Snowshoe Hare use of Silviculturally Altered Conifer Forests in The Greater Yellowstone Ecosystem

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Abstract

Information about snowshoe hare habitat use in key Canada lynx recovery areas, such as the Greater Yellowstone Ecosystem, is critical for the conservation of lynx. Although research conclusions differ in regard to the types and ages of forests preferred by snowshoe hares, restrictions on silvicultural practice have been implemented by forest managers to protect snowshoe hares in this area. However, some research suggests that regenerating lodgepole pine stands associated with silvicultural treatments benefit snowshoe hares. We evaluated three indices of snowshoe hare use within a timber management area in southwest Montana, inside the Greater Yellowstone Ecosystem (1999–2012) to assess the relative use of forest types. We analyzed: 1) 11 years of data collected from 280 pellet plots using linear mixed models and AIC_c model selection, 2) 13 years of track counts from 2,202 km of roadway travel using Chi-squared goodness-of-fit tests of proportional segment lengths and the associated cover types, and 3) 76 nights over one winter of live-trapping using a hare/night index. Overall, we observed the greatest use within the youngest two classes of regenerating lodgepole pine stands that were associated with clear cutting and pre-commercial thinning. These results suggest snowshoe hares prefer silviculturally influenced 30–60 years old lodgepole pine forests

Key words: Snowshoe hare, *Lepus americanus*, lodgepole pine, *Pinus contorta*, pellet plots, track counts, pre-commercial thinning, clear-cutting

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Introduction

Snowshoe hares (*Lepus americanus*) are an important prey species throughout the boreal forests of North America (Murray et al. 2008). Many forest carnivores feed on snowshoe hares and, in some instances, depend on them for survival (Hodges 2000a). Snowshoe hare are the primary prey base of Canada lynx (*Lynx canadensis*), such that lynx populations are directly linked to snowshoe hare populations (Ruggiero et al. 2000). In 2000, the Canada lynx was listed as threatened in the contiguous United States under the Endangered Species Act (US Fish and Wildlife Service 2000). The Greater Yellowstone Ecosystem (GYE) has been designated as critical habitat for sustaining and recovering lynx (US Fish and Wildlife Service 2014). This area encompasses Yellowstone and Grand Teton National Parks, as well as the surrounding mountain ranges in southwestern Montana, northwestern Wyoming, and southeastern Idaho. Based on historical evidence, the GYE has likely only supported small resident populations of lynx, though this area may be important for dispersal and connectivity (US Fish and Wildlife Service

2017) and is home to the most southern population of naturally occurring lynx (Squires et al. 2003). However, relatively limited research has been conducted on lynx or snowshoe hares within the GYE compared to other portions of their range.

Snowshoe hares are generally found in forests with dense understory where horizontal cover is high (Litvaitis et al. 1985, Berg et al. 2012, Holbrook et al. 2017). Snowshoe hares rely on dense cover for concealment from ground and avian predators, as well as adequate forage to survive the harsh winter months (Litvaitis et al. 1985, Zimmer et al. 2008a, Berg et al. 2012). Snowshoe hares feed on a variety of plant species. During the winter in the GYE they feed mainly on low hanging needles and twigs of lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*) and subalpine fir (*Abies lasiocarpa*) (Zimmer et al. 2008a). As a result, snowshoe hares select for forest types that offer an optimal combination of cover and forage (Zimmer et al. 2008a;b).

While various landscape level factors such as climate, fire, insect infestation, and ungulate browsing have the potential to affect forest age and structure, managers can often have direct control over silvicultural practices in order to influence snowshoe hare habitat. In many parts of their range, snowshoe hares are more abundant in younger classes of regenerating conifer stands with high stem densities (Litvaitis et al. 1985, Hodges 2000b, Fuller et al. 2007). For example, one study within the GYE concluded that snowshoe hares were more likely to be found in relatively young classes of regenerating lodgepole pine forests (Zimmer et al. 2008b). However, other studies in the GYE indicate that snowshoe hares are more abundant in late successional forest types, associated with a multi-storied canopy and dense understory (Hodges et al. 2009, Berg et al. 2012). There have been relatively few snowshoe hare studies within the GYE and the results are not consistent as to what forest stand types snowshoe hares are more likely to use (Zimmer et al. 2008b, Hodges et al. 2009, Berg et al. 2012). Consequently, there are still many uncertainties regarding the best timber management practices to employ in the GYE to promote snowshoe hare habitat.

Although the GYE is associated with Yellowstone National Park, much of the snowshoe hare habitat in this region is under the jurisdiction of the U.S. Forest Service, which has a multi-use management mandate that allows timber management prescriptions. These activities can result in drastic changes to vegetation and cover and cause significant impacts on snowshoe hare populations (Murray et al. 2008). Clear-cutting and pre-commercial thinning are two of the main silvicultural treatments affecting forests in the GYE. Clear-cutting involves harvesting all the trees in a stand, thereby removing the cover on which hares rely. Snowshoe hares may avoid clear-cut areas immediately after treatment (Ferron et al. 1998). However, human replanted clear-cuts typically result in dense regenerating conifer forests which provide desirable cover for snowshoe hares (Litvaitis et al. 1985, Hodges 2000b, Fuller et al. 2007). Pre-commercial thinning involves selectively removing trees to attain a prescribed density or spacing to reduce competition, reduce fuel load, and promote tree growth, thus reducing the time stands take to reach maturity (Griffin and Mills 2007). Research has suggested that pre-commercial thinning negatively impacts snowshoe hares for at least the first two to five years post-treatment due to a decrease in horizontal cover (Griffin and Mills 2007, Homyack et al. 2007, Abele et al. 2013). However, research in the GYE found that the long-term effects of pre-commercial thinning may benefit snowshoe hares (Zimmer et al. 2008b). It was concluded that thinning reduced self-pruning of lodgepole pine trees so that trees in thinned stands maintained lower lateral branches, which provided favorable cover and forage during winter months when the stands are in early stages of succession (Zimmer et al. 2008b).

We assessed the relative use of snowshoe hares among forest types within a silviculturally-impacted portion of the GYE, using three indices of snowshoe habitat use, during a 13-year period in southwest Montana. Our goal is to provide insight into snowshoe hare use among common forest types within a silviculturally altered portion of the GYE to inform forest managers on snowshoe hare habitat management practices. By associations, these techniques will also favor Canada lynx. We predict that we will observe the greatest relative snowshoe hare use in early to mid-successional lodgepole pine stands based on previous work done within the area (Zimmer et al. 2008b). Therefore, the objective of this study was to evaluate the association between snowshoe hare use and vegetative cover types using long term indices.

Study Area

Our study area was located in the Bear Creek drainage of southwest Montana in the Custer-Gallatin National Forest approximately 8 km from the town of Gardiner, MT (Fig. 1). The study area was approximately 11.7 km^2 (1172 ha) of a US Forest Service timber management area. The elevation ranged from approximately 2100–2600 m, with winter snow depths during the study period averaging 83 cm at a SNOTEL location at 2560 m in elevation approximately 4 km from our study area (NRCS 2017).

The Bear Creek study area is a mosaic of conifer forests resulting from various silvicultural treatments intermixed with old growth stands. Predominate conifer species include lodgepole pine, Douglas fir, subalpine fir, and Engelmann spruce (*Picea engelmannii*). The forest cover types sampled in this study area were grouped into eight classifications based on dominant species and age classes using standard classifications for the region (Table 1; Mattson and Despain 1985).

Materials And Methods

Pellet Plots

We counted snowshoe hare fecal pellets from 2002–2012 as an index of snowshoe hare use in the Bear Creek study area, using surveying methods similar to Litvaitis et al. (1985) and Ferron et al. (1998). We selected 29 sample sites in our study area with three to four of the sites in each of the eight dominant cover types (Table 1; Figure 1). We identified forest stands of each cover type that were large enough to contain the configuration of pellet plots and randomly oriented the sites within these stands. Sites consisted of 10, 1-m radius plots established in two parallel lines, 50 m apart with 5 plots on each line. Plots were spaced 20 m apart along transects. This resulted in a sampling effort of 30 to 40 pellet plots in each of the eight cover types for a total of 290 plots. We systematically counted and removed snowshoe hare fecal pellets from each plot every spring after snow had completely melted. No other lagomorph species had been documented or observed in this study area. Thus, we were confident pellets were deposited from snowshoe hares only. We additionally counted and cleared pellet plots again in the fall during the years of 2009–2012. For these years, we totaled annual counts so that for all years, pellet counts represented an annual accumulation of pellets.

We used linear mixed effects models to evaluate the association between snowshoe hare use, as indexed through pellet plot counts, and forest stands in the Bear Creek study area. We excluded pellet counts from site 29, as field investigation into this site revealed that the forest characteristics did not fall into any defined cover type categories. We conducted mixed effects multiple regression using package ‘lme4’ (Bates et al. 2015) in program R (R Core Team 2017). We set the response variable to mean pellet counts at each site for each year. To meet assumptions of homogeneous variance and normally distributed error, we added 0.01 to the mean pellet counts and log-transformed the values. We included random intercept terms for ‘site’ and ‘year’ in all models to account for the inclusion of counts from the same site each year and to account for study area wide effects related to environmental conditions, population changes or changes in sampling frequency

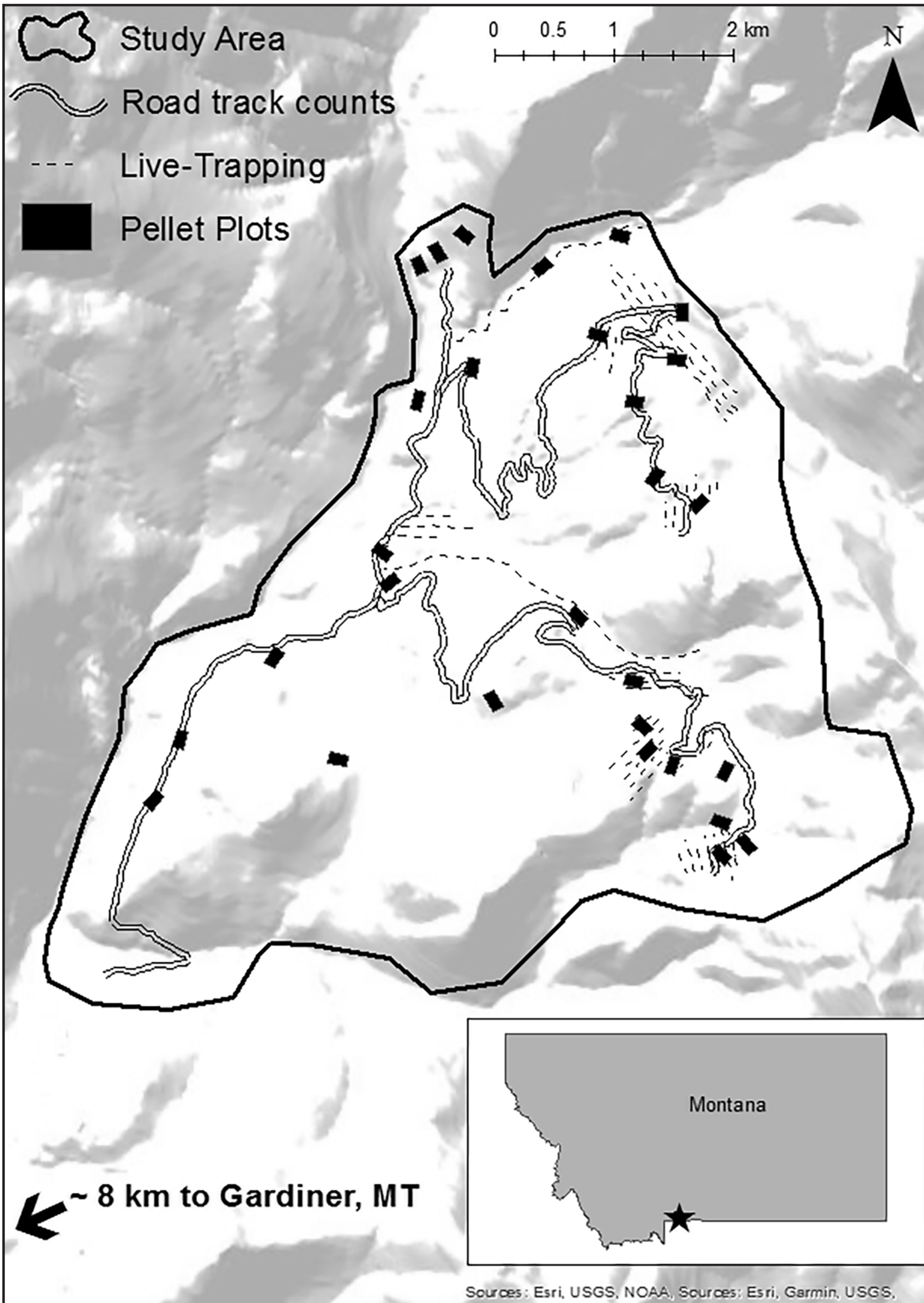

Figure 1. Location of the Bear Creek study area (1172 ha) and distribution of pellet plots, road track counts, and live-traps implemented to evaluate snowshoe hare use of coniferous forests.

Table 1. Dominant forest cover types within the Bear Creek study area where three indices of snowshoe hare use were implemented during 1999–2012.

Forest Cover Types*	Abb.*	Descriptions*	Proportion of Study Area (%)
Young regenerating lodgepole pine	LP0	Dense regenerating lodgepole pine stands resulting from clear-cutting between 1974–1976.	15
Middle-aged regenerating lodgepole pine	LP1	Regenerating lodgepole pine stands resulting from clear-cutting between 1950–1955 and Pre-commercial thinning 18 to 27 years later.	16
Mature lodgepole pine	LP2	Closed canopy dominated lodgepole pine stands estimated to be 100–300 years old with limited understory comprised of small to medium Englemann spruce and subalpine fir seedlings and saplings.	18
Late successional lodgepole pine	LP3	Broken canopy old growth lodgepole pine stands estimated to be > 300 years old. Small to large Englemann spruce and subalpine fir seedlings and saplings in understory.	13
Mixed forest	MF	Old growth late successional stands with varied age classes of trees and multiple species represented in the overstory	8
Spruce - fir	SF	Mature forests dominated by Englemann spruce and subalpine fir in both overstory and understory, typically found along drainage corridors in this area.	16
Douglas fir	DF	Old growth Douglas fir stands with a broken canopy, lacks understory, some spruce and fir present.	8
Sanitation salvage	SS	Mature mixed forest stands defined by a partial harvest of dead trees that occurred in 1986. Broken overstory with dense regenerating understory.	6

*Cover type classifications, abbreviations and descriptions were developed by Mattson and Despain 1985 with the exception of Sanitation salvage.

that could have been influencing all sites on an annual basis (Zuur 2009).

To address the association between snowshoe hare use and forest stand attributes, we reclassified the cover types into groupings based on stand commonalities described in cover type descriptions (Mattson and Despain 1985) and confirmed in the field (Table 2). The fixed effects for our models were developed using combinations of the groupings of cover types that were developed based on common stand attributes (Table 2).

We developed six *a priori* candidate models to test biological hypotheses regarding snowshoe hare use among the forest stands in our study area (Table 3). To compare silvicultural treatments to the absence of silviculture represented by late successional stands (Table 3), we considered M2 as the null model, instead of the intercept only model (M0). We ranked models using Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002; "AICcmodavg" package for R; Mazerolle 2017). The model with the lowest AIC_c was considered the most parsimonious. We calculated evidence ratios using AIC_c weights (ω_i) to demonstrate model support (Burnham and Anderson 2002). We evaluated model fit using marginal R^2 as a description of the variation accounted for by the fixed effects and conditional R^2 as a description of the variation accounted for by both the fixed effects and random effects in each model (Nakagawa and Schielzeth 2013; "MuMIn" package for R; Barton 2018). Models were developed using groupings of categorical variables that were not combined in the same way within each competing model, therefore models were non-nested and model averaging was not considered (Burnham and Anderson 2002). We reported on all parameter estimates due to the non-sequential model fitting approach and discussed effects of both informative and uninformative parameters based on an 85% confidence interval (Arnold 2010).

Table 2. Forest cover type groupings based on stand commonalities for modeling snowshoe hare use based on pellet counts within the Bear Creek study area from 2002–2012.

Grouping	Description
Regenerating	Young successional lodgepole forests (LP0 + LP1)
Late Successional	Young successional lodgepole forests (LP0 + LP1)
DF	Stands dominated by Douglas fir Same as DF cover type (DF)
LP	Forests dominated by lodgepole pine (LP0 + LP1 + LP2)
MIX	Forests with a Mixed spp. overstory (MF + SS)
SF	Same as spruce-fir cover type (SF)
Understory_LP	Forest with lodgepole in understory same as Regenerating (LP0 + LP1)
Understory_SF	Forests with spruce and sub-alpine fir in the understory (LP3 + MF + SS + SF)
Young	The youngest age stand, same as LP0 cover type (LP0)
Middle	Middle-aged stand, same as LP1 cover type (LP1)
Mature	Old aged stand, same as LP2 cover type (LP2)

Table 3. Six a priori models designed to test alternative hypotheses regarding the association of snowshoe hare pellet counts and forest stand characteristics in the Bear Creek study area from 2002–2012

Models*	Variables/Tested hypothesis
M0	Intercept only Hypothesis: Cover type is not a good predictor of snowshoe hare use as measured through mean pellet counts
M1	Regenerating Hypothesis: Mean pellet plot counts are only associated with the two regenerating lodgepole pine stand types
M2	Late Successional (Null) Hypothesis: Mean pellet plot counts are only associated with the late successional forest stand types indicating a lack of any timber management
M3	DF + LP + MIX + SF Hypothesis: Mean pellet plot counts are associated with the dominant overstory species of the site based on a reclassification of cover type categories.
M4	DF + Understory_LP + Understory_SF Hypothesis: Mean pellet plot counts are associated with the dominant conifer understory species of the site based on a reclassification of cover type categories.
M5	Young + Middle + Mature + Late Successional Hypothesis: Mean pellet plot counts are associated with age class of the site based on a reclassification of cover type categories

* Random intercepts for site and year included in all models.

Road Track Counts

We counted snowshoe hare tracks by travelling a road network within the Bear Creek study area during January–March, 1999–2012, except 2005 (Figure 1). We used a track-intercept design identical to Zimmer et al. (2008b). Track counts from 1999–2003 were published in previous work (Zimmer et al. 2008b) and were also included in our results in order to better understand trends over a longer time span. We divided the approximately 18-km road network into segments based on the cover type on either or both sides of the road (Table 1). Road segments with differing cover types on each side of the road were assigned combination classifications resulting in 11 unique road segment classifications (Table 2). We travelled the road network on snow machines 12–72 hours after snowfall events. We recorded fresh snowshoe hare tracks per road segment once for each time they intersected the roadway, regardless of the direction of the tracks, and recorded the time since snowfall.

We standardized snowshoe hare track counts by dividing the number of tracks by nights since last snowfall. We conducted Chi-square goodness-of-fit tests using Program R (R Core Team 2017) to assess if the proportion of tracks on each road segment classification was proportional to the respective distance. We averaged all survey counts from each year into a single measure to account for repetition of sampling and conducted tests of each individual year to assess changes in snowshoe hare use over the study period.

Live-Traps

We live-trapped snowshoe hares in the Bear Creek study area to assess use of different forest cover types during January–March, 2009. The labor and resources required to continue this effort was not available in any other winter of the study. Capture methods were similar to those used by Mills et al. (2005) and Berg and Gese (2010). All trapping protocols were approved by the Montana Fish, Wildlife and Parks Institutional Animal Care and Use Committee (IACUC # 8-2008). We set 80-traps with 50-m spacing between traps within each cover type. The cover types trapped were young regenerating lodgepole pine, middle-aged regenerating lodgepole pine, mature lodgepole pine, late successional lodgepole pine, and spruce-fir (Table 1). We modified trapping grids within each cover type by adjusting individual gridline lengths to preserve the 50-m spacing and to conform to the size and shape of the forest stands within the Bear Creek study area (Figure 1). This resulted in spatially independent sub-grids within the cover types, with the exception of the young regenerating lodgepole pine cover type and the mature lodgepole pine cover type which had stand sizes large enough to support a single contiguous trapping grid.

We checked traps daily and marked first time captures with unique numbered ear tags (National Band and Tag Company, 721 York St, PO Box 72430 Newport, KY 41072, USA, style 681). We documented location of capture, sex, body measurements and collected biological samples for additional research interests and released hares on site. Upon recapture, we recorded ear tag numbers, capture location, and re-collected measurements prior to release. Our trapping effort was divided into two trapping periods for each cover type. The first trapping period lasted 7–13 days followed by a 13–32 day rest between sequences then a final trapping period of 5–7 days. The length of the trapping periods was inconsistent due to adjustments made to minimize the impact on captured snowshoe hares while maximizing sample size (Mills et al. 2005). Forest carnivores, namely red fox (*Vulpes vulpes*) and American marten (*Martes americana*), at times discovered traplines, harassing and occasionally killing hares inside traps, causing us to end the trapping period.

In order to account for heterogeneity in trapping effort we calculated the number of unique snowshoe hares captured per trap night for each cover type trapping grid as an index of relative abundance (Dice 1931) or snowshoe hare use. Previous research in northern Montana found no justification for assuming unequal trappability of individual snowshoe hares or at different sites (Mills et al. 2005), thus we considered captures per night comparable among cover types. We summed the number of unique snowshoe hares captured in each cover type and divided it by the number of nights that traps were open for each respective cover type trapping grid. We also measured individual trapping period hare movements by comparing hare capture records with trap locations and ArcMap software and tools (ESRI 2011).

Results

Habitat Use: Pellet Plots

We surveyed 280 plots in the Bear Creek study area for 11 consecutive years during 2002–2012 resulting in 8,832 snowshoe hare fecal pellets counted. Average pellet counts per cover type varied between 0.36 in the Douglas fir cover type and 8.77 in the young regenerating lodgepole pine cover type (Fig. 2).

Results from the AIC_c model selection indicated that the model developed based on the dominant conifer understory species (M4) best explained mean snowshoe hare pellet plot counts among the candidate models and had 79% of the support of the data (Table 4). The remaining five models received relatively little support (Table 4). Evidence ratios between the top model and competing models suggested the top model was supported 3.95 times more than the second ranked model and 558 times more than the null model (M2).

The top model indicated that snowshoe hare pellet counts were associated with the conifer understory species as defined by the cover type classifications found in the Bear Creek study area. The estimated mean pellet counts were 0.05 (85% C.I. = 0.01,

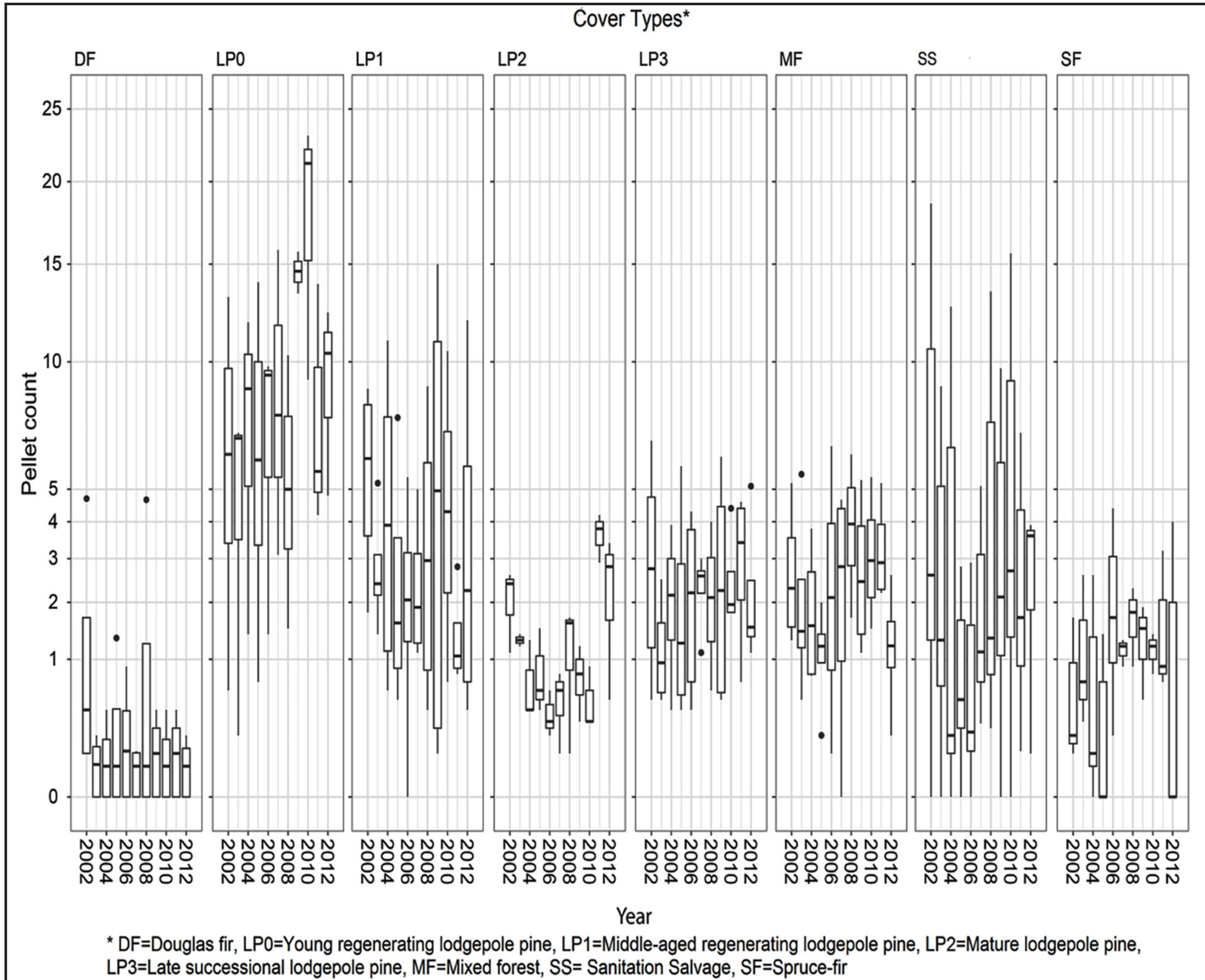

Figure 2. Boxplots of the average pellets recorded per cover type by year in the Bear Creek study area during 2002–2012 as an index of snowshoe hare use.

0.14), 3.19 (85% C.I. = 1.60, 6.36), and 1.14 (85% C.I. = 0.64, 1.59) pellets per plot for sites with Douglas fir, lodgepole pine, and spruce and subalpine fir dominance in the understory, respectively (Table 5). Sites that were dominated by lodgepole pine understory had approximately 61 times more pellets per plot than sites whose understories were dominated by Douglas fir, and approximately 3 times more than sites in which the understory was dominated by spruce and subalpine fir (Table 5). The marginal R^2 for the top model was 0.35 indicating 35% of the variation in pellet counts was accounted for by the fixed factors, the redefined cover types, while the conditional R^2 suggested that 72% of the variation was accounted for by both the fixed and random factors of year and site (Table 4).

Habitat Use: Road Track Counts

We counted a total of 14,324 snowshoe hare tracks intersecting the roadway by travelling approximately 2,202 km on snow machines over 13 winters during 1999–2012. The number of surveys conducted per year ranged from 5 in 2010 to 17 in 2002, due to the variability in snow events and timing. The annual average number of snowshoe hare tracks per night varied between 3.87 in the spruce-fir cover type and 386.51 in the middle-aged regenerating lodgepole pine cover type.

Snowshoe hare track counts of each individual year indicated that snowshoe hares did not use the cover type combinations proportional to availability the road segments (*P* < 0.001 each year). Small sample sizes of track counts for the individual years of 1999 and 2001 resulted

Table 4. Support for candidate models using AIC_c to test models developed from hypotheses regarding the association between snowshoe hare pellet counts and forest stand characteristics within the Bear Creek study area during 2002–2012.

Models*	K	AICc	∆AICc	ω_i	cR2	mR2
M4 = DF + Understory_LP + Understory_SF	6	1015.09	0.00	0.79	0.72	0.35
M3 = DF + LP + MIX + SF	7	1017.84	2.75	0.20	0.72	0.35
M1 = Regenerating	5	1026.30	11.21	0.00	0.71	0.09
M2 = Late Successional (Null)	4	1027.74	12.65	0.00	0.71	0.02
M5 = Young + Middle + Mature + Late Succesional	7	1029.41	14.32	0.00	0.72	0.15
M0 = Intercept only	4	1029.77	14.68	0.00	0.72	0.00

* Random intercepts for site and year included in all models.

Table 5. Estimates from the most parsimonious model (M4 = DF + Understory_LP + Understory_SF), determined through AIC_c, for explaining snowshoe hare pellet plot counts in the Bear Creek study area during 2002–2012.

Variable (understory spp.)	Estimate	Std. Error	Mean Pellet Count*	(85% CI)- Mean Lower*	(85% CI)- Mean Upper*
Douglas fir (DF)	-2.78	0.62	0.05	0.02	0.14
Understory_LP	1.16	0.47	3.19	1.60	6.37
Understory_SF	0.02	0.31	1.14	0.64	1.60

*Calculated using the inverse transformation (exponentiated coefficients -0.01) in violations of Chi-square test assumptions which prohibited us from conducting analysis for these years. We observed that segments defined by Douglas fir (DF) on both sides of the road as well as segments defined by meadows on both sides of the road were consistently used less than expected. Segments defined by middle-aged regenerating lodgepole pine stands on both sides (LP1) were consistently used more than expected. Track counts in the segments defined by young regenerating lodgepole pine stands on both sides (LP0) trended upward as time progressed (Fig. 3).

We found the highest positive difference between the observed proportion of tracks and the expected proportion of tracks on road segments defined by middle-aged regenerating lodgepole pine stands on both sides (LP1), with the exception of 2009, when the highest positive difference was documented on road segments with young regenerating lodgepole pine stands on both sides (LP0; Fig. 3). We observed the highest negative difference between the observed and expected proportion of use on road segments with Douglas fir (DF) stands on both sides each year. We observed the greatest change of use from the road segments in the young regenerating lodgepole pine stands (LP0). We documented a -0.08 proportional difference between observed and expected track counts in 2000, indicating use less than expected, and by the last year of the study (2012) we observed a 0.11 difference, indicating use greater than expected.

Habitat Use: Live-Trapping

We live-trapped a total of 59 unique snowshoe hares from all trapping grids within the Bear Creek study area during January–March of 2009. Nine of the 59 hares were recaptured in a second cover type trapping grid resulting in those individuals being considered unique snowshoe hares twice, once for each cover type. Our traps were set for a total of 76 nights for all five of the 80-trap grids combined, equating to 6,080 trap nights. The number of unique snowshoe hares captured in each trapping grid range from four in the mature lodgepole pine cover type to 20 in the young regenerating lodgepole pine cover type (Table 6).

The number of snowshoe hares captured per trap night was highest in young regenerating lodgepole pine stands (1.33 hares/night), followed by the spruce-fir stands (1.15 hare/night), middle-aged regenerating lodgepole pine stands (0.90 hares/night), late successional lodgepole pine stands (0.79 hares/night) and mature lodgepole pine stands (0.29 hares/night; Table 6). Recaptured snowshoe hare average movements, within a single trapping session, ranged from 85 m– 231 m. Notably, we observed two individual movements of >500 m within a single trapping period.

Discussion

Our pellet plot analysis revealed that relative snowshoe hare use was greatest in areas found in the two youngest classes of lodgepole pine stands (categories LP0 and LP1) that progressed in age from approximately 27–37 and 50–60 years old during the study. A considerable amount of variation in our pellet plot counts was explained by our site and year random effects with a higher range in variation among sites. We recognize that variation attributed to each site is likely related to site characteristics that we did not measure, however, we accounted for these potential effects in our models with the inclusion of the random effect variables. Annual variation may be related to the maturing and changing of forest stands over the study period. Specifically, we would expect to see the greater variations we observed over time in cover types that were going through successional changes related to silviculture and less variation in mature, stable forest types (Figure 2).

Our road track count analysis suggested that use of young regenerating lodgepole pine (LP0) and middle age regenerating pine stands (LP1) was higher than expected based on proportional availability of road segments in these same stands. Long-term,

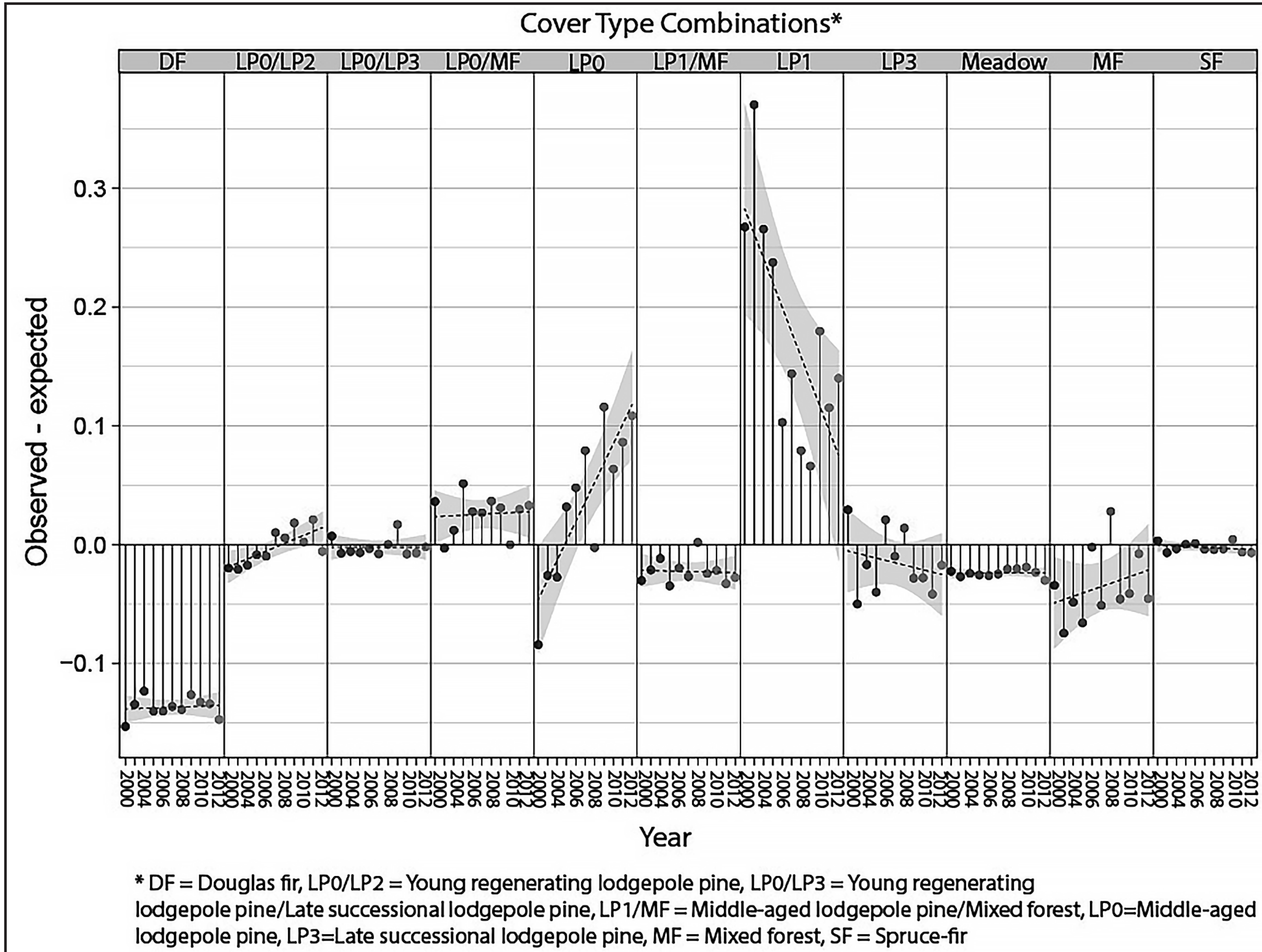

Figure 3. The difference between the observed and expected proportion of standardized track counts based on cover type combinations of road segments of individual years within the Bear Creek study area during 1999–2012 assessing snowshoe hare use among cover types

Table 6. Snowshoe hare live-trapping capture results from the Bear Creek study area during January–March of 2009 to assess relative snowshoe hare use among five dominant cover types.

Cover Type*	Traps	Nights	Individual Hares Captured	Hares / Night
Young regenerating lodgepole pine	80	15	20	1.33
Middle-aged regenerating lodgepole pine	80	20	18	0.90
Mature lodgepole pine	80	14	4	0.29
Late successional lodgepole pine	80	14	11	0.79
Spruce - fir	80	13	15	1.15

* Developed from Mattson and Despain (1985)

annual data also allowed us to assess trends and changes of use over time. Notably, we found that the young regenerating lodgepole pine stands were not used more than expected until they reached an age of approximately 31 years post clear-cutting. We recognize that track counts can be considered a weak index of snowshoe hare use due to the high variability of snowshoe hare activity and that tracks that were observed near the ends of each segment may have been correlated with the adjacent segment cover types. However, by standardizing counts and repeating our surveys multiple times per year over 13 years we feel that our results accurately demonstrate the disparity in relative use of cover types by hares. Our track count results were also corroborated by results from the pellet plot sampling.

The greatest numbers of snowshoe hares captured per night were in the young regenerating lodgepole pine stands. These stands were approximately 34 years old. We recognize that inferences about snowshoe hare use may be limited by a lack of replication of our efforts across space for each of the cover types or across time to account for annual variation. Also, the unstandardized shapes of the trapping grids have the potential to bias the number of snowshoe hares that encountered our 80-trap array. Nevertheless, results of our live-trapping effort were fairly consistent with the other indices of use. This consistency not only lends itself to strengthening our conclusions from individual indices, but more importantly solidifies our inferences regarding snowshoe hare use on a broader scale. The congruity of our results suggests that within the Bear Creek study area, within this time period, we were accurately observing snowshoe hare use among cover types. Collectively, our three independent indices suggest that relative snowshoe hare use was high in the younger classes of lodgepole pine stands.

The relative high use of the available cover types by snowshoe hares may be related to forage preferences of snowshoe hares. Other research related to snowshoe hare diet observed that lodgepole pine is a preferred food source for snowshoe hares during winter months due to a higher nutritional quality than other available forage (Sullivan and Sullivan 1988, Zimmer et al. 2008a, Ellsworth et al. 2013, Hutchen and Hodges 2018). However, the mature forest stands in our study area may have had slightly less horizontal cover than the younger regenerating lodgepole pine stands, as did some mature mixed conifer forests in the southern GYE (Berg et al. 2012). Thus, our findings may also be correlated to the structural density of younger lodgepole pine stands (Fuller et al. 2007, Zimmer et al. 2008b). We observed that the young regenerating lodgepole pine stands appeared to be at an age when self-pruning was limited and tree size was large enough to still provide cover during periods of deep snow accumulation. We also observed that middle-aged lodgepole pine stands had maintained low lateral branches, likely due to pre-commercial thinning. This provided snowshoe hares with low hanging branches for cover and forage, especially during periods of deep snow (Ivan et al. 2014).

Our pellet plot count index of snowshoe hare use was based on annual accumulations of pellets, thus our counts were related to habitat use of all seasons combined. Snowshoe hare track counts and live-trapping occurred in the winter, thus were only reflective of snowshoe hare use during the winter season. Similar results among methods suggest that young and middle-aged regenerating lodgepole pine stands were disproportionately used throughout seasons and throughout the study period. Although conditions and needs are likely to change throughout the year, winter is a season of increased predation pressure and decreased availability of forage species for snowshoe hares (Zimmer et al. 2008a, Squires et al. 2010). Thus, winter habitat is likely to be a central aspect to the survival of snowshoe hares. Quality habitat, as defined by Hall et al. (1997), is related to environmental conditions that allow individuals or populations to persist. Our study suggests that young and middle-aged regenerating lodgepole pine stands likely provided the cover and forage that snowshoe hares needed to survive the crucial winter months and thus should be considered a main component of quality snowshoe hare habitat in the northern GYE.

Forest stand size and connection to other stands are factors that may have also influenced snowshoe hare use in our study area. Snowshoe hare movements based on live-captures indicated that snowshoe hares used multiple stands within our study area. The intense timber management in our study area produced a mosaic of varied forest stand types and ages which may also benefit lynx (Holbrook et al. 2019). Holbrook et al. (2017) noted the importance of multi-use lands, such as National Forests, for snowshoe hares, which may be a reflection of the potential positive effects silviculture and a mosaic of smaller stands can have on snowshoe hare habitat. Snowshoe hares may be able to take advantage of multiple forests types for forage and cover if the heterogeneity of a landscape is such that hares can easily relocate if conditions or needs change (Hutchen and Hodges 2018).

Silvicultural practices have been restricted to maintain older seral classes of forests within the GYE (US Forest Service 2007). However, our results indicate the two youngest regenerating lodgepole pine forests were preferred by snowshoe hares within our study area, conflicting with recent policy related to silvicultural practices in the GYE. Pre-commercial thinning specifically has been restricted in lynx recovery areas, including the GYE. However, our results suggest that middle-aged regenerating lodgepole pine stands which had been thinned were generally used more by snowshoe hares than mature forest types. Zimmer et al. (2008a;b) suggested that delayed self-pruning due to pre-commercial thinning may extend the time that middle-aged lodgepole pine stands provide suitable forage and cover for hares and documented that these stands, which had been thinned, typically retained branches within 2-m of the ground. We advocate for more specific research into seasonal and long-term use of these silviculturally influenced cover types as well as stable mature stands, as use may relate to shifting resource needs and availability as well as life cycle events. We also advocate for more research on the effects pre-commercial thinning on snowshoe hare use, based on the relatively high use of middle-aged regenerating stands (LP1) within our study area, which had been the result of pre-commercial thinning. Our results suggest that silvicultural practices have the potential to at least create a temporal window of high snowshoe hare use of regenerating lodgepole pine stands.

Conclusions

Our research indicated that snowshoe hare use was greatest in lodgepole pine stands that were ≤ 60 years post clear-cut based on 13 years of data, and our results were consistent across three indices of snowshoe hare habitat use. Overall, we conclude that snowshoe hares demonstrate a preference for lodgepole pine stands that are approximately 30–60 years post-disturbance. We found evidence of an upward trend in snowshoe hare use in young regenerating lodgepole pine stands (LP0). This trend becomes apparent around 30 years post-disturbance. Comparably, there was a decreasing trend in the middle-aged lodgepole pine stand (LP1; Figure 3). We hypothesize that we were observing a shift in use from the middle-aged regenerating lodgepole pine stand to the young regenerating lodgepole pine stands due to the structural maturity in the younger stand and the onset of self-pruning in the middle-aged stands. We observed that snowshoe hare use was generally not as high in mature forest types. However, we did observe some use by snowshoe hares in the mature stand types as well as relative consistency of use over time (Figure 1, Figure 2). Thus we agree with past research that use of mature stands may be more temporally stable and thus important for long-term snowshoe hare habitat (Hodges 2000b).

Regional and intra-regional differences should be considered as our findings are translated by managers outside of our study area, since our study site represents such a small proportion of the GYE. Resource managers must also take into consideration important factors related to Canada lynx other than snowshoe hares, such as lynx reproductive success, other prey species and lynx hunting success (Ivan and Shenk 2016, Holbrook et al. 2019). Ultimately, as resource managers manage forests for snowshoe hares, we recommend that they reconsider blanket prohibitions on silvicultural practices and continue long-term research on the effects of silviculture on snowshoe hares.

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