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RESEARCH ARTICLE

Short-term response of snowshoe hares to western larch restoration and seasonal needle drop

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Old-growth western larch has been degraded throughout much of its historic range due to extensive timber harvest and fire suppression. We examined the effects of a restoration treatment of western larch on snowshoe hares, a denizen of the boreal forest serving as a focal animal species to indicate the health of the restored ecosystem. We implemented a restoration treatment using "doughnut thinning" to accelerate development of old-growth attributes in larch stands and simultaneously examined the short-term effects on snowshoe hare density, survival, and movement. Although typical forest management activities tend to have adverse effects on hares especially in the short term, we found that the restoration treatment did not affect hare density or survival in the short term. In addition, despite significant decreases in cover coinciding with the larch needle drop, we found evidence of year-round immigration into larch stands by hares suggesting larch stands are suitable year-round hare habitat. Taken together, our findings suggest that a larch restoration treatment designed to accelerate the development of old-growth attributes can be implemented so as to have no measurable short-term detrimental effects on hares.

Key words: habitat, *Larix occidentalis*, *Lepus americanus*, movement, restoration treatment, SECR

Implications for Practice

- Accelerating a forest towards restoration can be compatible with conservation of native fauna.
- Release treatments interspersed with uncut forest can mitigate negative impacts of widespread thinning on fauna sensitive to forest management.
- Restoration thinning treatments can have no short-term negative effects on snowshoe hares, a focal species for northern U.S. forestry practices.
- It is important to monitor immediate effects of treatments fostering restoration especially when full ecosystem recovery may take decades.

Introduction

In much of the world, forest management is undergoing a paradigm shift away from managing strictly for timber production towards a trend of restoration (Hobbs & Norton 1996; Sarr et al. 2004; Puettmann et al. 2009). Particularly on public lands in the western United States, managers are shifting from commercial harvest and reduction of fire risk towards restoration of ecological processes (Brown 2005). For example, the Bureau of Land Management (BLM), an agency that manages about 100 million hectares in the United States, has drastically shifted its focus from a resource extraction perspective prior to the 1990s (Wood 2006) to an emphasis on restoration of land (USDI 2008).

Western larch (*Larix occidentalis*) forests are of particular interest for restoration. Larch is found on mesic-to-moist sites in British Columbia, Washington, Oregon, Idaho, and Montana (Schmidt et al. 1976; Fiedler & Harrington 2004). Due to its desirable qualities such as high strength and hardness, western larch is one of the most important timber species in western North America (Schmidt et al. 1976). For example, in 1970 approximately 3.5 million cubic meters of larch were harvested in the northern Rocky Mountains (Schmidt et al. 1976). Extensive larch harvests throughout its range have shifted the forest structure from large old-growth larch stands to dense mixed-conifer forests comprised of mainly saplings and small trees (Fiedler & Harrington 2004; Brown 2005). The impacts of commercial harvesting on larch stands were compounded by the active fire suppression regimes of the last 100 years. Western larch forests historically were characterized by frequent mixed-intensity fires and are extremely fire resistant (Fiedler & Harrington 2004). These fires are vital for larch germination and regeneration. Modern fire suppression has shifted historical larch habitats to favor overstocked forests of shade-tolerant conifers resulting in a decline in the lifespan of all tree species, higher severe wildfire risk, and a decline in the extent of western

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larch (Fiedler & Harrington 2004). The removal of large, mature larch via extensive timber harvesting and the reduction of larch regeneration potential resulting from fire suppression make western larch a highly suitable candidate for restoration. As such, one of the few remaining old-growth larch stands was successfully restored (Fiedler & Harrington 2004; Brown 2005). Nonetheless, there remains a pressing need to restore the more characteristic larch forests comprised of mainly saplings and small trees.

Forest restoration success, however, should be judged not only on stand composition and structure but also by effects on native focal species (Hobbs & Norton 1996). One such focal species for boreal forests is the snowshoe hare (*Lepus americanus*), an important prey species for a plethora of carnivores including the federally threatened Canada Lynx (*Lynx canadensis*). Hares prefer dense understories (Adams 1959; Litvaitis et al. 1985; Koehler & Brittell 1990; Ferron et al. 1998) and can be adversely affected, at least in the short term, by forest management treatments like thinning or clear-cutting that reduce visual and thermal cover (Sullivan & Sullivan 1988; Ausband & Baty 2005; Sullivan et al. 2010; Bois et al. 2012). Although the effects on hares of traditional silvicultural techniques have received attention, little research has addressed the effects of forest restoration on snowshoe hares.

Although thinning can also be a key tool for restoring forest stands, its effects on snowshoe hares would generally be expected to be negative. For example, precommercial thinning (PCT) negatively affects snowshoe hare abundance and habitat use (Ausband & Baty 2005; Homyack et al. 2007; Sullivan et al. 2010; Abele et al. 2013), a finding that contributed to a moratorium on PCT of U.S. federal lands in designated lynx habitat (Ruediger et al. 2000).

However, alternative thinning practices have been shown to have less impact on snowshoe hares. For example, thinning a circular patch of 10 m radius (79 m^2) and surrounding it with a 10–50 m radius buffer of unthinned forest actually increased hare abundance relative to untreated stands in the short term (3 years) (Bull et al. 2005). Thinning three quarters of a stand and leaving the remaining quarter unthinned in quarter hectare (2,500 m^2) patches had no adverse effect on hare abundance compared to unthinned stands in the short term (<3 years) (Griffin & Mills 2007). Thus, small-scale thinning may be neutral or even positively affect hare abundance, at least in the short term, perhaps by providing forage in the open areas close to cover provided by the unthinned areas.

We examined the short-term effects on hare vital rates (survival and density) of a forest restoration thinning treatment designed to promote restoration of larch stands to historic (pre-European settlement) conditions using a replicated Before-After-Control-Impact (BACI) design. The release treatment involved thinning around the largest larch trees in the area to promote faster growth towards historic conditions of larger trees while leaving a large portion of the grid unthinned. We tested the immediate effects of the restoration treatment by examining changes in hare density, survival, and covariates affecting survival after the restoration treatment was applied.

In addition to its need for restoration, western larch is of special interest for snowshoe hare ecology and for management because it is a deciduous conifer. Larch stands undergo dramatic structural changes when they seasonally lose their needles. Open canopies tend to decrease both habitat use (Hodson et al. 2010; Lewis et al. 2011; Thornton et al. 2013) and survival of snowshoe hares (Griffin & Mills 2009). Because larch stands become more open when their deciduous needles drop in the fall potentially increasing predation pressure and/or reducing forage availability, we were interested in whether hares left larch stands when the needles dropped. If hares left, then the restoration treatment would be expected to have much less of an effect on them because they are only present in the stand for some of the year. Therefore, we also tested the following predictions. (1) Radiocollared hares would emigrate from larch stands when the needles drop in the fall and would immigrate back when the needles grow back in the spring. (2) Summer (needles on) local hare density in larch forests would be significantly greater than in winter (needles off). (3) Hares that continue to use areas with bare larch trees in the winter would have a lower survival than those using the surrounding larch-free areas, which provide more cover.

Methods

Study Site

We sampled hares from two larch stands in areas of the Upper Blackfoot region of western Montana on land managed by the BLM with a history of timber management (Appendix S1, Supporting Information). Marcum Mountain (Marcum) (lat 46.99°N, long −112.91°W) and Chamberlain Creek (Chamberlain) (lat 46.96°N, long −113.24°W) are approximately 30 km apart at similar elevations (Marcum: 1,450–1,600 m, Chamberlain: 1,600–1,800 m).

Marcum has a relatively diverse larch stand with an average basal area of 11 m^2/ha, ranging from saplings to greater than 20 cm diameter at breast height (dbh) and has greater than 7,000 trees/ha. In contrast, most of the larch in Chamberlain are saplings (<10 cm dbh) resulting from fire regeneration with some areas greater than 7,000 trees/ha but most less than 2,000 trees/ha and an average basal area of 5 m^2/ha. However, some larger larches (>20 cm dbh) also remain in small quantities (roughly 10 trees/ha) throughout the stand. Both stands are approximately 35 ha and the surrounding forest has little to no larch present. Other prominent tree species in both areas include Douglas-fir (*Pseudotsuga menziesii*), Subalpine fir (*Abies lasiocarpa*), Lodgepole pine (*Pinus contorta*), and Engelmann spruce (*Picea engelmannii*).

Common predators of snowshoe hares likely present at both areas include Canada lynx (*Lynx canadensis*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), American marten (*Martes americana*), long-tailed weasel (*Mustela frenata*), Golden Eagle (*Aquila chryseatos*), Great Horned Owl (*Bubo virginianus*), Barred Owl (*Strix varia*), Northern Goshawk (*Accipiter gentilis*), and Red-tailed Hawk (*Buteo jamaicensis*).

Experimental Restoration Treatment

The goal of the restoration treatment was to accelerate the growth of large larch trees to better resemble our reference ecosystem, which was characterized by larch trees of the large (38.1–53.2 cm dbh) and very large (>53.3 cm dbh) size classes (Appendix S1). Thus, the treatment aimed to accelerate the development of the largest larch trees by eliminating inter- and intraspecific competition. Within each of the two study areas, we established two grids (a treatment and a control each approximately 15 ha). With only two replicates, we chose to designate the grids with bigger larch trees to receive the restoration treatment, as they are better suited to achieve the restoration goal.

BLM contractors applied a restoration prescription to the treatment grid approximately halfway through the study (summer 2014 for Chamberlain and fall 2014 for Marcum). The treatment involved "doughnut thinning" around large larch trees with chainsaws. Specifically, all larch trees above a specified dbh were designated as "leave" trees and all stems greater than 2.5 cm dbh within 5 m of the leave tree were felled in place. We chose 5 m because larch experiences a substantial drop-off in crown development when there are other stems present within 5 m (Schmidt 1997).

We chose a dbh threshold for leave trees that resulted in approximately one-third of the stand being thinned to a density of 400 trees per hectare. [Correction added on 26 September 2017, after first online publication: The data "40" in the preceding sentence has been changed to "400".] This left two-thirds of the stand unthinned, which was the major difference between this restoration treatment and traditional PCT. We chose to thin approximately one-third of the stand because it was close to the thinning extent of the two studies that showed no adverse effects of thinning on hares (Bull et al. 2005; Griffin & Mills 2007) and because experience indicated that it should be a sufficient level to achieve the forest restoration objective. Using stem densities from our vegetation sampling (see below), we determined that the dbhs for leave trees to thin around should be 15 cm for Chamberlain and 22 cm for Marcum. These radii provided an approximate guideline but contractors were instructed to adjust that guideline as they saw fit to ensure that approximately one-third of the stand was treated. In addition, BLM contractors left cut stems where they fell (i.e. no slashing of cut trees). The control grid received no thinning treatments.

Vegetation Sampling

We measured stand level vegetation characteristics and structural changes from the restoration treatment at 10 random points within each grid following protocols of Lewis et al. (2011). At each point, we established circular plots of 5 m radii as the basis of vegetation sampling. We estimated stem density by counting all stems greater than 1 m tall and greater than 2.5 cm dbh. We also counted total number of larch stems.

We used photographs analyzed in Adobe Photoshop to estimate horizontal cover and canopy closure (Goerz, Kumar, & Mills in preparation). Horizontal cover was estimated by photographing a coverboard (100 cm × 50 cm) and counting the number of unobstructed coverboard pixels in Adobe Photoshop. This number was then divided by the total number of pixels comprising the coverboard to yield an estimate of the proportion of the coverboard unobstructed by vegetation. This estimate was then subtracted from one to give percent horizontal cover. We estimated horizontal cover at three different compass azimuths, the first chosen randomly and the last two 120° apart from the first. Similarly, we estimated canopy closure at the center of each plot using a fisheye lens mounted to a camera. We again used Adobe Photoshop to divide the number of pixels unobstructed by cover by the total number of pixels and subtracted that number from one to estimate canopy closure. We measured these vegetation characteristics once in summer and winter for the control grids and twice (once before and once after restoration treatment) in summer and winter for the treatment grids.

Snowshoe Hare Capture/Handling

Control and treatment grids consisted of 80 live traps on Marcum and 78 on Chamberlain with 50 m spacing. In each area, control and treatment grids were separated by at least 100 m, greater than the mean maximum distance moved over 4-day capture periods by hares in this region (Mills et al. 2005).

We trapped all four grids for four consecutive nights twice in summer and twice in winter from summer 2013 to winter 2015. We also continued to trap Chamberlain in summer 2015 yielding two primary trapping occasions pre-thinning and three post-thinning. Post-thinning trapping began 1 week after completion of the thinning treatment (summer 2014 for Chamberlain and fall 2014 for Marcum).

We used collapsible Tomahawk live traps 51 × 18 × 18 cm (Tomahawk Live Trap Company, Tomahawk, WI, U.S.A.), baited with alfalfa cubes and apple pieces. We weighed all hares, determined sex, measured right hind foot length, and determined breeding status (lactating or pregnant, testes abdominal, or testes scrotal). We marked all hares greater than 500 g with a unique numbered ear tag and a very high frequency (VHF) radiocollar (Wildlife Materials, Murphysboro, IL, U.S.A.) weighing less than 40 g and equipped with a mortality sensor. All capture and handling procedures were approved by Institutional Animal Care and Use Committee under a permit issued to L.S.M.

Radio-telemetry of Snowshoe Hares

We tracked hares using radio-telemetry to monitor survival and determine locations. We monitored survival year-round on a biweekly basis. In the spring and fall (seasons of larch needle drop), we visually determined hare locations weekly by honing in on them. We then established a circular plot of 5 m radius centered around the hare location and recorded the number of larch stems, dbh for all larch stems, and the total number of stems as described above.

Statistical Analysis

We used *t*-tests to compare vegetation characteristics. We compared initial vegetation structure at control versus treatment grids pre-treatment with unpaired *t*-tests. We compared vegetation structure winter versus summer and pre- versus post-restoration treatment with paired t-tests.

We performed a known-fate analysis with staggered entry (Pollock et al. 1989) in Program MARK (White & Burnham 1999) to examine the effects of various larch and thinning covariates on snowshoe hare survival. As we were mostly interested in the effects of six specific covariates on hare survival and less interested in the actual estimate of survival itself, we only included models that included our specific covariates of interest. Specifically, we tested the following binary individual covariates: *study area* (Marcum vs. Chamberlain), *grid* (restoration vs. control) and *slash* (whether or not the hare was ever found in cover provided by the felled trees created by restoring grid). We also included a covariate, *DBH*, the average sum of all larch dbhs found within 5 m of the hare averaged across all relocations. Finally, we also included two time-varying covariates: L (leaf off vs. leaf on) and R (before or after the restoration treatment). We also considered models with three biologically relevant interactions: $grid{\times}R$ represented a difference in control and treatment grids only after the restoration treatment was applied, $slash{\times}R$ represented a difference in cover use only after the restoration treatment was applied, and $DBH{\times}L$ represented whether larch trees being bare or full of needles had a greater effect on hares that used areas with more larch. We also included a null model, S(.), for constant survival.

We ranked models using Akaike information criterion corrected for small sample size (AICc) and used AICc differences (ΔAICc) and Akaike weights (w_i) to evaluate model support. We considered models with $\Delta\text{AICc} \leq 2$ to be indistinguishable from each other and models with $\Delta\text{AICc} > 7$ to have little support (Burnham et al. 2011).

We performed a spatial mark recapture analysis using the Package SECR (Efford 2004; Borchers & Efford 2008) in Program R (version 2.15.1, R Development Core Team 2012) to determine hare densities. Traps that caught nontarget species or were otherwise unable to capture a hare were considered inoperable for that night. We originally considered models with half-normal and hazard detection functions and varied g_0, the probability of detection given the individual's activity center is at the detector, to include: a constant detection probability, a time-varying detection probability, and two-class finite mixture allowing for heterogeneity in detection probability. We specifically wanted to include models that attempted to account for individual heterogeneity because it has been shown to affect hare abundance estimation (Boulanger & Krebs 1994, 1996).

We fit models with the full likelihood, ranked them using AICc and used AICc differences (ΔAICc) and Akaike weights (w_i) to evaluate model support. We found that the model that contained the half-normal detection function and a constant detection probability contained the majority of the Akaike weights (>0.60) for 3 out of 4 grids during the summer of 2013, so we used it for all subsequent analyses. In this case, we did not model average because we were comparing density estimates from year to year and did not want to confound actual changes in density with apparent changes in density due to differences in model weight.

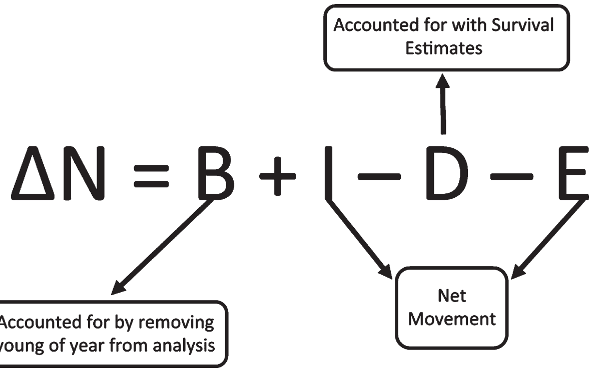

Figure 1. Conceptual representation on how index of net movement was derived from a traditional BIDE (Births + Immigrants − Deaths − Emigrants) equation. Changes to the population size due to births were accounted for by removing young of year. Deaths were accounted for using the site-specific survival estimates. The remainder ($I-E$) yields an estimate of net movement.

To examine whether hare movement in larch stands corresponds to larch needle phenology, we estimated hare immigration/emigration from winter to summer (25 weeks) and from summer to winter (25 weeks) in Chamberlain (logistical constraints prevented us from trapping Marcum in summer 2014). Although radio-telemetry data can directly measure individual temporary emigration from a sampled stand (permanent emigration and death are confounded), we were interested in population level movement of hares back into (immigration) and out of (emigration) our focal stands. We therefore relied on an index derived from our density and survival data (Fig. 1).

To estimate immigration and emigration from winter to summer we first multiplied the density estimates produced by the spatially explicit capture-recapture (SECR) model by the grid size to approximate the number of hares on the grid in winter, producing a "scaled abundance." We then used an adult hare density estimate that excluded juveniles based on a weight threshold (juveniles were <700 grams) to calculate a summer adult hare scaled abundance. Next we used the known-fate model-averaged weekly survival estimates multiplied by the winter scaled abundance to approximate the number of hare deaths to subtract from the winter scaled abundance. After these corrections, the change in population size from winter to summer was considered an index of net emigration or immigration (Fig. 1).

Rates from summer to winter were similarly indexed calculating a summer hare scaled abundance for all hares (juveniles and adults) to compare to the scaled abundance the following winter. Although hares added by birth after summer densities were estimated could bias our index, we believe such bias is minimal (Appendix S2).

Results

Site Vegetation

At the Marcum area, initial vegetation characteristics were similar between the control and pre-treatment grids, with no significant differences in any vegetation characteristics. At the Chamberlain area, the pre-treatment grid had a trend towards greater number of larch stems (two sample t-test, $n = 10$, $t = -1.94$, $p = 0.07$), number of total stems (two sample t-test, $n = 10$, $t = -2.04$, $p = 0.06$), and sum of larch dbhs (two sample t-test, $n = 10$, $t = -2.07$, $p = 0.05$) compared to the control (Table S1).

As expected for deciduous larch stands, summer had more cover than the winter (Fig. 2). Horizontal cover was significantly greater in the summer in Marcum (two sample t-test, $n = 20$, $t = -8.26$, $p < 0.001$) and Chamberlain (two sample t-test, $n = 20$, $t = -5.69$, $p < 0.001$). Similarly, canopy cover was significantly greater in the summer in Marcum (two sample t-test, $n = 20$, $t = -6.00$, $p < 0.001$) and Chamberlain (two sample t-test, $n = 20$, $t = -4.38$, $p < 0.001$).

After the restoration thin in fall 2014, Marcum had less horizontal cover (two sample t-test, $n = 10$, $t = -2.76$, $p = 0.02$) and canopy cover (two sample t-test, $n = 10$, $t = -6.15$, $p < 0.001$) compared to the summer of 2013 (Fig. S1). However, no significant difference was found in cover between the winter of 2013/2014 and the winter of 2014/2015. In fact, no other vegetation characteristics were significantly different after the restoration thin at either Marcum or Chamberlain.

Hare Survival

We monitored survival from July 2013 to December 2014 on 47 hares (24 at Chamberlain and 23 at Marcum) of which 20 died (9 at Chamberlain and 11 at Marcum). The model-averaged estimate of weekly survival was 0.97 (95% CI = 0.92–0.99). Five of the nine models, including the null model, all had ΔAICc ≤ 2 indicating roughly equal support (Table 1). The beta coefficients for all covariates (*study area*, *grid*, *slash* [use of slash], *DBH* [use of larch areas], *L* [larch bare vs. full], *R* [pre vs. post-restoration], *grid×R*, *slash×R*, *DBH×L*) had 95% CIs that included 0 indicating nonsignificance of covariates on survival rate.

Hare Density

We had 700 (502 at Chamberlain and 198 at Marcum) captures of 335 (225 at Chamberlain and 110 at Marcum) individual snowshoe hares. We estimated hare density four times (two pre-restoration treatment and two post) on control and treatment grids at Marcum and five times at Chamberlain (two pre-restoration treatment and three post) (Fig. 3). Densities within each area were similar across treatments and years, with all but three falling within the 95% confidence intervals of the other estimates from that area.

Hare Movement

We found that net movement of hares tended towards year-round (both summer to winter and winter to summer) immigration into larch stands. Specifically, our index of net movement indicated that immigration overwhelmed emigration in almost all cases (Table 2). We were only able to estimate net movement from Marcum from summer 2013 to winter 2013/2014 because we were unable to trap it in the summer of 2014.

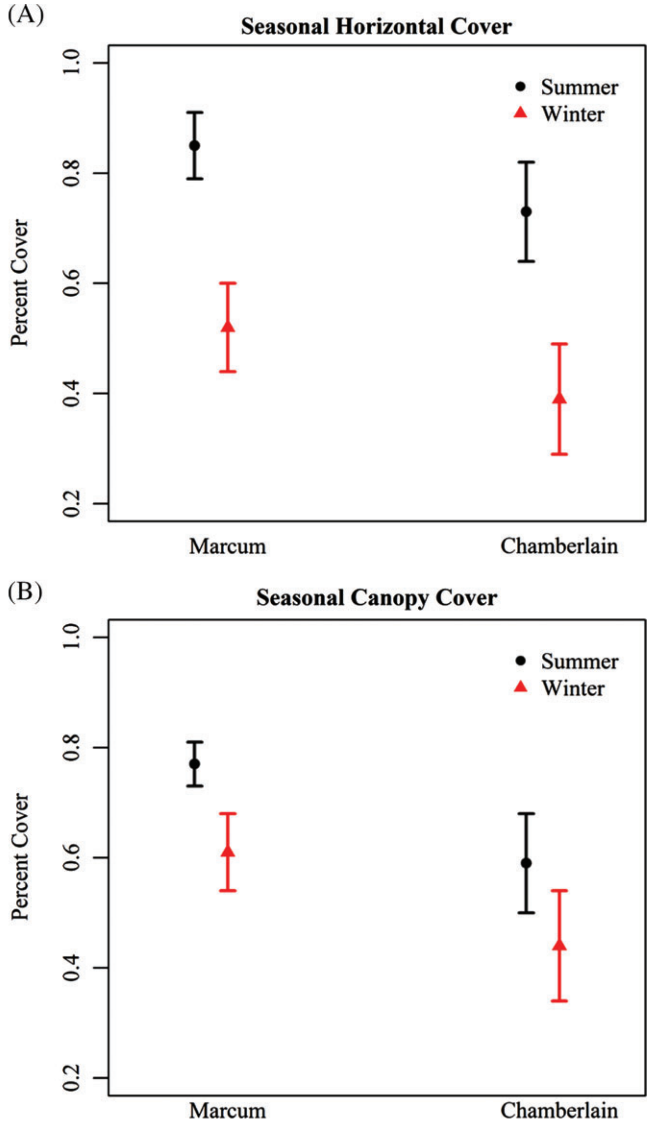

Figure 2. Seasonal changes in horizontal and canopy cover at two different predominately western larch study areas in western Montana from 2013 to 2015. The summer always had significantly more cover (two sample t-test, $n = 20$, $p < 0.001$). Twenty random points were visited at each area once in the summer and once in the winter and compared with a paired t-test. Cover was estimated by photographing a horizontal coverboard and the forest canopy using a fisheye lens and analyzing the photographs in Adobe Photoshop. Error bars represent ± 95% CI.

Discussion

Overall, we found little support for short-term effects of the restoration treatment on snowshoe hares. The Chamberlain site showed no declines in hare density post-treatment. Although densities in Marcum did decline during the 1 week post-treatment fall sampling, these decreases occurred in both

Table 1. Known-fate models in Program MARK of 47 collared snowshoe hares from July 2013 to December 2014 in western Montana. Models were ranked by Akaike's information criterion adjusted for small sample size (AICc). Covariates included: study area (Marcum vs. Chamberlain), grid (treatment vs. control), slash (whether or not the hare was ever found in cover provided by the felled trees created by restoring grid), DBH (average sum of all larch dbhs found within 5 m of the hare), L (larch trees bare vs. full with needles), and R (before or after the restoration treatment). We also considered models with the following interactions: grid×R (difference in control and treatment grids only after the restoration treatment), slash×R (difference in cover use only after the restoration treatment), and DBH×L (whether bare larch trees vs. larch trees full of needles had a greater effect on hares that used areas with more larch). We also included a null model, S(.), which represented constant survival. *K* indicates the number of estimated parameters.

Model	K	*AICc*	*ΔAICc*	*AICc Weights*	*Model Likelihood*	*Deviance*
{S(slash×R)}	3	172.67	0.00	0.24	1.00	166.63
{S(L)}	2	173.25	0.58	0.18	0.75	169.23
{S(slash)}	2	173.80	1.13	0.14	0.57	169.78
{(DBH×L)}	4	174.64	1.97	0.09	0.37	166.57
{S(.)}	1	174.65	1.98	0.09	0.37	172.64
{S(R)}	2	174.98	2.31	0.08	0.32	170.96
{S(DBH)}	2	175.21	2.54	0.07	0.28	171.19
{S(study area)}	2	176.04	3.37	0.05	0.19	172.02
{S(grid)}	2	176.26	3.60	0.04	0.17	172.24
{S(grid×R)}	4	177.87	5.20	0.02	0.07	169.80

treatment and control grids and were transient, with all other densities in summer and winter being similar. Therefore, we attribute the effect to seasonal habitat use (Wolff 1980; Koehler & Brittell 1990; Bull et al. 2005).

Although landscape-level reduction in tree density from PCT is known to decrease hare abundance (Ausband & Baty 2005; Homyack et al. 2007; Sullivan et al. 2010; Abele et al. 2013), small patch thinning treatments can have neutral to positive effects on hares at least in the short term. For example, Bull et al. (2005) found an increase in hare abundance 3 years post-thin of 10 m circular patches and Griffin and Mills (2007) found no short-term effect of the thinning treatment with 2,500 m^2 unthinned patches. Our results further support the idea that a thinning treatment that retains unthinned patches minimizes short-term impact on snowshoe hare density. However, an important caveat to these findings is that all these studies only addressed short-term effects of less than 4 years.

Several factors likely underlie the lack of effects of our restoration thinning treatment on hare densities. First, we left two-thirds of the grids unthinned. This restoration treatment did not substantially change the measured stand level vegetation characteristics. Although cover was significantly lower after the restoration thin on Marcum, this is likely a seasonal effect as the pre-treatment measurements were taken in the summer and the post-treatment measurements were taken in the fall. Second, as the area thinned was small relative to the effective area sampled, hare use of thinned areas could change without affecting density. Finally, we emphasize that our short-term study cannot test for potential longer-term effects of the treatment on density that may occur.

Density estimates from this study are generally higher than densities from a long-term study of hare populations at 16 sites ($n = 259$ density estimates) in northwest Montana (Mills unpublished data). Mean density at Marcum (0.82 hares/ha) fell in the 86% quantile of the long-term data and mean density at Chamberlain (1.31 hares/ha) fell in the 98% quantile. In addition, the maximum density at Chamberlain (1.92 hares/ha) was greater than any density from the long-term study. These findings suggest that larch forests can sustain high densities of snowshoe hares in the southern part of their range.

We found little support for any covariates affecting hare survival. There were no differences between grids or study areas in survival and no effect of the restoration treatment or larch phenology on survival. Although the effects of thinning on hare survival are not well studied, the few studies that address this question had similar findings (Sullivan & Sullivan 1988; Abele et al. 2013).

The changing stand structure created by the larch needle phenology also had no effect on survival. As expected, we found that both horizontal and canopy cover are significantly reduced in winter when larch trees drop their needles. Open habitats typically have fewer hares (Wirsing et al. 2002) and have been linked to the creation of population sinks through decreased survival (Griffin & Mills 2009). In addition, lower understory cover reduces hare survival (Sievert & Keith 1985). However, we found no effect of the larch seasonal cover reduction on hare survival. Because we obtained weekly estimates of vegetation characteristics from locations occupied by hares we were able to improve power to test for covariate effects on survival that accounted for the specific habitat characteristics of areas used by each hare each week, increasing confidence that we would have detected strong effects if they existed.

Snowshoe hares may adopt behavioral changes to compensate for reduced cover and forage caused by the annual needle drop. Although western larch was the most prevalent tree species at the areas, other conifer species were also present preserving some year-round cover for hares. Hares could modify their behavior when the needles drop and avoid areas with compromised cover. Hares are known to preferentially browse and rest in high cover microhabitats (Hodges & Sinclair 2005; Hodson et al. 2010). It is also possible that either snow depth or hardness at the areas increased the difficulty of predation on hares by terrestrial predators (Murray & Boutin 1991) in such a way as to compensate for increased predation risk in open larch stands rendering hare survival unaffected.

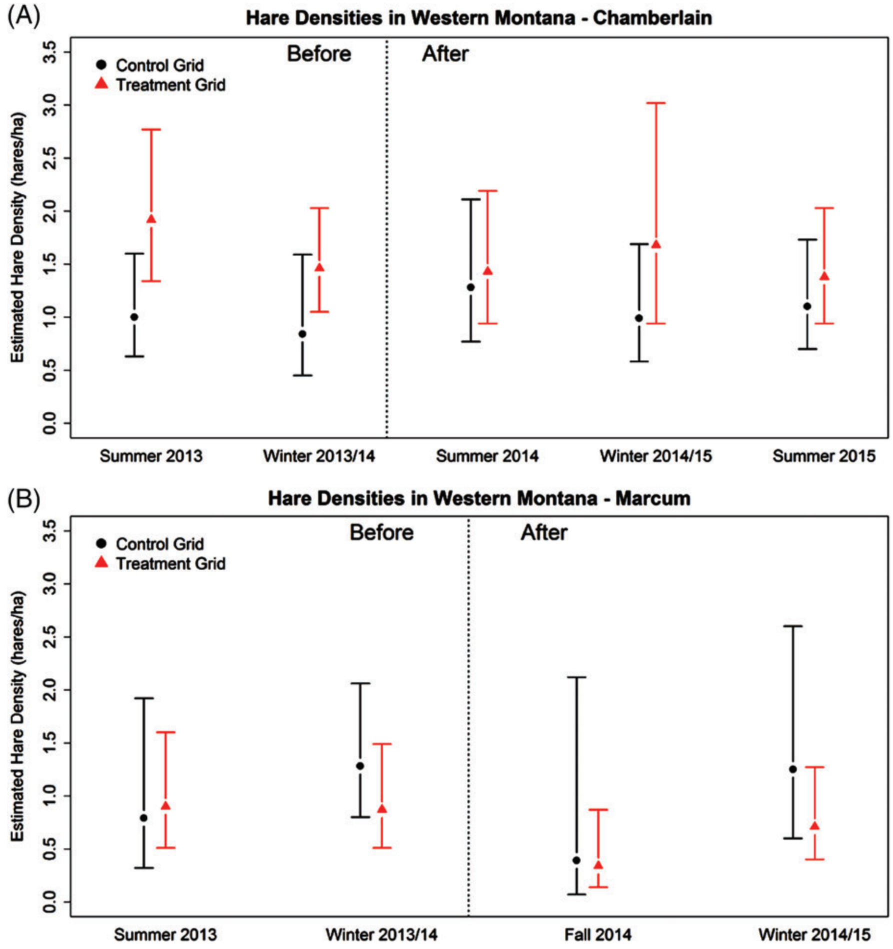

Figure 3. Density estimates of snowshoe hares on control and treatment grids in western Montana from 2013 to 2015 before and after a restoration treatment. Densities were obtained using the Package SECR in Program R. Grids were approximately 16 hectares in size and had about 80 traps. The restoration treatment (represented by the dotted line) was implemented in July 2014 for Chamberlain and October 2014 for Marcum. Error bars represent ± 95% CI.

We also found little support for larch needle phenology impacting hare use of larch stands. Hares were consistently immigrating to the stand even as the needles were dropping in the fall. Despite the relatively crude nature of our movement index the high levels of immigration indicate at the very least that hares were not substantially leaving the stands. Hare use of larch year-round is an important finding in the context of larch restoration because if hares abandon larch stands during the leaf off season then the restoration treatment would have less of an effect on them. Instead, our finding of year-round use of larch stands implies a strong role for both larch and larch restoration for snowshoe hares.

Despite the general trend of year-round immigration, hare density in the summer (needles on) was not significantly different than in winter (needles off). As net immigration was high but densities remained unchanged, it is possible that these areas might be acting as population sinks for hares. Although the larch needle phenology did not affect survival, it is possible that other stand level attributes decreased survival in the study site compared to a greater landscape, leading to local sink dynamics (Griffin & Mills 2009).

Consistent seasonal hare densities and year-round immigration into larch stands suggest a lack of seasonality in hare use of larch stands, a somewhat surprising result given that hares may move from more open areas in the summer with abundant herbaceous forage to more dense coniferous areas in the fall and winter (Wolff 1980; Sullivan et al. 2010). Hares prefer understories with more cover (Koehler & Brittell 1990; Ferron et al. 1998; Bois et al. 2012) and sites with more canopy cover are more likely to be colonized and less likely to go extinct (Thornton et al. 2013). In addition, hare pellet densities increase with cover (Lewis et al. 2011). Nonetheless, we have found that hares stay in larch stands year-round, with survival unaffected by the seasonal cover changes mediated by larch needle phenology.

Given the challenge of evaluating restoration success (Ruiz-Jaen & Aide 2005), we targeted a priori a focal species (Mills et al. 2013) that should respond to changes in forest stand structure (e.g. act as an indicator species) and serve as a strong interactor and keystone prey species for multiple carnivores. We measured restoration success using multiple criteria (Ruiz-Jaen & Aide 2005). One criterion was accelerating the transition of the stand towards historic old-growth stand structure, which

Table 2. Net seasonal movement of snowshoe hares in western larch stands in western Montana. Movement was indexed using modifications to a traditional BIDE (Births + Immigrants − Deaths − Emigrants) equation (Fig. 1). Positive numbers for net movement indicate net immigration whereas negative numbers indicate net emigration. We were only able to estimate net movement from Marcum from summer 2013 to winter 2013/2014 because we were unable to trap it in the summer of 2014. Each period was approximating 25 weeks (January–July).

Period	*Study Area*	*Grid*	*Net Movement*
Summer 2013–winter 2013/2014	Chamberlain	Treatment	+7
Summer 2013–winter 2013/2014	Chamberlain	Control	+5
Winter 2013/2014–summer 2014	Chamberlain	Treatment	−2
Winter 2013/2014–summer 2014	Chamberlain	Control	+6
Summer 2014–winter 2014/2015	Chamberlain	Treatment	+15
Summer 2014–winter 2014/2015	Chamberlain	Control	+5
Summer 2013–winter 2013/2014	Marcum	Treatment	+6
Summer 2013–winter 2013/2014	Marcum	Control	+13

we accomplished by thinning around the largest larch trees available. Another criterion was not impacting hares as a focal species, which was also successful at least for the short term monitored. Although restoration would be expected to affect different species in different ways (Gaines et al. 2007), our targeted focal species connects clearly to both the treatment and the greater ecosystem effects.

We found that stand structure changes arising from both a restoration treatment and from inherent phenologic changes in western larch have no short-term impact on hare movement, habitat use or vital rates. Hares use larch habitat year-round, which suggests that any management activities that disturb the stand have the potential to affect hares. However, our findings show that a restoration treatment can be implemented in a manner that not only restores degraded habitat but also has no measurable short-term detrimental effects on a strongly interacting focal species.

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LITERATURE CITED

Abele SL, Wirsing AJ, Murray DL (2013) Precommercial forest thinning alters abundance but not survival of snowshoe hares. Journal of Wildlife Management 77:84–92

Adams L (1959) An analysis of a population of snowshoe hares in northwestern Montana. Ecological Monographs 29:141–170

Ausband DE, Baty GR (2005) Effects of precommercial thinning on snowshoe hare habitat use during winter in low-elevation montane forests. Canadian Journal of Forest Research 35:206–210

Bois G, Imbeau L, Mazerolle MJ (2012) Recovery time of snowshoe hare habitat after commercial thinning in boreal Quebec. Canadian Journal of Forest Research 42:123–133

Borchers DL, Efford MG (2008) Spatially explicit maximum likelihood methods for capture-recapture studies. Biometrics 64:377–385

Boulanger J, Krebs CJ (1994) Comparison of capture–recapture estimators of snowshoe hare populations. Canadian Journal of Zoology 72:1800–1807

Boulanger JG, Krebs CJ (1996) Robustness of capture–recapture estimators to sample biases in a cyclic snowshoe hare population. Journal of Applied Ecology 33:530–542

Brown H (2005) Ecological restoration in Montana's western larch. Fire Management Today 65:28–35

Bull EL, Heater TW, Clark AA, Shepherd JF, Blumton AK (2005) Influence of precommercial thinning on snowshoe hares. Research Paper PNW-RP-562, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, 16 p

Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65:23–35

Efford M (2004) Density estimation in live-trapping studies. Oikos 106:598–610

Ferron J, Potvin F, Dussault C (1998) Short-term effects of logging on snowshoe hares in the boreal forest. Canadian Journal of Forest Research 28:1335–1342

Fiedler CE, Harrington MG (2004) Restoring vigor and reducing hazard in an old-growth western larch stand (Montana). Ecological Restoration 22:133–134

Gaines WL, Haggard M, Lehmkuhl JF, Lyons AL, Harrod RJ (2007) Short-term response of land birds to ponderosa pine restoration. Restoration Ecology 15:670–678

Griffin PC, Mills LS (2007) Precommercial thinning reduces snowshoe hare abundance in the short term. Journal of Wildlife Management 71:559–564

Griffin PC, Mills LS (2009) Sinks without borders: snowshoe hare dynamics in a complex landscape. Oikos 118:1487–1498

Hobbs RJ, Norton DA (1996) Towards a conceptual framework for restoration ecology. Restoration Ecology 4:93–110

Hodges KE, Sinclair ARE (2005) Browse site selection by snowshoe hares: effects of food supply and predation risk. Canadian Journal of Zoology 83:280–292

Hodson J, Fortin D, Bélanger L (2010) Fine-scale disturbances shape space-use patterns of a boreal forest herbivore. Journal of Mammalogy 91:607–619

Homyack JA, Harrison DJ, Krohn WB (2007) Effects of precommercial thinning on snowshoe hares in Maine. Journal of Wildlife Management 71:4–13

Koehler GM, Brittell DJ (1990) Managing spruce-fir habitat for lynx and snowshoe hares. Journal of Forestry 88:10–14

Lewis CW, Hodges KE, Koehler GM, Mills LS (2011) Influence of stand and landscape features on snowshoe hare abundance in fragmented forests. Journal of Mammalogy 92:561–567

Litvaitis JA, Sherburne JA, Bissonette JA (1985) Influence of understory characteristics on snowshoe hare habitat use and density. Journal of Wildlife Management 49:866–873

Mills LS, Griffin PC, Hodges KE, McKelvey K, Ruggiero L, Ulizio T (2005) Pellet count indices compared to mark-recapture estimates for evaluating snowshoe hare density. Journal of Wildlife Management 69:1053–1062

Mills LS, Zimova M, Oyler J, Running S, Abatzoglou JT, Lukacs PM (2013) Camouflage mismatch in seasonal coat color due to decreased snow duration. Proceedings of the National Academy of Sciences 110: 7360–7365

Murray DL, Boutin S (1991) The influence of snow on lynx and coyote movements: does morphology affect behavior? Oecologia 88:463–469

Pollock KH, Winterstein SR, Bunck CM, Curtis PD (1989) Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15

Puettmann KJ, Coates KD, Messier C (2009) A critique of silviculture: managing for complexity. Island Press, Washington D.C.

R Development Core Team (2012) R version 2.15.1. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Ruediger B, Claar J, Gniadek S, Holt B, Lewis L, Mighton S, et al. (2000) Canada lynx conservation assessment and strategy. Forest Service Publication R1-00-53, USDA Forest Service, USDI Fish and Wildlife Service, USDI Bureau of Land Management, and USDI National Park Service, Missoula, Montana, 142 p

Ruiz-Jaen MC, Aide TM (2005) Restoration success: how is it being measured? Restoration Ecology 13:569–577

Sarr D, Puettmann K, Pabst R, Cornett M, Arguello L (2004) Restoration ecology: new perspectives and opportunities for forestry. Journal of Forestry 102:20–24

Schmidt WC (1997) Stand density in relation to biological functions in young western larch forests. Pages 101–111. In: Bamsey C (ed) Stand density management: planning and implementation. Clear Lake Ltd., Edmonton, Alberta, Canada

Schmidt WC, Shearer RC, Roe AL (1976) Ecology and silviculture of western larch forests (no. 1520). US Department of Agriculture, Forest Service

Sievert PR, Keith LB (1985) Survival of snowshoe hares at a geographic range boundary. Journal of Wildlife Management 49:854–866

Sullivan TP, Sullivan DS (1988) Influence of stand thinning on snowshoe hare population dynamics and feeding damage in lodgepole pine forest. Journal of Applied Ecology 25:791–805

Sullivan TP, Sullivan DS, Lindgren PMF, Ransome DB (2010) Long-term responses of mammalian herbivores to stand thinning and fertilization in young lodgepole pine (*Pinus contorta* var. *latifolia*) forest. Canadian Journal of Forest Research 40:2302–2312

Thornton DH, Wirsing AJ, Roth JD, Murray DL (2013) Habitat quality and population density drive occupancy dynamics of snowshoe hare in variegated landscapes. Ecography 36:610–621

USDI (United States Department of the Interior), Bureau of Land Management (2008) General statement. Bureau of Land Management, Washington D.C., 679 p

White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120–S139

Wirsing AJ, Steury TD, Murray DL (2002) A demographic analysis of a southern snowshoe hare population in a fragmented habitat: evaluating the refugium model. Canadian Journal of Zoology 80:169–177

Wolff JO (1980) The role of habitat patchiness in the population dynamics of snowshoe hares. Ecological Monographs 50:111–130

Wood RS (2006) The dynamics of incrementalism: subsystems, politics, and public lands. Policy Studies Journal 34:1–16

Supporting Information

The following information may be found in the online version of this article:

Appendix S1. Historic and current site evaluations.
Appendix S2. Determining immigration bias due to late births.
Table S1. Comparison of vegetation characteristics between grids in western Montana prior to the restoration treatment.
Figure S1. Changes in horizontal and canopy cover from Marcum Mountain in western Montana after a restoration treatment was implemented.

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