Precommercial Thinning Reduces Snowshoe Hare Abundance in the Short Term

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ABSTRACT Management of young forests is not often considered in conservation plans, but young forests provide habitat for some species of conservation concern. Snowshoe hares (Lepus americanus), critical prey of forest carnivores including the United States federally threatened Canada lynx (Lynx canadensis), can be abundant in young montane and subalpine forests with densely spaced saplings and shrub cover. Precommercial thinning (PCT) is a silvicultural technique that reduces sapling and shrub density on young forest stands. We tested for effects of PCT on snowshoe hare abundance for 2 years after experimental treatment at 3 replicate study areas. We also tested the effectiveness of a precommercial thinning with reserves (PCT-R) prescription, where 20% of the total stand was retained in uncut quarter-hectare patches. All stands were in montane–subalpine coniferous forests of western Montana, USA, where there is a persistent population of Canada lynx. Posttreatment changes in abundance were strongly negative on stands treated with standard PCT prescriptions (100% of the stand was treated), relative to both controls and stands treated with PCT-R. Trapping, snowtrack, and winter fecal-pellet indices indicated that snowshoe hares used the quarter-ha retention patches more than thinned portions of the PCT-R-treated stands in winter. We suggest that managing forest landscapes for high snowshoe hare abundance will require adoption of silvicultural techniques like PCT-R for stands that will be thinned, in addition to conservation of structurally valuable early and late-successional forest stands. (JOURNAL OF WILDLIFE MANAGEMENT 71(2):559–564, 2007)

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Young forest stands provide valuable, if transient, habitat for many species (Hejl et al. 1995, Askins 2001, Hunter et al. 2001, Litvaitis 2001), but high sapling densities can decrease future timber yields (Marzluff et al. 2002). Therefore, young stands are often converted to more open forest by precommercial thinning (PCT). Silvicultural goals of PCT include increased tree growth rates (Daniel et al. 1979, Johnstone 1985, Homayak et al. 2005), increased frequency of favored tree species (Carey and Johnson 1995), decreased fire risk (U.S. Forest Service and U.S. Bureau of Land Management 2004), and decreased time to develop old-growth characteristics (DeBell et al. 1997, Tappeiner et al. 1997).

Snowshoe hares (Lepus americanus) are critically important prey for federally Threatened Canada lynx (Lynx canadensis; U.S. Fish and Wildlife Service 1999), especially in winter (Squires and Ruggiero 2007), when a lynx may eat between 0.8–1.6 hares per day (Mowat et al. 2000). Snowshoe hares are typically most abundant where sapling and shrub thickets provide forage and cover (e.g., Dolbeer and Clark 1975, Wolfe et al. 1982, Koehler and Brittell 1990, Hodges 2000); this can include late-seral stands (Beauvais 2000, Buskirk et al. 2000, Griffin and Mills 2004), especially in winter (P. C. Griffin and L. S. Mills, University of Montana, unpublished data). At the scale of the larger forest ecosystem, snowshoe hare populations require a constant availability of forests with dense understory cover. Stands with high sapling density may also be net sources of emigrant snowshoe hares that supplement nearby open habitats (Wolff 1980, Wolff 1981, Griffin 2003). If PCT dramatically decreases snowshoe hare abundance in such stands, the Canada lynx could be seriously impacted. Alternatively, the increased availability of herbaceous forage may favor snowshoe hare survival and increase hare density after thinning (Adams 1959, Black 1965, Sullivan and Sullivan 1988).

The assumption that PCT reduces snowshoe hare abundance (U.S. Forest Service and U.S. Bureau of Land Management 2004) has not been tested with a replicated, controlled experiment and direct measures before and after treatment. In a retrospective study, Etcheverry et al. (2005) found no strong evidence of lowered snowshoe hare abundance in PCT stands. Ausband and Baty (2005) also found, based on index counts, no clear evidence of changes in use of habitat by snowshoe hare after PCT.

We used mark–recapture trapping to test the prediction that treatment with PCT would decrease snowshoe hare abundance in thinned stands relative to paired, untreated control stands. Changes in control stands should reflect seasonal and annual changes that are independent of any thinning effect. Evidence of a PCT treatment effect would be consistently negative changes in abundance on treated stands at all study areas, beyond any changes observed at control stands. We also tested whether a novel PCT treatment that left isolated patch reserves of unthinned forest (PCT-R) would lead to changes in snowshoe hare abundance that were intermediate between PCT-treated and control stands.

STUDY AREA

There were 3 replicate study areas in montane–subalpine coniferous forests of western Montana, USA. The Cold Creek (T21N, R17W, Section 30) and Beaver-Finley

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(T16N, R16W, Section 33) study areas were in the Mission Mountains. Spring Creek (T16N, R14W, Sections 22 and 23) study area was in the Swan Mountains. At these sites' elevations (1,450–1,700 m), lodgepole pine (Pinus contorta), Douglas-fir (Pseudotsuga menziesii), western larch (Larix occidentalis), subalpine fir (Abies lasiocarpa), and Engelmann spruce (Picea engelmannii) dominated. Lodgepole pine and Douglas-fir provide relatively high-quality winter forage for hares (Wirsing and Murray 2002). Various montane and subalpine shrubs and forbs provided some cover and forage in summer and autumn.

subalpine shrubs and forbs provided some cover and forage. Various montane and Douglas-fir provide relatively high-quality winter forage for spruce (P. C. Griffin and L. S. Mills, unpublished data).

We evaluated changes in the response variable, estimated hare abundance, N, in single stands. Stands were ≥30 ha; this size is typical in the relatively heterogeneous stand structures of western Montana (Mills et al. 2005). In 5-day trapping sessions in the region we have caught 0–22 individuals in comparably sized young stands, and 0–28 individuals in comparably sized old-growth stands (P. C. Griffin and L. S. Mills, unpublished data).

Within each stand we marked 5 parallel trap lines 50 m apart, each with 10 traps spaced at 50-m intervals; these formed a 50-trap, rectangular, 9-ha grid. Trapping grids were ≥50 m from stand edges. Assuming a 100-m fixed-width boundary strip (Keith 1990), each trapping grid effectively trapped approximately 25 ha. Before and after treatments, we sampled sapling density at ≥5 6.5-m-radius plots per stand (Table 1).

We used mark–recapture trapping to estimate pretreatment N. This was in July 1999 at Spring Creek and July 2000 at Cold Creek and Beaver-Finley; PCT treatment followed within one month, in August. For 2 years after treatment we estimated N with one trapping session at the end of each summer and 2 trapping sessions each winter. Sessions were 4–6 consecutive nights (x̄ = 5.5 nights). We trapped all 3 stands at a study area simultaneously. We baited traps with weed-free alfalfa, pelleted horse feed, and apple, and checked them every morning. We marked hares uniquely with numbered tags in each ear, weighed, sexed, and released them. Because the number of recaptures was too small to distinguish reliably between alternative closed population models in a framework such as CAPTURE (White et al. 1982) or MARK (White and Burnham 1999), we used the Lincoln–Petersen estimator adjusted for small sample size (Chapman 1951, Seber 1982) or MARK (White and Burnham 1999), we used the Lincoln–Petersen estimator adjusted for small sample size (Chapman 1951, Seber 1982) to estimate N (Menkens and Anderson 1988, McKelvey and Pearson 2001). We pooled captures from the first 3 days of the trapping session to form the initial sample period; the latter

Table 1. Abundance of snowshoe hares (no. of individuals) before any precommercial thinning treatment at 3 study areas in western Montana, USA, July 1999 (Spring Creek study area) and July 2000 (Cold Creek and Beaver-Finley study areas), and sapling density (saplings/ha) of coniferous trees on control stands before and after treatment with standard precommercial thinning (PCT) or precommercial thinning with reserves (PCT-R).

<table>
<thead>
<tr>
<th>Area</th>
<th>Treatment</th>
<th>Hares before treatment</th>
<th>Sapling density before treatment</th>
<th>Sapling density after treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>SDb</td>
<td>2b</td>
<td>4b</td>
</tr>
<tr>
<td>Spring Creek</td>
<td>Control</td>
<td>13.5</td>
<td>6.75</td>
<td>9,135</td>
</tr>
<tr>
<td></td>
<td>PCT</td>
<td>8.0</td>
<td>1.8</td>
<td>6,665</td>
</tr>
<tr>
<td></td>
<td>PCT-R</td>
<td>5.0</td>
<td>0.0</td>
<td>2,554</td>
</tr>
<tr>
<td>Cold Creek</td>
<td>Control</td>
<td>8.8</td>
<td>1.3</td>
<td>2,757</td>
</tr>
<tr>
<td></td>
<td>PCT</td>
<td>0.0</td>
<td>0.0</td>
<td>2,977</td>
</tr>
<tr>
<td></td>
<td>PCT-R</td>
<td>3.0</td>
<td>2.0</td>
<td>5,295</td>
</tr>
<tr>
<td>Beaver-Finley</td>
<td>Control</td>
<td>5.7</td>
<td>1.1</td>
<td>3,011</td>
</tr>
<tr>
<td></td>
<td>PCT</td>
<td>12.2</td>
<td>2.6</td>
<td>2,723</td>
</tr>
<tr>
<td></td>
<td>PCT-R</td>
<td>7.4</td>
<td>0.6</td>
<td>3,163</td>
</tr>
</tbody>
</table>

a Standard PCT treatment thinned 100% of stand area, while PCT-R treatment left 20% of the stand area unthinned in randomly distributed quarter-hectare patches.

SD of abundance and SE of sapling density are to the right of means.
Table 2. Relative score of Akaike’s Information Criterion corrected for small sample size (AICc), Akaike weight, and number of parameters for 9 repeated-measures mixed models of changes in snowshoe hare abundance after no treatment (control), treatment with standard precommercial thinning (PCT), or treatment with precommercial thinning with reserves (PCT-R). Each of 3 study areas in western Montana, USA, had 3 stands (control, PCT, and PCT-R) where snowshoe hare abundance was estimated once before treatment and 6 times after treatment. All trapping occurred during 1999–2002. Models are uniquely lettered. Models with fixed factors for treatment had separate parameters for each treatment or had control and PCT-R treatments grouped. Models with fixed factors for season had separate parameters for summer, first winter, and second winter, or they had both winters grouped.

<table>
<thead>
<tr>
<th>Model and description</th>
<th>ΔAICc</th>
<th>AICc wt</th>
<th>No. of parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>D. 3 treatments, 3 seasons</td>
<td>0.0</td>
<td>0.67</td>
<td>11</td>
</tr>
<tr>
<td>G. Control + PCT-R, 3 seasons</td>
<td>3.0</td>
<td>0.15</td>
<td>10</td>
</tr>
<tr>
<td>C. 3 treatments, 2 seasons</td>
<td>3.5</td>
<td>0.11</td>
<td>10</td>
</tr>
<tr>
<td>B. 3 treatments, no seasons</td>
<td>5.9</td>
<td>0.035</td>
<td>9</td>
</tr>
<tr>
<td>F. Control + PCT-R, 2 seasons</td>
<td>6.6</td>
<td>0.025</td>
<td>9</td>
</tr>
<tr>
<td>E. Control + PCT-R, no seasons</td>
<td>9.5</td>
<td>0.006</td>
<td>8</td>
</tr>
<tr>
<td>I. No treatment effect, 3 seasons</td>
<td>11.5</td>
<td>0.002</td>
<td>9</td>
</tr>
<tr>
<td>H. No treatment effect, 2 seasons</td>
<td>14.6</td>
<td>0.0004</td>
<td>8</td>
</tr>
<tr>
<td>A. No treatment effect, no seasons</td>
<td>17.7</td>
<td>0.0001</td>
<td>7</td>
</tr>
</tbody>
</table>

trap-nights formed the second sample period. Abundance estimates for each stand appeared independent; very few snowshoe hares (5 of 290) were captured at >1 stand in a session.

For all posttreatment trapping sessions, ΔN in a stand was the change in individual hares, relative to pretreatment N. Positive ΔN values reflected increases; negative ΔN values reflected decreases. Each study stand had 6 post–treatment ΔN estimates. We assumed that changes in snowshoe hare abundance on control stands represented the natural temporal variation at each study area.

To estimate treatment effects, we compared the model parsimony of 9 biologically motivated candidate models for ΔN; these were univariate analysis of variance mixed models with repeated measures. Of 9 candidate models for ΔN (Table 2), the simplest included no effect of treatment type or season (model A). We made 3 models (models B, C, and D) with separate parameter estimation for each treatment type (control, PCT, PCT-R). Based on the possibility that snowshoe hare habitat quality on PCT-R-treated stands was comparable to control stands, we made 3 other models (models E, F, and G) that grouped control and PCT-R treatment types together, in contrast to the PCT treatment type. Three models had no effect of season (models A, B, and E). Three models with effects of 2 seasons pooled all winter estimates in contrast to summers (models C, F, and H). Three other models differentiated 3 seasons: first winter, second winter, and summers (models D, G, and I).

Using estimates from the highest-ranked model, we considered marginal mean differences of ΔN to be the treatment effect sizes. Model parsimony rank was based on Akaike’s Information Criterion modified for small sample size (AICc; Hurvich and Tsai 1989, Burnham and Anderson 2002). Models with lowest AICc, scores are considered to have the most parsimonious fit to the data and they have the highest Akaike weights; other models within 2 AIC, units may be equally parsimonious (Burnham and Anderson 2002).

Within PCT-R-treated stands only, we tested for associations between snowshoe hares and retention patches, based on 3 relative use indices (the no. of individuals caught/100 trap-nights, snowtrack counts, and winter fecal-pellet counts). Unlike mark–capture estimators that have associated estimates of precision, these indices have generally positive but unknown relationships to true abundance (Nichols and Pollock 1983, Nichols 1992, Rexstad 1994). Because retention patches in PCT-R-treated stands were quarter-hectare units defined by the trapping grid, some traps and pellet trays were located on outside corners of retained patches, and some 50-m transect segments were along edges of retained patches. We considered those traps, trays, and transect segments ‘next to’ a retention patch. In contrast, we considered traps, trays, and transect segments ‘away from’ retention patches if they were surrounded by thinned portions of the stand. To test whether retained patches influenced index counts, we used mean next to versus away from counts from single stands as data pairs for paired t-tests. Alpha was 0.05 for statistical significance, but we were more interested in the magnitude of any effect.

Twice per winter in each PCT-R-treated stand, we counted snowshoe hare snowtrack crossings for each 50-m transect segment of the 5 450-m trap lines. Poor snow conditions precluded reliable counts once in December 2001. Counts of 1-year fecal-pellet accumulation (Krebs et al. 1987, Krebs et al. 2001, Mills et al. 2005, Murray et al. 2005) were not feasible after PCT-R because cut saplings covered the ground too completely in places. Instead, we could reliably count winter fecal pellets by systematically staking 50 plastic trays (52 × 25 × 0.5 cm) on the ground in late autumn, before snow accumulation. We counted pellets in trays shortly after snowmelt, censoring data from dislodged, broken, or steeply angled (≥30°) trays; these totaled 8.1% of all trays.

RESULTS

Snowshoe hare abundance decreased on PCT-treated stands more than would have been expected without any change in sapling density. Snowshoe hare abundance at different study stands varied before treatment (Table 1). Based on the highest-ranked model for ΔN in our study (Table 2), average post-treatment abundance changes indicate a loss of −3.0 snowshoe hares (SE = 1.7) on PCT-treated stands, compared to control stands. Similarly, the relative decline on PCT-treated stands, when compared to PCT-R-treated stands, was −4.4 hares (SE = 1.7). However, there was only a minimal difference in ΔN between control and PCT-R-treated stands (x = 1.4 snowshoe hares, SE = 1.7). The 2 models with Akaike model weights of 0.15 and 0.11 also had parameter estimates for treatment effect sizes that were nearly equivalent to those from the highest-ranked model.

Changes in snowshoe hare abundance due to season were
negligible, compared to the effect of PCT treatment. The estimated marginal mean of $\Delta N$ was 0.6 hares higher ($SE = 1.8$) in summers than in the first winter after treatment, and 1.1 hares higher ($SE = 1.7$) in summers than in the second winter after treatment. The estimated marginal mean of $\Delta N$ was 0.5 hares higher ($SE = 1.8$) in the first winter compared to the second winter.

Snowshoe hare trapping, snowtrack, and pellet indices from PCT-R-treated stands suggested that, in winter, microhabitats next to aggregate retention patches were used preferentially more than thinned portions of the stand. We trapped 90% more individuals, counted 86% more snowtracks, and counted 510% more pellets next to retained patches than away from retained patches (Table 3).

### DISCUSSION

We found that PCT decreased snowshoe hare abundance, compared to both control and PCT-R treatments. If our experimental observations are representative of PCT effects in young stands across the range of Canada lynx, then standard PCT may lead to an ecologically significant loss of snowshoe hares from the Canada lynx prey base. Canada lynx in their southern range already persist at the lower threshold of required snowshoe hare density, with starvation an important cause of lynx mortality (Aubry et al. 2000, Mowat et al. 2000). Potentially compounding any local snowshoe hare declines due to PCT, logistics may dictate that many stands in a landscape be thinned at nearly the same time.

In contrast to PCT, there was no clear negative effect of PCT-R treatment. Changes in snowshoe hare abundance in PCT-R-treated stands appeared comparable to control stands. Our study was too short to address whether PCT-R may extend the time that stands provide good-quality snowshoe hare habitat (e.g., Doerr and Sandburg 1986).

In this controlled experiment, PCT decreased snowshoe hare abundance, at least during 2 years after thinning. The untreated control stands in each study area represented ecological benchmarks; in contrast to those, snowshoe hare abundance on PCT-treated stands declined by about 3 hares per approximately 25 ha. That this relative reduction on PCT-treated stands was detectable despite having only 3 replicate study areas underscores the large effect size.

Random treatment assignment in any experiment reduces the possibility that some unknown factor other than treatment type is the cause of observed differences across treated experimental units. In this experiment, PCT and PCT-R treatments were always randomly assigned. The nonrandom assignment of the control at the Cold Creek study area was not ideal, but it does not change the conclusion that PCT leads to declines in hare abundance.

Snowtrack, winter capture, and winter pellet counts indicated behavioral preference for retained patches in winter. There may be summer hiding cover in thinned microhabitats, but once deep snow blankets the ground the only cover in precommercially thinned areas comes from scattered single saplings.

### MANAGEMENT IMPLICATIONS

Where high snowshoe hare abundance is a goal, standard PCT should be avoided. The PCT-R retains some natural variation in young stand structure, and may maintain snowshoe hare abundance at levels comparable to unthinned stands, at least in the short term. It is possible to use PCT-R treatments other than the one we used; we suggest that PCT-R should retain a spatially well-distributed selection of the very densest patches of saplings.

### ACKNOWLEDGMENTS

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### LITERATURE CITED


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