{-1}). Mean values with different letters were significantly different by DMRT ($P = 0.05$).



and species diversity of all vascular plants were similar among stands.

In the PCT + fertilization study, there were no significant differences among stands with respect to density for any of the herbivores. Thus, these stands were pooled to compare fertilized with unfertilized stands at $n = 8$. Mean crown volume index values of herbs and shrubs were similar between fertilized and unfertilized stands (Table 3). Again, mean total species richness and species diversity of all vascular plants and mean structural diversity of conifers were similar between stands (Table 3). Mean species diversity of conifers was significantly ($F_{[1,1]} = 606.95$, $P = 0.03$) greater in the fertilized (1.36) than unfertilized (1.02) stands.

Regression analyses

Among managed stands, mean density of conifers that had developed below the crop tree layer (i.e., ingress density) was inversely and exponentially related ($R^2 = 0.43$, $P < 0.01$) to crop tree density (i.e., thinning density) at least up to 1700 stems·ha^{-1} (Fig. 2*a*). This inverse relationship was even stronger among stands grouped by treatment history ($R^2 = 0.71$, $P = 0.04$, for stands 20 years post-PCT and $R^2 = 0.67$, $P = 0.01$, for stands 15 years post-PCT with fertilization treatments). This understory layer of coniferous foliage likely contributed to the significant quadratic relationship ($R^2 = 0.36$, $P = 0.01$) between hare habitat use and thinning density of conifers from about 250 to 1700 stems·ha^{-1} (Fig. 2*b*). There were no other relationships between relative habitat use of hares and stand structure variables.

As for snowshoe hares, a significant quadratic relationship was observed between thinning density and habitat use by both moose ($R^2 = 0.30$, $P = 0.03$; Fig. 3*a*) and mule deer ($R^2 = 0.34$, $P = 0.02$; Fig. 4). A significant quadratic relationship ($R^2 = 0.52$, $P < 0.01$) was also observed among these thinned stands between shrub abundance and habitat use by moose (Fig. 3*b*). This correlation between shrub abundance and moose was increased when considering stands 20 years post-PCT ($R^2 = 0.95$, $P = 0.01$) and stands 15 years post-PCT with fertilization ($R^2 = 0.96$, $P < 0.01$) separately (Fig. 3*c*). Significant positive relationships were also observed between plant species diversity and moose within stands 15 years post-PCT, both unfertilized ($R^2 = 0.73$, $P = 0.01$) and fertilized ($R^2 = 0.52$, $P = 0.04$) (Fig. 3*d*).

Discussion

Snowshoe hares

The responses of snowshoe hares to PCT at 15–20 years after treatment followed a pattern similar to that recorded at earlier stages of stand development in these same stands (Sullivan et al. 2006*a*, 2007). Hares clearly preferred high-density thinned (>1500 stems·ha^{-1}) and unthinned (>2600 stems·ha^{-1}) stands of pine. Such dense stands provided sufficient cover of coniferous trees, and in the lower-density stands, this cover was provided by the lateral branches of the abundant understory conifer layers (advance regeneration) (Litvaitis et al. 1985; Koehler 1990). The increase in relative habitat use by hares in the lower-density stands was 1.90 times higher than that reported by Sullivan et al. (2006*a*) at 10 years after the onset of treatments. It could be argued that our current (2008) pellet counts represented a multiyear (2004–2008) count that was significantly more than the annual counts from a 5-year period reported by Sullivan et al. (2006*a*). However, only those pellets on the surface of the forest floor were counted in 2008 and were likely deposited in the last year or two.

The important point is that thinned stands change through time, particularly those at lower (<2000 stems·ha^{-1}) densities, often with substantial development of the coniferous understory. This aspect of succession seems to be overlooked by most studies that were relatively short-term, investigated recent PCT treatments, and concluded that PCT was detrimental to snowshoe hare populations (Koehler 1990; Ausband and Baty 2005; Bull et al. 2005; Griffin and

Table 2. Crown volume index (mean ± SE, n = 4 replicate stands) of herbs and shrubs, tree density, and diversity measurements for the five stand treatments in the pre-commercial thinning (PCT) study.

						Significance	
Habitat attributes	Low	Medium	High	Unthinned	Old growth	$F_{[4,12]}$	P
Volume ($m^3·0.01\ ha^{-1}$)							
Total herbs	8.05±0.30	10.13±1.82	7.79±0.30	8.15±3.37	7.74±2.94	0.59	0.68
Total shrubs	28.61±7.21	12.36±5.55	6.84±3.01	14.86±8.11	7.16±2.45	2.90	0.07
Density of trees (no. of stems·ha^{-1})							
Overstory (>3 m height)	1010±90b	1267±109b	1592±60b	5666±1192a	1203±231b	14.00	<0.01
Understory(<3 m height)	1653±285	948±236	750±246	666±202	8030±5303	1.70	0.22
Diversity							
Conifer species diversity	1.10±0.29	1.45±0.19	1.21±0.08	1.41±0.19	0.52±0.33	2.22	0.13
Conifer structural diversity	1.94±0.01a	1.80±0.08ab	1.75±0.07ab	1.58±0.10b	0.89±0.19c	29.09	<0.01
Total species richness	20.67±2.73	18.00±1.48	17.25±3.07	17.92±2.04	16.09±2.14	1.01	0.44
Total species diversity	1.41±0.26	1.14±0.14	0.67±0.19	1.00±0.28	1.20±0.18	2.13	0.14

Note: Columns of mean values with different letters were significantly different by DMRT.

Table 3. Crown volume index (mean ± SE, n = 8 replicate stands) of herbs and shrubs and diversity measurements for fertilized and unfertilized stands in the fertilization study.

			Significance	
Habitat attributes	Fertilized	Not fertilized	$F_{[1,1]}$	P
Volume ($m^3·0.01\ ha^{-1}$)				
Total herbs	12.32±2.57	8.51±1.13	0.41	0.64
Total shrubs	13.78±3.45	15.62±4.32	0.06	0.85
Diversity				
Total species richness	15.96±0.83	18.04±0.94	3.71	0.31
Total species diversity	1.43±0.19	1.29±0.19	25.88	0.12
Conifer species diversity	1.36±0.10	1.02±0.18	606.95	0.03
Conifer structural diversity	1.72±0.06	1.88±0.03	4.00	0.30

Mills 2007). Alternatively, maintaining understory complexity (cover), particularly of conifers, may mitigate the negative effects of PCT on hares, partially by reducing predation pressure during winter seasons when deciduous shrubs provide little or no cover (Beaudoin et al. 2004; Etcheverry et al. 2005; Homyack et al. 2007). Herb and shrub vegetation may also respond to PCT, but this seemed to have little effect on relative habitat use by hares in our study or those earlier investigations (Sullivan et al. 2006*a*, 2007).

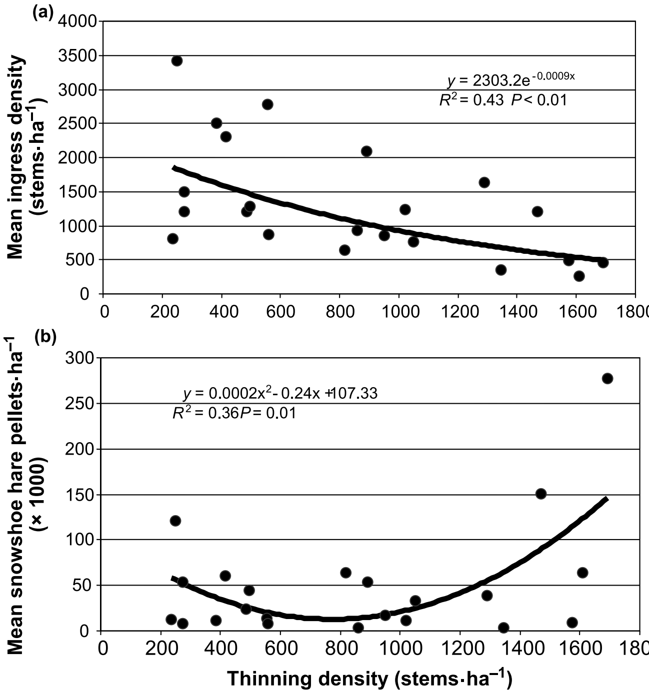
Several studies have recommended PCT with reserves of unthinned patches within target stands to provide some natural variation of young stand structure (Ausband and Baty 2005; Bull et al. 2005; Griffin and Mills 2007). This approach presumably includes hiding cover from predators in retention patches that would be high-density stands or thickets of conifers. Our data support this premise in terms of a positive relationship of hare habitat use with conifer density. However, in some situations, reserves of unthinned stands or a reduction in spacing distances between crop trees (e.g., high-density stands) might compromise silvicultural objectives and cost efficiencies of PCT treatments. Therefore, alternative prescriptions of a range of stand densities (particularly to ≤1000 stems·ha^{-1}) with fertilization could help offset the reduced abundance of hares associated with PCT.

Mule deer and moose

The highest relative habitat use by mule deer was in the very low density (250 stems·ha^{-1}) stands with comparable mean pellet-group counts across the low-, medium-, and high-density stands. The lack of formal significant differences among stand densities for deer habitat use was also reported by Sullivan et al. (2006*b*, 2007). However, the comparable mean abundance of deer pellet-groups in thinned (15–20 years post-PCT) young stands and old-growth stands indicated that these managed forests may be moving towards winter range conditions suitable for mule deer (Armleder et al. 1994). Although fertilization enhanced relative habitat use by deer in summer (but not winter) months at 10 years after initiation of treatments (Sullivan et al. 2006*b*), such results were not evident in our current measurement of these same stands. It was possible that the fertilization effect may have waned in these stands as the last fertilizer application was in the spring of 2003. The lack of positive responses by the understory vegetation in fertilized stands in 2008 may have resulted in less use of these stands by deer than recorded earlier (Sullivan et al. 2006*b*).

The significant quadratic relationship between thinning level and both deer and moose indicated that lower-density stands were preferred by these ungulates, at least 15 and

Fig. 2. Relationship between PCT density and (*a*) understory conifer development (ingress; stems·ha^{-1}) and (*b*) relative habitat use by snowshoe hares (*Lepus americanus*; number of pellets·ha^{-1}) 15 and 20 years after pre-commercial thinning (PCT).



20 years post-PCT. Lower thinning densities were likely attractive as these stands provided important security cover in the form of abundant ingress of understory conifers, while also providing enhanced forage opportunities from an abundant shrub layer. Higher density stands were likely attractive for the cover provided by the dense canopy of pine. At 15 and 20 years post-PCT, moderate thinning densities (~1200 stems·ha^{-1}) may have been less attractive for deer and moose as such densities were too high to allow for an abundant understory of shrubs and conifers (forage and security cover) and too low to provide sufficient overstory cover. Although heavily thinned stands appeared to have increased use by both deer and moose relative to lightly thinned stands, Doerr and Sandburg (1986) predicted that their observation of greater habitat use of thinned than unthinned stands by black-tailed deer, at 18 years after PCT, was only temporary as understory conifers were released and displaced the forage plants in thinned stands. Though we concur with this prediction, we also suggest that heavier thinnings (e.g., densities < 500 stems·ha^{-1}) might maintain favourable forage and cover conditions for ungulates for many more years compared with conventional thinnings to densities greater than 1000 stems·ha^{-1}.

Although deer may be attracted to heavily thinned stands, in part, for the abundant forage provided within these stands, no significant relationship between deer and either herbs or shrubs was observed. Relative habitat use by moose, on the other hand, was highly and positively correlated with shrub abundance, particularly within fertilized stands, indicating that abundance of shrubs likely reflected a vegetation response detected by moose, but perhaps was less important to deer. Moose preference for fertilized and relatively open

Fig. 3. Relationship between relative habitat use by moose (*Alces alces*; pellet-groups·ha^{-1}) and (*a*) pre-commercial thinning (PCT) density and (*b*) shrub abundance 15 and 20 years post-PCT, (*c*) shrub abundance 20 years post-PCT and 15 years post-PCT with fertilizer, and (*d*) total plant species diversity 15 years post-PCT with and without fertilizer.

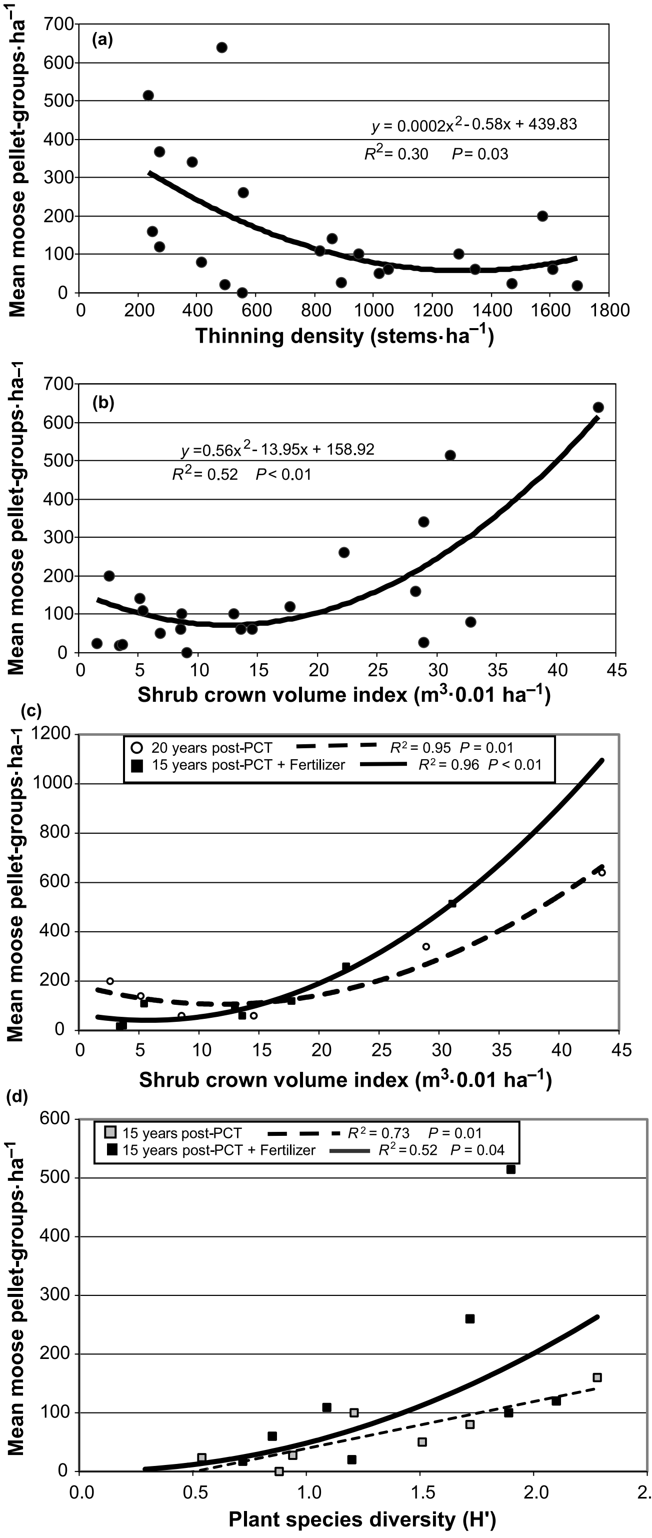
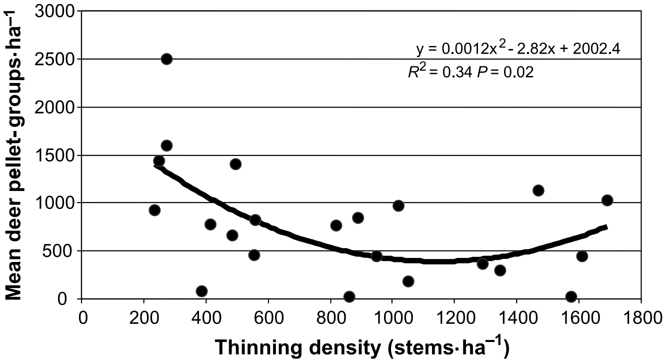


Fig. 4. Relationship between pre-commercial thinning (PCT) density and relative habitat use by mule deer (*Odocoileus hemionus*; pellet-groups·ha^{-1}).



stands was similar for forestry–moose interactions in Scandinavia (Lavsund 1987; Ball et al. 2000). Moose often browse both conifers and deciduous trees in fertilized plantations, creating a difficult regeneration problem in forests of northern Europe (Edenius 1993; Ball et al. 2000). Moose will also select for cover provided by very dense stands with little shrub production (Peek et al. 1976), and this likely explained the slight increase in moose pellets-groups observed within stands with very low abundance of shrubs.

Moose diets include a wide variety of plants, particularly deciduous woody species, that change depending on seasonal requirements, as well as the availability, phenology, nutrient status, and palatability of the forage species (Peek et al. 1976; Lautenschlager et al. 1997). Habitats with a diverse assortment of forage species may, therefore, be attractive to moose and may explain the positive relationship observed between total plant species diversity and moose.

Experimental and sampling design

Our study is the first long-term (15 and 20 years since the initiation of PCT and fertilization) evaluation of the responses of these three mammalian herbivores to silvicultural treatments of second-growth lodgepole pine forests. To augment the 20-year response dataset on PCT, which was deficient because of loss of stands to MPB attack, we added the same stand treatments (low-, medium-, and high-density, unthinned, and old-growth) from the 15-year study area for a total of four replicate sites (Hurlbert 1984). The investigation of mammal responses to fertilization had two replicate sites at 15 years after the start of treatments. As discussed by Lindgren et al. (2007), the scope of our inferences may be extrapolated to lodgepole pine stands and habitats throughout the southern interior of BC. These inferences were responses of relative habitat use of snowshoe hares, deer, and moose to silvicultural practices of PCT and fertilization at 15–20 years after the onset of treatments.

Our sampling design represented a cumulative total of fecal pellets and pellet-groups that were counted and removed from permanent plots. Initially, in the 1998–2003 period, we counted and removed all pellets and pellet-groups from each plot in spring and autumn of each year. Thus, we had an annual and seasonal distribution of pellets and pellet-groups among stands. In the current study, we sampled all plots once in May 2008, with the sample representing the 5-year period 2003–2008. However, as we counted only those fecal pellets on the surface of the forest floor, it was very likely that the majority of pellets and pellet-groups had been deposited in the last year or two. Hodges and Mills (2008) 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 and configuration to sample concurrently for habitat use by the three mammalian herbivores. Thus, we used 5 m^2 circles, which were large for hares but adequate for deer and moose. Our study was a multistand sampling regime (30 stands in four geographic locations) with the number of sample plots ranging from 55 to 145 per stand, depending on area of the 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. A discussion of the limitations of fecal pellet group counts for deer and moose with respect to relative deposition of pellet-groups and importance of a given microhabitat or part of a stand, changes in defecation rates with forage quality and season, and timing of deposition of pellet-groups, particularly during winter, was provided by Sullivan et al. (2006*b*).

Management implications

Our hypothesis that large-scale PCT and repeated fertilization at 15–20 years after the onset of treatments would enhance relative habitat use by hares, mule deer, and moose in managed compared with unmanaged stands was partly supported. Relative habitat use by snowshoe hares was indeed highest in the unthinned and high density (1290 to 1580 stems·ha^{-1}) stands. However, the substantial increase in understory conifers in lower-density ($\leq$1000 stems·ha^{-1}) stands, both fertilized and unfertilized, provided essential cover for hares. This change in stand structure presumably increased hare habitat use at 15–20 years compared with 10 years since the onset of PCT and fertilization treatments. Within managed stands, habitat use by deer and moose was highest in heavily thinned stands, presumably for the forage and security cover provided by the abundant understory of shrubs and conifers, respectively.

Thus, both forest and wildlife managers should consider the long-term nature of understory development in young stands managed for timber production. In particular, heavy thinning ($\leq$1000 stems·ha^{-1}) will yield larger-diameter trees and vegetative understories suitable for use by these three herbivores. For snowshoe hares, ingress of understory conifers and shrubs may take up to 15–20 years or longer to create suitable habitat for this species. Results from short-term (<5 years after PCT) investigations of habitat use by hares should be interpreted accordingly, as these results may change dramatically with vegetative succession.

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