

SNOWSHOE HARE HABITAT USE AND SILVICULTURAL INFLUENCES IN THE
GREATER YELLOWSTONE ECOSYSTEM

by

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ABSTRACT

Snowshoe hares (*Lepus americanus*) are the main prey base of the Canada lynx (*Lynx canadensis*) and are an important food source for many forest carnivores. Snowshoe hare research in the Greater Yellowstone Ecosystem is lacking and current research conclusions differ in regards to the types and ages of forests that snowshoe hares prefer. The US Forest Service has implemented limitations and prohibitions on silviculture in this area based on previous snowshoe hare studies. However, some research in the Greater Yellowstone Ecosystem suggests that regenerating lodgepole pine (*Pinus contorta*) stands that are associated with silviculture benefit snowshoe hares. We implemented three snowshoe hare use indices in southwest Montana within a portion of the Custer-Gallatin National Forest during 1999–2012 to assess snowshoe hare use of forest cover types in Greater Yellowstone Ecosystem. Our study area was located in a designated US Forest Service timber management area where a history of silviculture has resulted in a heterogeneous landscape of multiple successional stages intermingled with other old growth stands. We analyzed 11 years of snowshoe hare pellet plot surveys using linear mixed models and AIC_c model selection. Our results suggested that the understory conifer species was the best predictor of use and that the youngest two classes of regenerating lodgepole pine stands had the greatest snowshoe hare use. We analyzed 13 years of snowshoe hare track counts on roads within our study area using Chi-squared goodness-of-fit tests based on proportional road segment lengths and the associated cover types. We observed the greatest snowshoe hare habitat use in the youngest two classes of regenerating lodgepole pine stands. We live-trapped snowshoe hares for one winter in our study area and observed the greatest number of hares captured per night in the youngest lodgepole pine stands. The findings from our 13 year study suggest that snowshoe hare use was greatest in early successional lodgepole pine forests that were approximately 30–60 years old and associated with clear cutting and pre-commercial thinning.

CHAPTER ONE

INTRODUCTION AND LITURATURE REVIEW

Introduction

Snowshoe hares (*Lepus americanus*) are an important prey species throughout the boreal forests of North America (Murray et al. 2008). Many forest carnivores including coyotes (*Canis latrans*), red fox (*Vulpes vulpes*), great horned owls (*Bubo virginianus*), great gray owls (*Strix nebulosi*), goshawks (*Accipiter gentilis*), American martens (*Martes americana*), and Canada lynx (*Lynx canadensis*) selectively 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. Therefore, lynx populations are directly linked to snowshoe hare populations (Ruggiero et al. 2000). The Canada lynx has been listed as threatened under the Endangered Species Act (US Fish and Wildlife Service 2000). In the contiguous United States, Canada lynx persist at low numbers and relatively little is known about them or the ecology of their main prey base (Murray et al. 2008). In order to better understand and conserve this elusive feline, a more comprehensive understanding of snowshoe hares is required.

The Greater Yellowstone Ecosystem (GYE) has been identified as a critical area for sustaining and recovering Canada 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. Federally managed lands in the GYE include portions of the

Beaverhead-Deerlodge, Bridger-Teton, Caribou-Targhee, Custer-Gallatin, and Shoshone National Forests. This region is home to the most southern population of naturally occurring Canada lynx (Squires et al. 2003). The GYE is also crucial to conserving and connecting viable snowshoe hare and lynx habitat across the Rocky Mountains (Murray et al. 2008). However, only limited research has been conducted on lynx or snowshoe hares within the GYE.

Snowshoe hares are found in mountainous terrain typified by coniferous forests, low temperatures, and deep snow. Snowshoe hares are winter specialists. Their color-changing coats and oversized feet help them survive extreme winters and the increased predation pressure that occurs during this time of year (Squires et al. 2010). The classic cyclic fluctuations of snowshoe hare populations typically occur every eight to eleven years (Hodges 2000a). The amplitude and duration of cyclic fluctuations vary among regions and some evidence suggests that populations may be acyclic in the GYE (Hodges 2000b, Hodges et al. 2009). Snowshoe hare densities are much lower in their southern ranges compared to densities in Alaska and Canada (Hodges 2000b) and relatively little is known about snowshoe hares in the western United States, especially the GYE. Much of what we do know about snowshoe hares has been extrapolated from studies in their northern ranges (Hodges 2000b). Snowshoe hare home range sizes are estimated to be 5-10 ha, with occasional forays of >500 m at night observed (Hodges 2000a). While snowshoe hares can live up to six years in the wild, most breeding hares in a population are yearlings due to the high predation rates (Hodges 2000a).

One challenge within snowshoe hare research is determining habitat use and preferences. Habitat preference is a result of disproportional use, whereas habitat use refers to any way an animal uses the resources in a habitat (Krausman 1999). Therefore, snowshoe hare presence indicates that some type of use is occurring. Snowshoe use is often assessed either indirectly through relative amounts of sign (e.g. tracks or scat), or through the direct observation of individuals. Snowshoe hare preferences are often evaluated by measuring the relative use of different areas. Indirect indices of snowshoe hare use are frequently implemented because they are typically less costly, easier to replicate, and produce results that are consistent with direct observations (Krebs et al. 1987, Mills et al. 2005, Burt et al. 2016).

Literature Review

Snowshoe hares are found in forests with dense understory where horizontal cover is high (Litvaitis et al. 1985b, Berg et al. 2012, Holbrook et al. 2017). Snowshoe hares rely on dense cover for concealment from ground and avian predators (Litvaitis et al. 1985b, Zimmer et al. 2008a). Dense understory vegetation also provides snowshoe hares with adequate forage to survive the harsh winter months (Zimmer et al. 2008a, Berg et al. 2012). Snowshoe hares feed on a variety of plant species, but 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). Higher nutritional

quality of lodgepole pine leads to higher use by snowshoe hares and possibly habitat selection (Holbrook et al. 2017).

In many parts of their range, snowshoe hares are more abundant in younger classes of regenerating conifer stands (Litvaitis et al. 1985b, Hodges 2000b, Fuller et al. 2007, Berg et al. 2012). The high stem densities in regenerating stands offer dense understories (Litvaitis et al. 1985b, Hodges 2000b). However, some studies in the GYE indicate that snowshoe hares are more likely to be found in late successional forest types (Hodges et al. 2009, Berg et al. 2012). Higher snowshoe hare abundances in late successional stands were attributed to a multi-storied canopy with a dense understory component (Berg et al. 2012). The understory structure and composition in successional stages of forests may vary regionally resulting in different levels of snowshoe hare use.

Habitat preferences by snowshoe hares may also vary within regions, specifically the GYE (Zimmer et al. 2008b, Hodges et al. 2009, Berg et al. 2012). During a six year study in Yellowstone National Park, Hodges et al. (2009) documented few, if any, snowshoe hares in the extensive dense regenerating lodgepole pine forests that resulted from the 1988 wildfires based on live-trapping and fecal pellet count surveys. Hodges et al. (2009) noted that hares were more prevalent in mature forests. Berg et al. (2012) concluded that snowshoe hares were likely to be found in mature forests in the southern portion of the GYE based on pellet plot counts, but also observed high hare numbers in dense 30–70 year old lodgepole pine stands. Zimmer et al. (2008b) recorded the highest snowshoe hare use based on track counts in approximately 50–55 year old lodgepole pine stands that had experienced pre-commercial thinning in the northern portion of the GYE.

The three aforementioned studies conducted within the GYE are the only known studies related to snowshoe hare use in relation to forest types in this area. Therefore, there are still many uncertainties as to how to best manage for snowshoe hares within the GYE.

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. Snowshoe hare occupancy rates and intensity of use have been found to be higher on multi-use lands as opposed to protected areas like National Parks (Holbrook et al. 2017). Many of the lands in the National Forest system allow for timber management prescriptions including cultivation and removal of wood products. These activities can result in drastic changes to vegetation and cover, which can have significant impacts on snowshoe hare populations (Murray et al. 2008).

Clear-cutting and pre-commercial thinning are two of the main silvicultural treatments that affect the boreal forest where snowshoe hares are found. 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, replanted clear-cuts result in dense regenerating conifer forests which provide desirable cover for snowshoe hares (Litvaitis et al. 1985b, Hodges 2000b, Fuller et al. 2007). Pre-commercial thinning is a process wherein timber managers selectively thin out stands by removing trees to attain a prescribed density or spacing to promote the growth of the remaining trees by reducing competition.

In the western United States, regenerating conifer forests are often prescribed pre-commercial thinning to reduce the time stands take to reach maturity (Griffin and Mills 2007). Short-term effects of pre-commercial thinning have been shown to negatively impact snowshoe hare populations (Griffin and Mills 2007, Homyack et al. 2007, Abele et al. 2013). Studies in northern Montana and Oregon indicated that pre-commercial thinning reduced the number of snowshoe hares for at least the first two to five years post-treatment due to a decrease in horizontal cover. However, Zimmer et al. (2008b) found, in the GYE, that snowshoe hares were using lodgepole pine stands that had been pre-commercially thinned approximately 30 years prior more than other available forest types, which included younger regenerating lodgepole pine stands that had not been thinned, and several mature forest types. Zimmer et al. (2008b) suggested that snowshoe hares were using the middle aged pre-commercially thinned stands because thinning had reduced self-pruning so that trees in these stands had lower lateral branches which provided favorable cover and forage, especially in winter. Lodgepole pine trees in lower density stands maintain lower live branches nearer to ground level (Anhold et al. 1996). Moreover, fluctuations in snowshoe hare use of forest stands are expected, as the structure of the stands change throughout post-disturbance succession (Hodson et al. 2011).

The U.S. Forest Service's guiding document for lynx management prohibits pre-commercial thinning throughout the intermountain west including the GYE, based on the assumption that this treatment is detrimental to snowshoe hare habitat (US Forest Service 2007). However, this directive may not appropriately consider the regional variation of

snowshoe hare habitats across the Rocky Mountains, the discrepancies about the preferred ages of forest stands in the GYE, or the long-term effects of silvicultural treatments. Therefore, research comparing long-term snowshoe hare use in forest types with varying silviculture treatments would inform the efforts of land managers to protect snowshoe hare habitat and contribute to Canada lynx recovery.

A common method for measuring snowshoe hare use is fecal pellet plot counts or pellet plots (Mac Lulich 1937, Krebs et al. 1987, Malloy 2000, Krebs et al. 2001, McKelvey et al. 2002, Murray et al. 2002, Mills et al. 2005, Murray et al. 2005, Homyack et al. 2006, Hodges and Mills 2008, Berg and Gese 2010). Pellet plots are a way to systematically sample for snowshoe hare fecal pellets (Krebs et al. 1987). Pellet plots are a simple and inexpensive way to quickly assess snowshoe hare presence as they are non-invasive and can be conducted during times of year with easier accessibility (Mills et al. 2005, Berg et al. 2012, Holbrook et al. 2017). Pellet plots can be implemented on a semi-annual basis to study seasonal variations in snowshoe hare use (Litvaitis et al. 1985a). Also, with advancements in DNA sampling, individuals can be identified from pellets, providing a non-invasive technique for more accurate abundance estimates (Schwartz et al. 2007). An obstacle, when conducting pellet plots counts, is that survey timing and the plot design are crucial for yielding consistent and representative pellet counts. Fecal pellet decomposition rates can vary regionally, usually requiring plots to be surveyed and cleared at least annually (Malloy 2000, Prugh and Krebs 2004, Murray et al. 2005). Multiple shapes and sizes of plots have been used in snowshoe hare research, however, large circular plots have been recommended for the large scale sampling

required in snowshoe hare's southern ranges because they are more intuitive and less time-consuming to establish and repeat (McKelvey et al. 2002, Murray et al. 2002).

Track counts are another indirect index and have been shown to estimate patterns of snowshoe hare use that are consistent with other indices (Litvaitis et al. 1985a, Thompson et al. 1989, Ausband and Baty 2005, Griffin and Mills 2007, Bois et al. 2012). Track counts are an inexpensive and non-invasive method for evaluating snowshoe hare use over large areas (Mills et al. 2005). However, weather and other environmental factors affect snowshoe hare activity and the visibility of tracks (Griffin and Mills 2007). Therefore, track counts are often paired with other indices to prevent misrepresentation of snowshoe hare abundance (Ausband and Baty 2005, Bois et al. 2012). The number of tracks encountered can be highly variable from one survey to the next due to changes or shifts in activity, thus repeated surveys are needed to better represent patterns and trends over time (Thompson et al. 1989). Track count surveys can be time-intensive because long transects are usually required to sufficiently cover the study area (Burt et al. 2016). Snowshoe hare track counts are not as commonly used to evaluate habitat use as other indices because tracks counts are dependent on conditions, difficult to implement systematically and are best paired with other methods. One study developed a simplified method to counted snowshoe hare tracks by traveling roadways on snow machines (Zimmer et al. 2008b). Zimmer et al. (2008b) found consistency between the results from the simplified methods and results from systematic transects of the entire study area, suggesting that these simplified methods may be a valuable tool for snowshoe researchers

in areas where snow machines can be used. According to Hodges et al. (2009) there is no evidence that snowshoe hares are affected by roadways in the literature.

The most direct way to measure snowshoe hare presence is through capture-mark-recapture or mark-recapture (Mills et al. 2005). Through capturing a target animal, researchers can be assured of their presence and thus use of that particular area. Mark-recapture models are the most reliable method for estimating snowshoe hare abundance (Mills et al. 2005). However, mark-recapture is logistically demanding and often too costly to implement because hares have to be live-trapped and handled. Therefore, capture related injury or death to individual hares is possible which may negatively affect the study population (Silvy 2012). Even though population inferences from mark-capture data are more reliable than other methods, estimates derived from mark-recapture models with small sample sizes are negatively biased (Mills et al. 2005). Therefore, it has been recommended that mark-recapture only be conducted after indirect indices indicate there is a sufficient snowshoe hare population (Murray et al. 2002, Mills et al. 2005, Berg and Gese 2010).

Other techniques for evaluating snowshoe hare presence are uncommon within the literature likely due to the inherent difficulty of visually observing snowshoe hares in dense understories and the lack of vocalizations by hares. Direct observations of snowshoe hares have been conducted at night with the aid of red lights (Finley 1959). However, the incidental nature of the detections prohibited any inferences regarding habitat use or abundance (Finley 1959). Camera trapping snowshoe hares may be a viable method for evaluating snowshoe hare presence (Villette et al. 2017). Camera traps

have not been frequently implemented to detect snowshoe hares and has not been fully assessed as an index of habitat use or abundance (Villette et al. 2017).

Snowshoe hare research most commonly uses variations of fecal pellet counts, live-trapping, and track count methods to assess snowshoe hare presence or habitat use. Only two known studies have implemented all three of the commonly used methods and have done so over limited time periods (Litvaitis et al. 1985a, Griffin and Mills 2007). The exact relationship between the different indices is often unknown and may not hold up over the long-term due to variability of snowshoe hare activity patterns and population fluctuations (Litvaitis et al. 1985a, Hodges 2000b, Griffin and Mills 2007). Litvaitis et al. (1985a) compared snowshoe hare track counts, pellet counts, and live-trapping in Maine for two years and indicated that the indices provided similar information regarding habitat use. The mixed hardwood and conifer forests of Maine are drastically different from the conifer and lodgepole pine forests in the western United States and the GYE. The performance of snowshoe hare use indices may vary based on habitat conditions, thus the relationship between the indices may not be consistent in different regions. Griffin and Mills (2007) documented the presence of snowshoe hares for one year pre-silvicultural treatment and two years post-treatment in northwestern Montana with track counts, pellet plots, and trapping. Griffin and Mills (2007) found consistency in the documented relative use of pre and post-treatment stands among indices. Griffin and Mills (2007) were only able to assess snowshoe hare use for two years immediately after logging activity in a study area outside the GYE. A study including all three of these indices over a longer time period would greatly expand the understanding of snowshoe

hares and their habitat preferences in a region crucial to Canada lynx and allow future researchers to better understand the efficacy of each of these methods.

Summary

Although little is known about Canada lynx in the GYE, there is current and historical documentation within this area signifying the importance of gaining a better understanding of snowshoe hare ecology (Murphy 2005). The GYE has been under represented in snowshoe hare research. Long-term studies within the GYE on snowshoe hares are notably lacking (Hodges 2000b). Some snowshoe hare studies within the GYE have documented high use in mature forests (Hodges et al. 2009, Berg et al. 2012). Research outside the GYE, has suggested that pre-commercial thinning can cause snowshoe hare avoidance in the short-term. These findings have shaped lynx habitat management directives for the region by disallowing pre-commercial thinning and emphasizing the protection of mature forest stands (US Forest Service 2007).

Research within in the GYE has inconsistencies in regards to snowshoe hare use of different successional stages of forest stands. Two studies have suggested that younger classes of forest are important for snowshoe hares (Zimmer et al. 2008b, Berg et al. 2012). Berg et al. (2012) documented high snowshoe hare use in some 30–70 year old lodgepole pine stands and Zimmer et al. (2008b) found the highest snowshoe hare use in 50–55 year old lodgepole pine stands that had experienced pre-commercial thinning. The inconsistencies recorded regarding snowshoe hare preferences in the GYE suggests that younger classes of forest may be overlooked but important, and that silvicultural treatments are not always detrimental to snowshoe hares.

Snowshoe hare studies, in general, have been unable to include multiple indices to assess snowshoe hare use. Individual indices of snowshoe hare use are susceptible to inaccuracies due to variations in snowshoe hare populations and activity patterns (Thompson et al. 1989, Hodges 2000b). Zimmer et al.'s (2008b) findings in the northern part of the GYE are inconsistent with most other research in the region. However, this study only included snowshoe hare track counts over a five year period (Zimmer et al. 2008b). Management decisions could be improved by research over a longer-term study that includes multiple indices in this same study area.

Objectives

To assess the relative relationship between snowshoe hare use and forest cover types within a silviculturally-impacted portion of the GYE we analyzed a 13 year collection of data on snowshoe hare habitat use from a study area in southwest Montana. We hypothesize that snowshoe hares disproportionately use different cover types within our study area based on previous research that recorded higher relative use in middle-aged lodgepole pine stands (Zimmer et al. 2008b). In order to evaluate the association between snowshoe hare use and the characteristics that define forest cover types we conducted 11 years of pellet plot sampling. To assess the proportional use of cover types adjacent to roadways in comparison to the proportional length of the road segments we also conducted 13 years of road track counts, including five years previously analyzed by Zimmer et al. (2008b). To assess the relative use of the five most dominant cover types within our study area, based on a direct index of the number of individuals captured, we conducted a mark-recapture effort for one winter. Our goal was to add insight to

silviculture programs to enhance habitat managers' abilities to effectively manage for snowshoe hare and thus Canada lynx using this long-term study which included three indices of snowshoe hare habitat use in a timber management area.

CHAPTER TWO

METHODS

Study Area

Our study area is located in Bear Creek drainage of southwest Montana in the Custer-Gallatin National Forest approximately 8 km from the town of Gardiner, MT (Figure 1). The study area is approximately 11.7 km² (1172 ha) of US Forest Service designated timber management area with documented treatments occurring since the 1940s. The elevational range of the study area is approximately 2100–2600 m. Snow typically covers this landscape from late October to May. Winter snow depths during the study period averaged 83 cm at a SNOTEL location at 2560 m in elevation, which is approximately 4 km from our study area (NRCS 2017). Our study area is nearly surrounded by the unharvested forests of the Absaroka-Beartooth Wilderness and Yellowstone National Park and, as part of the GYE, has been deemed important lynx habitat by the US Fish and Wildlife Service due to its connectivity to a large, contiguous, and intact landscape (US Fish and Wildlife Service 2014). Within this study area there has been historical documentation of Canada lynx (D.B. Tyers, USFS, unpublished data).

The Bear Creek study area is a mosaic of conifer forest types that are the result of various silvicultural treatments as well as old growth stands. Predominate conifer species include lodgepole pine, Douglas fir, subalpine fir, and Engelmann spruce (*Picea engelmannii*). The specific forest cover types sampled in this study area were grouped into eight classifications based on dominant species, age and composition using standard

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. ^a	Descriptions ^a	Proportion of Study Area ^b (%)	Horizontal Cover Average ^c (%)	Horizontal Cover ^c (S.D.)
Young regenerating lodgepole pine	LP0	Dense regenerating lodgepole pine stands resulting from clear-cutting between 1974–1976.	15	59	19.3
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	19	14.3
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	14	10.3
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	28	15.0
Mixed forest	MF	Old growth late successional stands with varied age classes of trees and multiple species represented in the overstory.	8	35	25.4

Table 1 (continued).

Forest Cover Types	Abb. ^a	Descriptions ^a	Proportion of Study Area ^b (%)	Horizontal Cover Average ^c (%)	Horizontal Cover ^c (S.D.)
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	20	15.6
Douglas fir	DF	Old growth Douglas fir stands with a broken canopy, lacks understory, some spruce and fir present.	8	5	6.1
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	29	16.2

^a Developed from Mattson and Despain (1985)

^b Determined by Zimmer et al. (2008b)

^c Measured in 2008 using US Forest Service methodology (Squires and DeCesare 2008)

Pellet Plots

Data Collection

We counted snowshoe hare fecal pellets from 2002–2012 as an index of snowshoe hare use, using pellet plot surveying methods in the Bear Creek study area, similar to Litvaitis et al. (1985a) 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 2). 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 (Figure 3). The plot arrangement resulted in rectangular sites with an outer boundary of 52 m x 82 m to include the transect lines and the plot radii. We determined site locations by locating stands that were large enough to contain a site and randomly placed and oriented sites within these stands while in the field. We recorded coordinates of corner plots with handheld GPS units and permanently staked the center of each plot for repeatability. To sample the plots, we used a 1-m string attached to the center stake and rotated it around while systematically counting and removing snowshoe hare fecal pellets from each plot. We visited plots every spring after snowmelt (typically mid-May to mid-June) during the 11 year study period. We additionally counted and cleared pellet plots again in the fall from 2009–2012. For these years, we totaled previous years fall counts and spring counts for comparison with single sampling years.

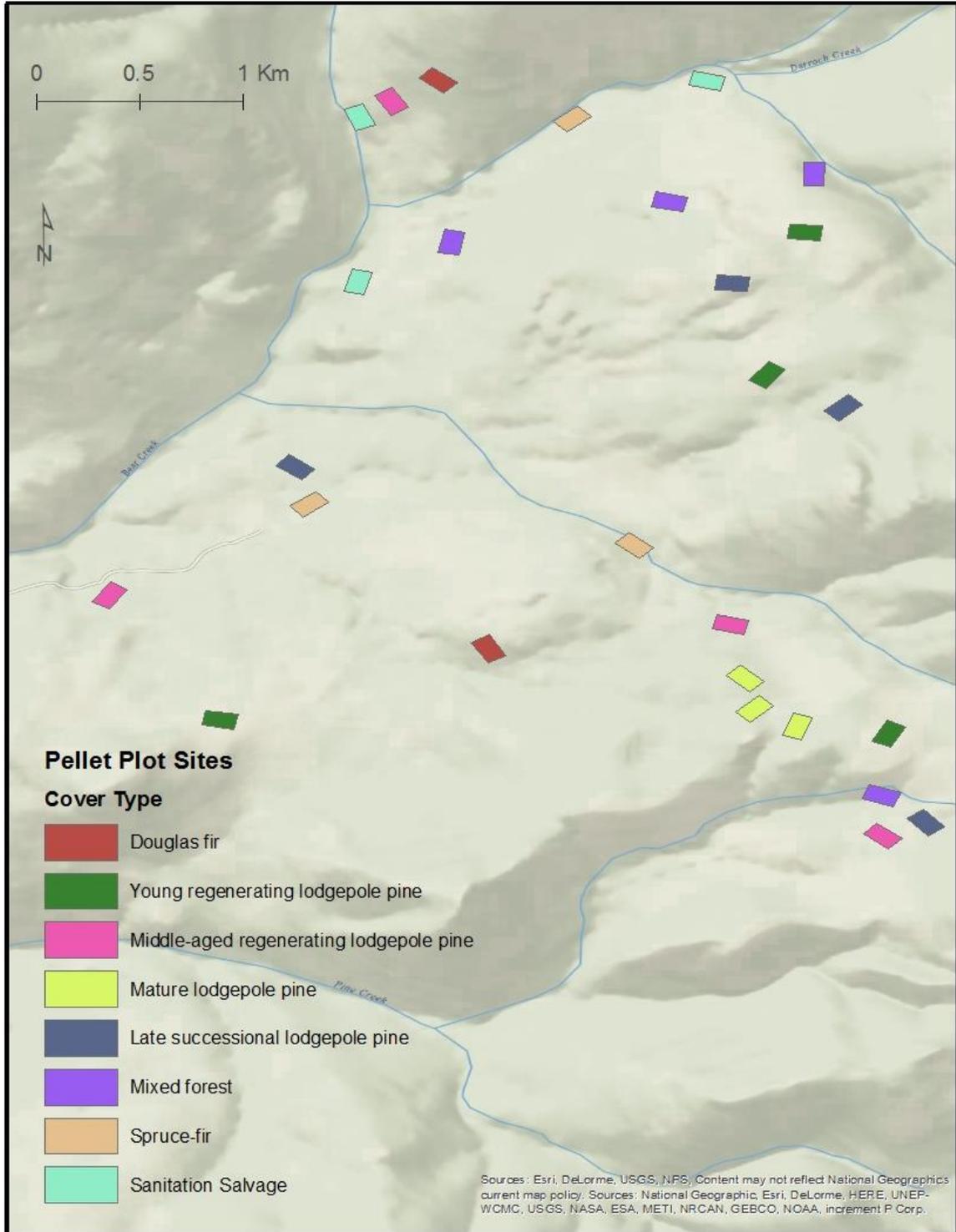


Figure 2. Locations of snowshoe hare pellet plot sites within the Bear Creek study area from 2002–2012 to assess snowshoe hare habitat use among cover types.

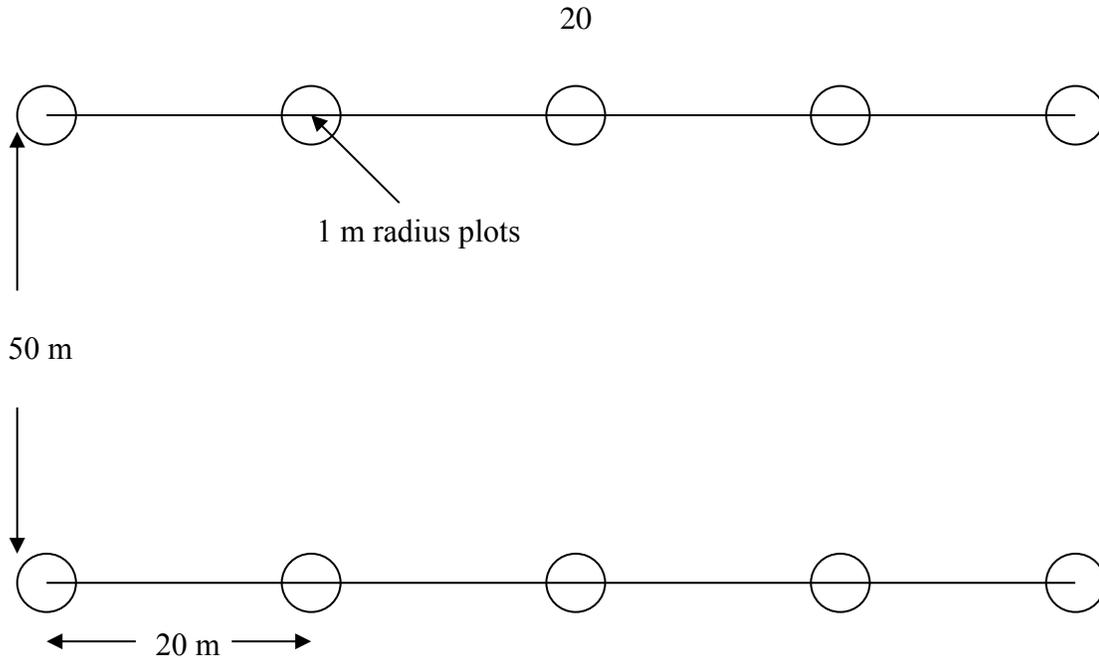


Figure 3. Arrangement of pellet plots within each of the 29 sample sites within the Bear Creek study area designed for counting snowshoe hare fecal pellets from 2002–2012.

We hypothesized that the cover type classifications (Mattson and Despain 1985) were not representative of forest stand characteristics that were likely the most influential in predicting snowshoe hare use within our study area. In order to gain more insight into the association between snowshoe hare use and forest stand attributes we reclassified the cover types into multiple alternative redefined categories. We developed redefined categories by grouping cover types based on commonalities described in cover type definitions (Mattson and Despain 1985) and common stand attributes observed in the field (Table 2). Redefined categories represented groupings that we hypothesized were more ecologically relevant for predicting snowshoe hare use.

Table 2. Redefined forest cover type categories developed based on stand commonalities that for modeling snowshoe hare use based on pellet counts within the Bear Creek study area from 2002–2012.

Redefined Categories	Description
Regenerating	Young successional lodgepole forests (LP0 + LP1)
Late Successional	Mature or late successional forest types (DF + LP3 + SS + MF + SF)
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)

Analysis

We used linear mixed effects models to evaluate the associations between snowshoe hare use, as indexed through pellet plot counts, and forest stands in the Bear Creek study area. We conducted analyses with the use of package ‘lme4’ (Bates et al. 2015) in program R (R Core Team 2017). We set the response variable to mean pellet counts for the ten plots at each site for each year. In order 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 excluded pellet counts from site 29, as investigation into these outlying data points revealed that the forest characteristics did not fall into any defined cover type categories. We included a random intercept term for ‘site’ in all models because we included counts from the same site each year which are repeated measures and are not independent (Zuur 2009). We also included a random intercept term for ‘year’ in all models because study area wide effects related to environmental conditions, population changes, or changes in sampling frequency could have been influencing all sites on an annual basis rendering counts within years not independent (Zuur 2009). The fixed effects for each model were developed using combinations of redefined categories of cover types (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). We treated M2 as our null model in order to compare silvicultural treatments to the absence of silviculture which is represented by late successional stands. 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 support for the top model (Burnham and Anderson 2002). Model validation was assessed 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). We considered multimodel inferencing by presenting results from all supported models ($\Delta AIC_c \leq 2$; Burnham and Anderson). 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). To the better understand the variability attributed to the year and site of sampling we graphed the conditional modes of the random effects (“sjPlot” package in R; Lüdecke 2018).

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	Hypothesis Reference
M0	Intercept only Hypothesis: Cover type is not a good predictor of snowshoe hare use as measured through mean pellet counts	Null
M1	Regenerating Hypothesis: Mean pellet plot counts are only associated with the two regenerating lodgepole pine stand types	Sullivan and Sullivan 1988
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	Hodges et al. 2009
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.	Holbrook et al. 2017
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.	Ellsworth et al. 2013
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.	Hodson et al. 2011

* Random intercepts for site and year included in all models

Road Track Counts

Data Collection

We travelled an established road network within the Bear Creek study area in order to count snowshoe hare tracks during January–March, 1999–2012, except 2005 (Figure 4). We used a track-intercept transect design similar to methods used by Thompson et al. (1989) and following the methods of Zimmer et al. (2008b). Track counts from 1999–2003 were published in previous work by Zimmer et al. (2008b). We included these years in our results as well to better understand snowshoe hare use trends over a longer time span. The total length of the road network was approximately 18-km in length. We divided the road network into segments based on changes in cover type on either or both sides of the road (Table 1). We grouped related road segments based on cover type, resulting in 11 unique road segment classifications (Table 4). Road segment lengths were measured using a hand-operated odometer wheel and ranged from 0.03 km to 1.48 km. We travelled the road network on a snow machine 12–72 hours after a snowfall event that was sufficient to cover old snowshoe hare tracks. We counted fresh snowshoe hare tracks that intersected the road from one side within each road segment. We recorded individual snowshoe hare tracks once for each time they intersected the roadway, regardless of the direction of the tracks. In instances when multiple sets of tracks were on top of each other we followed the tracks off of the roadway until they split apart and the number of tracks could be determined. We also recorded time after snowfall and road segments during each outing.

Table 4. The 11 cover type combination classifications along the road network within Bear Creek study area where snowshoe hare track counts were recorded during the winters of 1999–2012.

Cover Type Combinations*	Abbreviations*
Old growth Douglas fir stands on both sides of the road	DF
Young regenerating lodgepole pine stands resulting from clear-cutting between 1974–1976 on both sides of road	LP0
Young regenerating lodgepole pine stands resulting from clear-cutting between 1974–1976 on one side of road, mature lodgepole pine stand estimated to be 100–300 years old on other side of road	LP0/LP2
Young regenerating lodgepole pine stands resulting from clear-cutting between 1974–1976 on one side of road, late successional lodgepole pine stand estimated to be >300 years old on other side of road	LP0/LP3
Young regenerating lodgepole pine stands resulting from clear-cutting between 1974–1976 on one side of road, Mixed forest late successional stands with multiple conifer species in the overstory on the other side of the road	LP0/MF
Middle –aged regenerating lodgepole pine stands resulting from clear-cutting between 1950–1955 and Pre-commercial thinning 18 to 27 years later on one side of the road, Mixed forest late successional stands with multiple conifer species in the overstory on the other side of the road	LP1
Middle –aged regenerating lodgepole pine stands resulting from clear-cutting between 1950–1955 and Pre-commercial thinning 18 to 27 years later on both sided of the road	LP1/MF
Late successional lodgepole pine stands estimated to be >300 years old on both sides of road	LP3
Meadows found on both sides of the road	Meadow
Mixed forest late successional stands with multiple conifer species in the overstory on both sides of the road	MF
Spruce-fir stands late successional, dominated by Englemann spruce and subalpine fir found on both sides of the road	SF

*Developed from Mattson and Despain (1985)

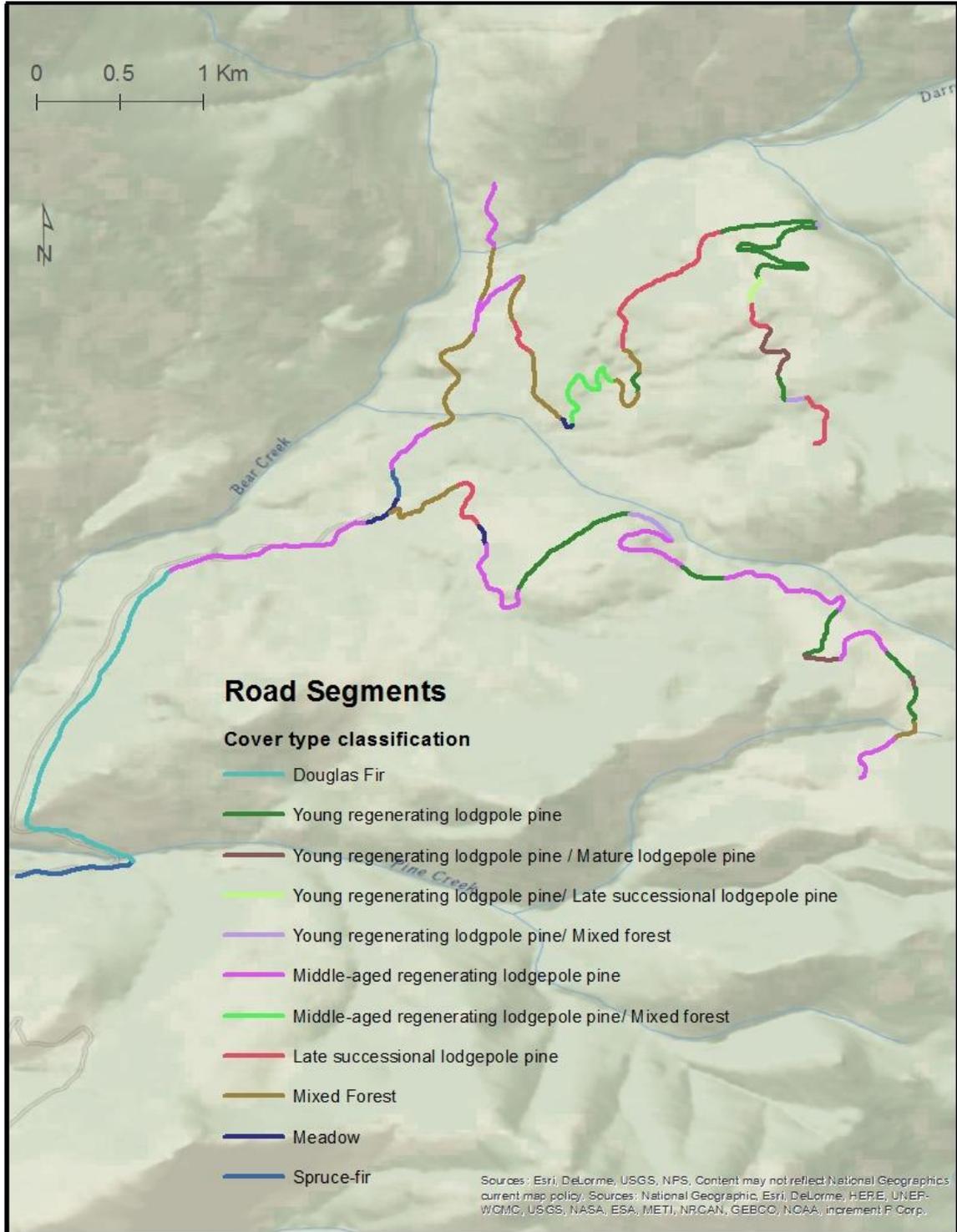


Figure 4. Location of the road network within the Bear Creek study area where snowshoe hare track counts were recorded during the winters of 1999–2012 to assess habitat use among cover types.

Analysis

We standardized snowshoe hare track counts by dividing the number of recorded snowshoe hare 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 counted on each road segment classification was equal to the respective proportion of the cover type combinations in regards to the total road network based on length using the standardized track counts. We combined all surveys from each year into a single measure to account for repetition of sampling. We conducted a Chi-square goodness-of-fit test on pooled track counts from surveys of all years to assess snowshoe hare use over the entirety of the study period. We also conducted Chi-square goodness-of-fit tests of combined surveys from each individual year to assess changes of snowshoe hare use within each cover type over time. We selected for this type of analysis to coincide with past research in this study area (Zimmer et al. 2008b).

Mark-Recapture

Data Collection

We conducted a mark-recapture live-trapping effort of snowshoe hares across the Bear Creek study area to assess snowshoe hare use of different forest cover types during January–March of 2009 similar to methods used by Mills et al. (2005), Hodges et al. (2009) and Berg and Gese (2010). All trapping protocols were approved by the Montana Fish, Wildlife and Parks Wildlife Division (Scientific Collectors Permit No. 2009-011). We established 80-traps grids with approximate 50-m trap spacing intervals within each of the five most dominant cover types in the Bear Creek study area. 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 in order 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 5). The young regenerating lodgepole pine cover type and the mature lodgepole pine cover type provided stand sizes that were large enough to support a single contiguous trapping grid. However, the smaller stand sizes of the middle-aged lodgepole pine and the late successional lodgepole pine cover type caused us to divide these trapping grids into three spatially separated sub-grids to remain within the representative cover type and to preserve the 80-trap overall trapping sample. The spruce-fir cover type was typically found along stream corridors within our study area resulting in narrow linear stand shapes. In order to trap solely within the spruce-fir cover type, we customized the spruce-fir trapping grid by aligning it into two spatially separated trap lines that acted as our sub-grids.

We checked traps at first light each morning by walking trap lines on snowshoes. We marked first time captures by attaching unique numbered tags to each ear. We use National Band wing bands (style 681) crimped through the ear cartilage as permanent ear tags. We documented location of capture and collected biological samples and measurements 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.

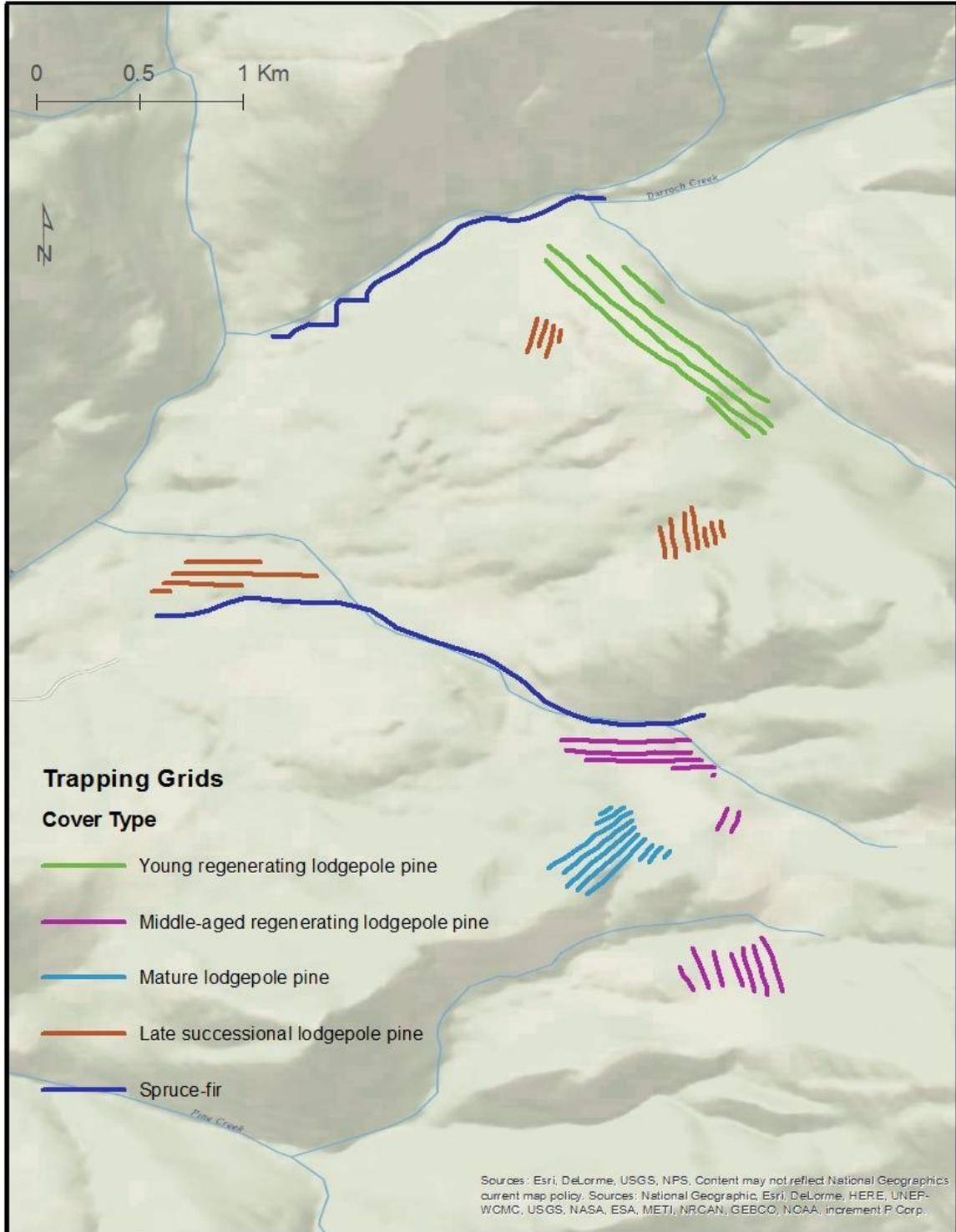


Figure 5. Location of snowshoe hare trapping grids in the Bear Creek study area during January–March of 2009. Trapping grids consisted of 80 traps per cover type to assess snowshoe hare use of the five dominant cover types in the study area.

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 when no trapping occurred then a final trapping period of 5–7 days. The length of the trapping periods were inconsistent due to adjustments made to minimize the impact on captured snowshoe hares while maximizing sample size (Mills et al. 2005).

Analysis

Our preliminary attempts to calculate abundance and density revealed violations of assumptions for mark-recapture population estimates (Otis et al. 1978, Seber 1982). Evidence of open populations, movement of individual snowshoe hares between grids, lack of replication, variability in recapture rates and small sample sizes led us to select a traditional technique of calculating the number of individuals captured per trap night as an index of relative abundance (Dice 1931) or snowshoe hare use of the sampled cover types. 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 individual 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 using plotted trapping grids and ArcMap software and tools (ESRI 2011).

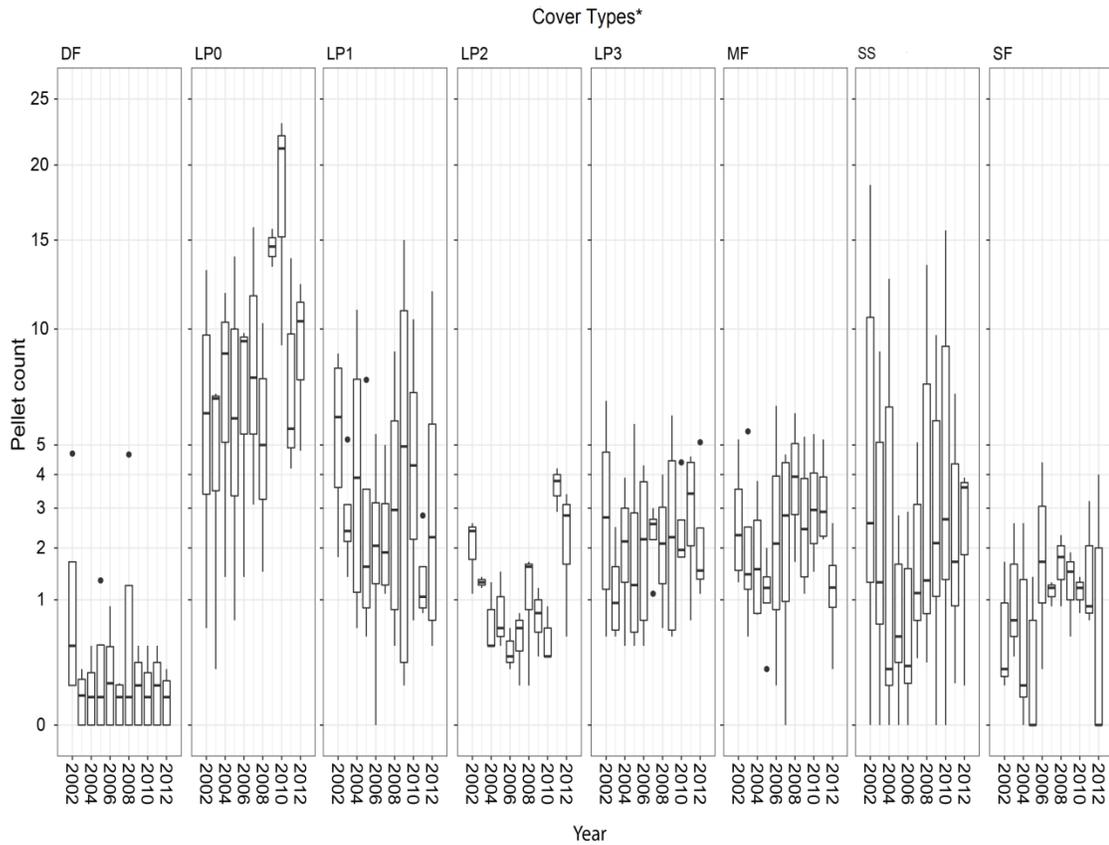
CHAPTER THREE

RESULTS

Pellet Plots

We counted 8,832 snowshoe hare fecal pellets in the Bear Creek study area by surveying 28 sites with ten plots at each site for 11 consecutive years during 2002–2012. Our average number of pellets per plot of all sites over the entire study period was 2.23. The maximum number of pellets at a single site in a single year was 231. We recorded zero pellets per site 34 times. 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 (Figure 6).

Results from the AIC_c model selection indicate M4 as the best model for explaining mean snowshoe hare pellet plot counts among the candidate models (Table 5). The remaining five models had a $\Delta AIC_c > 2$, therefore no inferences were made from these models. Model M4 had the highest relative support ($\omega_i = 0.79$) out of the six models considered. Evidence ratios between the top model and competing models suggested the M4 was supported 3.95 times more than the second ranked model and 558 times more than the null model (M2).



* DF=Douglas fir, LP0=Young regenerating lodgepole pine, LP1=Middle-aged regenerating lodgepole pine, LP2=Mature lodgepole pine, LP3=Late successional lodgepole pine, MF=Mixed forest, SS= Sanitation Salvage, SF=Spruce-fir

Figure 6. Boxplots of the average pellets counts recorded per cover type by year in the Bear Creek study area during 2002–2012 as an index of snowshoe hare use.

Table 5. 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	AIC_c	ΔAIC_c	ω_i	cR^2	mR^2
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 Successional	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

Results from the top model suggests that snowshoe hare pellet counts are 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 equal to 0.05 (85% C.I. = 0.01, 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 6). Sites defined by lodgepole pine being the dominant conifer species in the understory had approximately 61 times more pellets per plot than sites defined by Douglas fir in the understory, and approximately 3 times more than sites defined by spruce and subalpine fir in the understory.

Table 6. Estimates from the most parsimonious model ($M4 = DF + \text{Understory_LP} + \text{Understory_SF}$), determined through AIC_c , for explaining snowshoe hare pellet plot counts in the Bear Creek study area during 2002–2012. Estimates and standard errors were calculated from log transformed mean pellet counts at sites. Mean pellet count values and confidence intervals were calculated through transformations.

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)

The marginal R^2 for the top model was equal to 0.35 indicating 35% of the variation was accounted for by the fixed factors, the redefined cover types, while the conditional R^2 was equal to 0.72 suggesting 72% of the variation was accounted for by both the fixed and random factors of year and site. The variation among sites and years of sampling are represented with a plot of the conditional modes (Figure 7 and 8). In

addition to the classifications based on understory conifer species, unknown variables related to the year of sampling or the sample sites that we did not account for in the model are responsible for the observed variations.

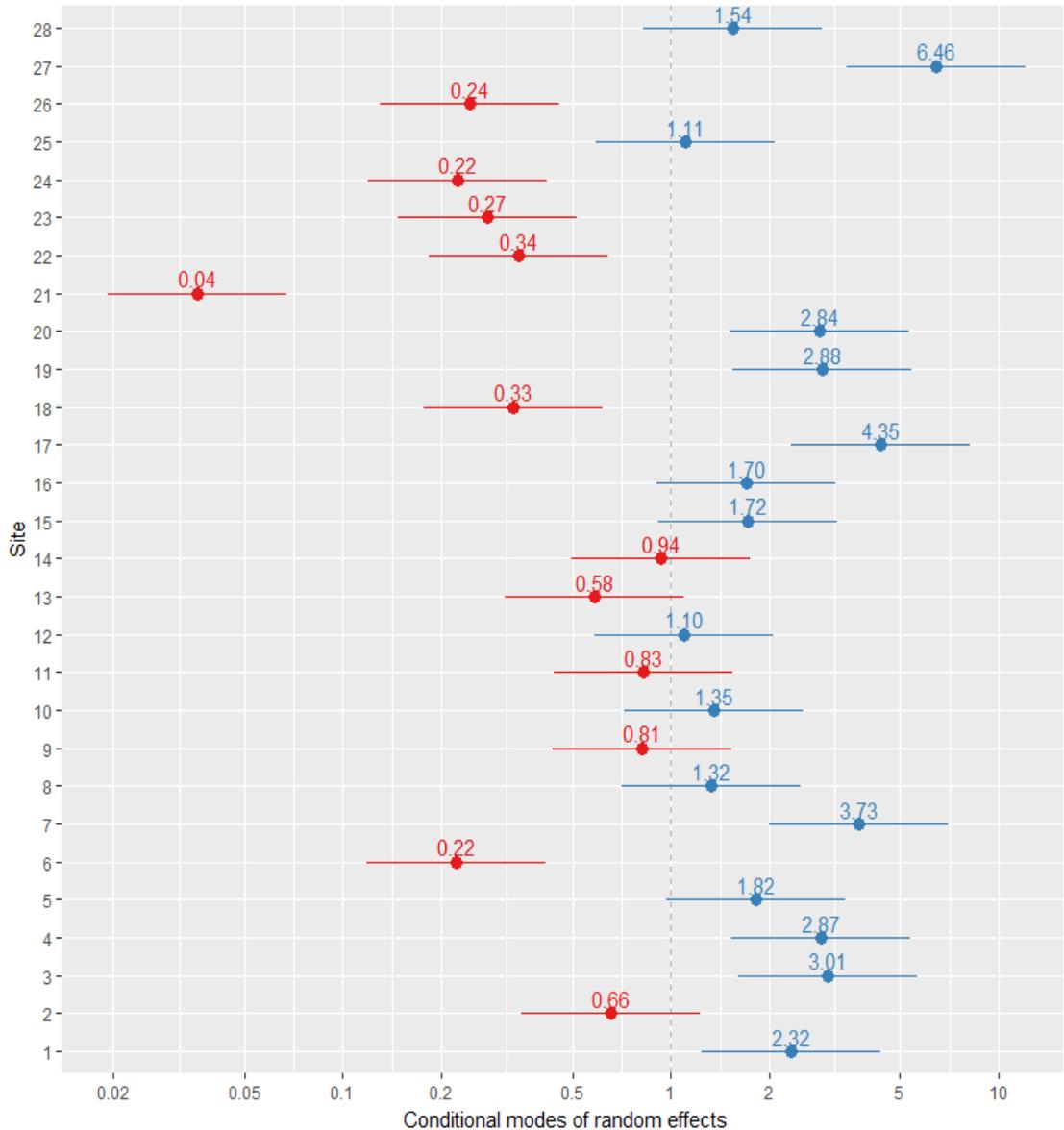


Figure 7. Exponentiated conditional modes (with 95% confidence bands) estimated for the sample sites in the Bear Creek study area from snowshoe hare pellet plot counts during 2002–2012. Individual random effects represent the variability attributed to the sample site. Estimated values can be interpreted as the multiplicative effect on mean pellet counts.

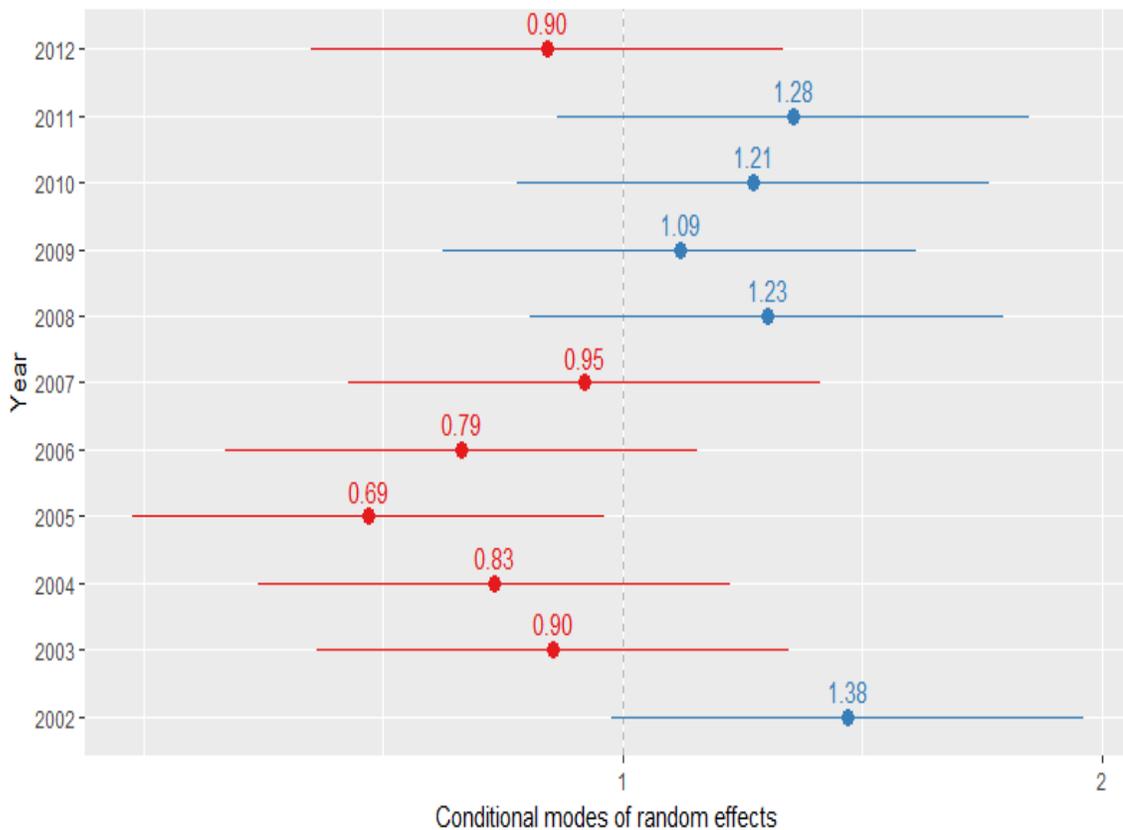


Figure 8. Exponentiated conditional modes (with 95% confidence bands) estimated for the year of sampling in the Bear Creek study area from pellet plot counts during 2002–2012. Individual random effects represent the variability attributed to the sample years. Estimated values can be interpreted as the multiplicative effect on mean pellet counts.

Road Track Counts

We counted a total of 14,324 snowshoe hare tracks intersecting the roadway and travelled 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. 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 (Figure 9).

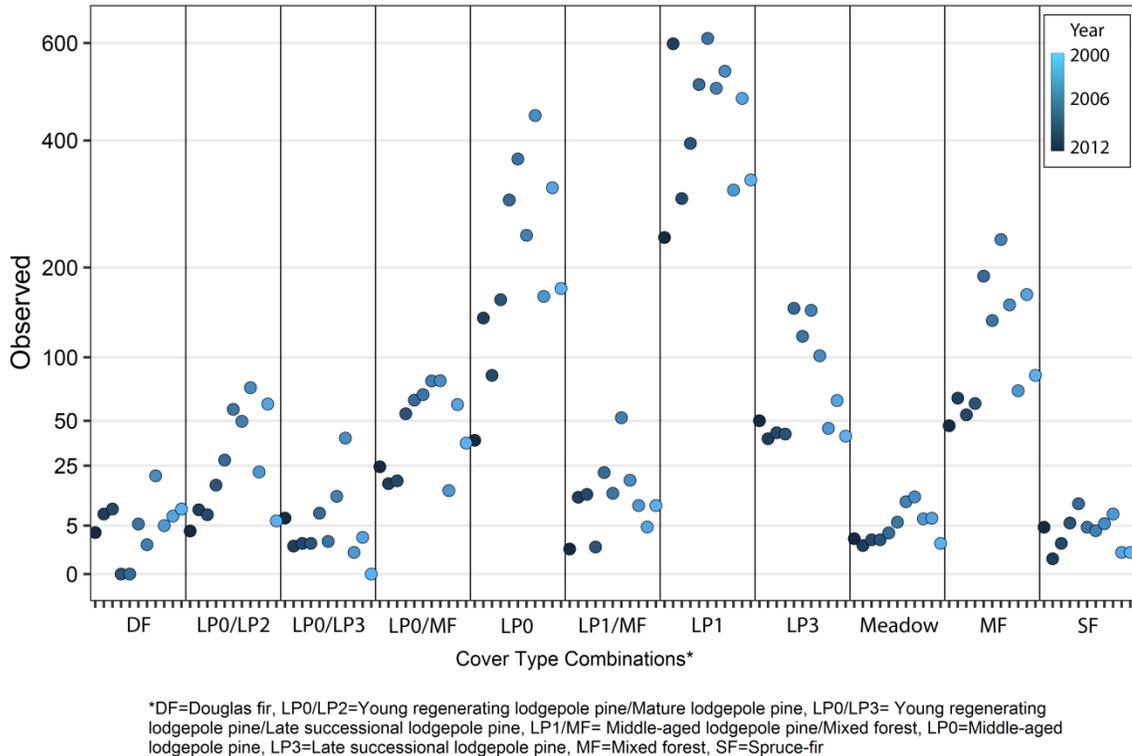


Figure 9. Number of observed standardized snowshoe hare tracks in each of the 11 cover type combinations by year in the Bear Creek study area during 1999–2012 as an index of snowshoe hare use.

Snowshoe hare track counts over all years of the study period indicated that snowshoe hares did not use the cover type combinations proportional to availability of measured road segments ($\chi^2 = 3447$, 10df, $P < 0.001$). Our Chi-squared analysis indicated that snowshoe hare use, indexed by tracks, was higher than expected in segments that were defined by young regenerating lodgepole pine stands on both sides of the road (LP0), a young regenerating lodgepole pine stand on one side and a mixed forest stand on the other (LP0/MF), and middle-aged regenerating stands on both sides of the road (LP1; Table 7). We found no significant difference ($P \geq 0.05$) between the observed and expected proportion of tracks on road segments defined by a young regenerating lodgepole pine stand on one side and a mature lodgepole pine stand on the other

(LP0/LP2) as well as segments defined by a young regenerating lodgepole pine stand on one side and a late successional lodgepole pine stand on the other (LP0/LP3). Our track counts indicated that use was less than expected for all other road segment types, which included Douglas fir on both sides (DF), middle-aged lodgepole pine on one side and mixed forest on the other (LP1/MF), late successional lodgepole pine stands on both sides (LP3), meadows on both sides, mixed forest stands on both sides (MF), and spruce-fir stands on both sides (SF).

When we combined the standardized number of snowshoe hare tracks over all the study period years we observed the highest positive difference between the observed and expected proportion of use on road segments that had middle-aged regenerating lodgepole pine stands on both sides of the road (LP1; Figure 10). We observed the highest negative difference between the observed and expected proportion of use on road segments with Douglas fir stands on both sides of the road (DF).

Snowshoe hare track counts of each individual year indicated that snowshoe hares did not use the cover type combinations proportional to availability of measured road segments ($P < 0.001$ each year). Small sample sizes of track counts for the individual years of 1999 and 2001 resulted in violations of Chi-square test assumptions which prohibited us from conducting analysis for these years. Snowshoe hare track counts indicated variability of proportional use across years with the exception of only three of the cover type combinations (Table 8). 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 (Figure 11). During 2000, track counts in segments defined by young regenerating lodgepole pine stands on both sides were lower than expected, from 2002 to 2004 there was no significant difference between observed and expected track counts, and from 2006 to 2012 track counts were higher than expected with the exception of 2008 when no significant difference was observed.

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; Figure 11). We observed the highest negative difference between the observed and expected proportion of use on road segments with Douglas fir stands on both sides (DF) 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.

Table 7. Chi-squared analysis of snowshoe hare use of cover types based on track counts from 1999–2012 in the Bear Creek study area.

Cover Type Combinations	Observed Tracks/night	Expected Tracks/night	Expected proportion of Tracks/night	Observed proportion of Tracks/night	Lower CI	Upper CI	Test Result*
Douglas fir	73.46	1635.06	0.15	0.01	0.01	0.01	-
Young regenerating lodgepole pine	2450.92	1941.56	0.18	0.22	0.21	0.24	+
Young regenerating lodgepole pine/Mature lodgepole pine	339.99	325.40	0.03	0.03	0.03	0.04	=
Young regenerating lodgepole pine/Late successional lodgepole pine	78.55	96.74	0.01	0.01	0.01	0.01	=
Young regenerating lodgepole pine/Mixed forests	532.97	235.81	0.02	0.05	0.04	0.06	+
Middle-aged regenerating lodgepole pine	5024.65	3241.27	0.30	0.46	0.45	0.47	+
Middle-aged regenerating lodgepole pine/Mixed forest	160.86	399.79	0.04	0.01	0.01	0.02	-
Late successional lodgepole pine	869.88	1022.67	0.09	0.08	0.07	0.09	-
Meadow	58.18	319.26	0.03	0.01	0.00	0.01	-
Mixed forest	1296.03	1636.08	0.15	0.12	0.11	0.13	-
Spruce-fir	50.34	82.20	0.01	0.00	0.00	0.01	-

*"-“ indicates less than expected ($P < 0.05$), “+” indicates greater than expected, and “=” indicates no significant difference between observed and expected.

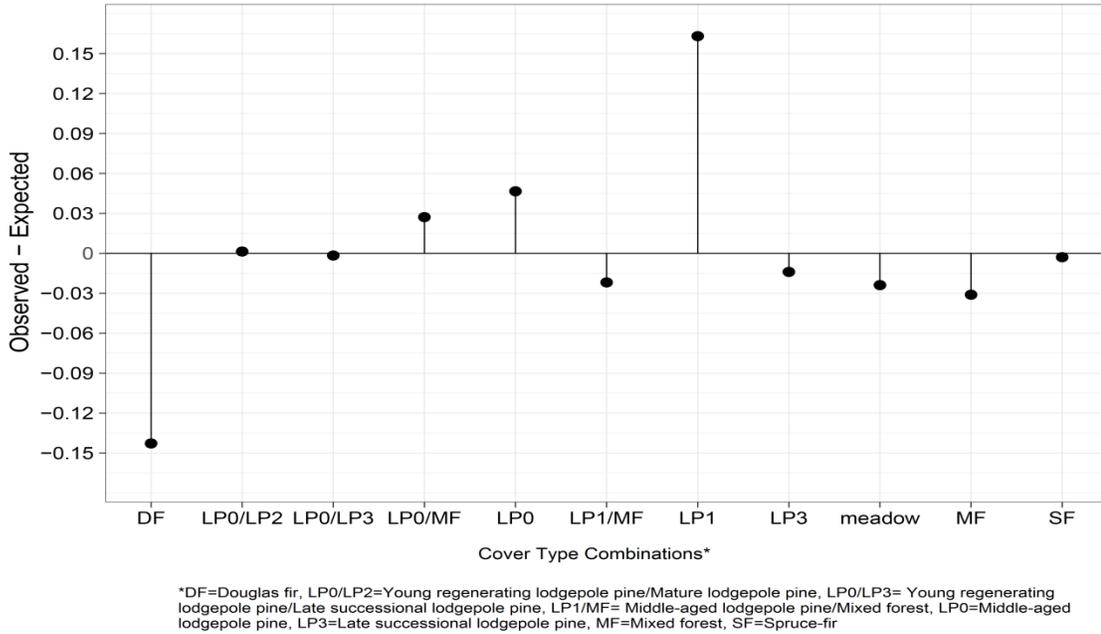


Figure 10. The difference between the observed and expected proportion of standardized track counts based on cover type combinations of road segments over all years within the Bear Creek study area during 1999–2012 assessing snowshoe hare use among cover type.

Table 8. Summary of Chi-squared test results of cover type use by snowshoe hare track count proportions in regards to proportional length of road segments in each cover type combination from 2000–2012 in the Bear Creek study area.

Cover Type Combination	Number of years "+"	Number of years "="	Number of years "-"
Douglas fir	0	0	11
Young regenerating lodgepole pine	6	4	1
Young regenerating lodgepole pine/Mature lodgepole pine	2	6	3
Young regenerating lodgepole pine/Late successional lodgepole pine	1	4	6
Young regenerating lodgepole pine/Mixed forests	8	3	0
Middle-aged regenerating lodgepole pine	11	0	0
Middle-aged regenerating lodgepole pine/Mixed forest	0	2	9
Late successional lodgepole pine	0	6	5
Meadow	0	0	11
Mixed forest	0	4	7
Spruce-fir	0	8	3

“+“ indicates less than expected (P<0.05), “=” indicates no significant difference, and “-” indicates less than expected between observed and expected.

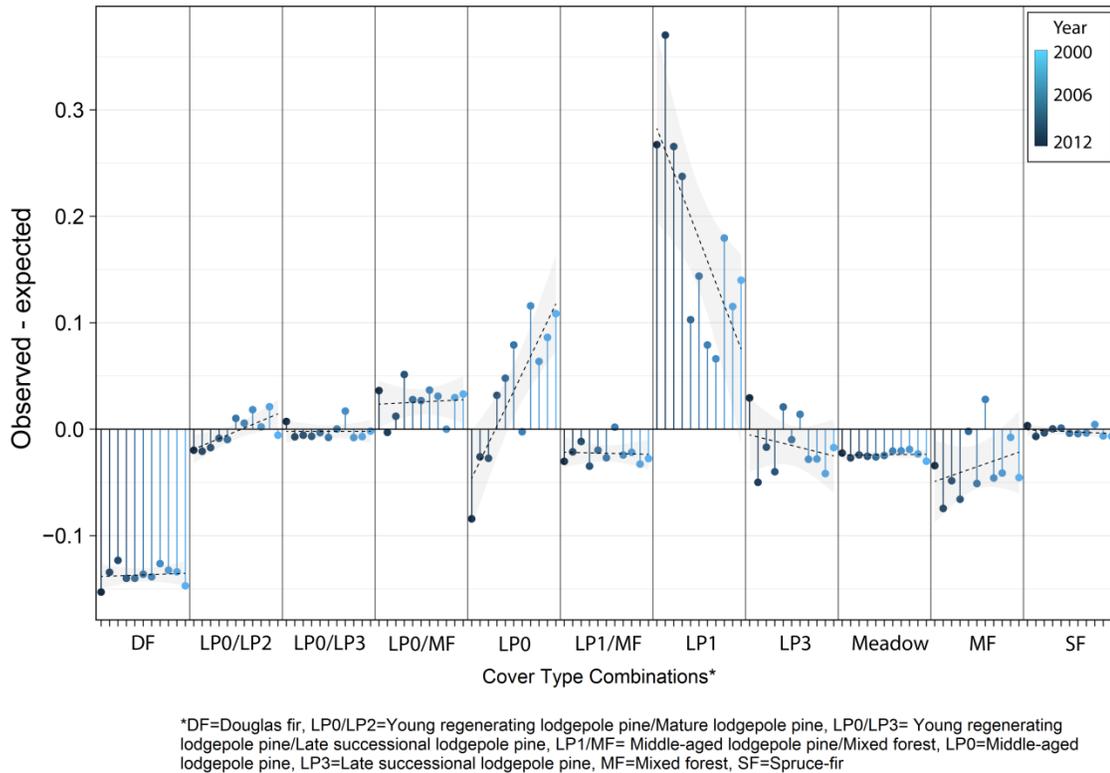


Figure 11. The differences between the observed and expected proportion of standardized track counts based on cover type combinations of road segments of individual years within the Bear Creek study area during 1999–2012 assessing snowshoe hare use among cover types.

Mark-Recapture

We captured and marked a total of 59 unique snowshoe hares within the Bear Creek study area during January–March of 2009. 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. Our non-target captures included gray jays (*Perisoreus canadensis*) and red squirrels (*Tamiasciurus hudsonicus*). The number of individual snowshoes 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 9).

Results from our calculations of individual snowshoe hares captured per trap night for each cover type indicated that the young regenerating lodgepole pine stands had the highest documented index of snowshoe hare use of 1.33 hare/night. We documented the second highest use in the spruce-fir stands at 1.15 hare/night, followed by the middle-aged regenerating lodgepole pine stands at 0.90 hares/night, the late successional lodgepole pine stands at 0.79 hares/night and the mature lodgepole pine stands at 0.29 hares/night (Table 9). The sum of the individuals captured was 68, which reflects that out of 59 unique individuals, nine were captured in multiple cover type trapping grids. We calculated that average maximum movements by individual snowshoe hares within trapping sessions ranged from 85 m–231 m. Notably, we observed two individual movements of >500 m within a single trapping period.

Table 9. 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)

CHAPTER FOUR

DISCUSSION AND MANAGEMENT IMPLICATIONS

Discussion

Our research indicates that snowshoe hare use was greater in lodgepole pine stand that were ≤ 60 years post clear-cut, than in mature stands based on 13 years of data including three indices of snowshoe hare habitat use. Our pellet plot analysis revealed that snowshoe hare use was highest in two classes of lodgepole pine stands (LP0 and LP1) that progressed from approximately 27–37 and 50–60 years old respectively. A considerable amount of variation in our pellet plot counts was explained by our site and year variables with a higher range in variation among sites (Figure 7 and 8). We hypothesize that the variation due to year was likely a reflection of the snowshoe hare population fluctuating and environmental variability through the study period. We recognize that variation attributed to each site is likely related to site characteristics that we did not measure.

Our road track count analysis suggests that use of road segments that travelled through young regenerating lodgepole pine (LP0) and middle age regenerating pine stands (LP1) was higher than expected based on proportional availability in these same stands, and when analyzed per year our findings were 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. We recognize that tracks that were observed near the ends of each segment are likely correlated with the adjacent segment cover types possibly confounding some of our results. However, by standardizing counts and repeating our surveys multiple times per year over 13 years we feel that our results demonstrate the disparity in relative use.

We found that the greatest numbers of snowshoe hares captured per night were in the young regenerating lodgepole pine stands and the third greatest in the middle-aged regenerating lodgepole pine stands based on our mark-recapture effort. These stands were approximately 34 and 57 years old respectively. We recognize that inferences about snowshoe hare use may be limited by our implementations of our live-trapping methods. Within this study we did not have the opportunity to replicate our efforts across space for each of the cover types or across time to account for annual variation. Also, we were unable to standardize the shapes of our trapping grids due to the heterogeneity of forest stand shapes and sizes. The irregular shapes of the trapping grids have the potential to bias the number of snowshoe hares that encountered our 80-trap array. Our results were similar to other findings in this study thus we concluded that in areas with higher snowshoe hare use we were more likely to capture hares and in areas with lower use we were less likely to capture hares.

Individual results from each method were not identical as we observed some differences in the rankings of the cover types. However, the greatest and least used cover types within our study area were validated by all the methods suggesting that overall our results accurately reflect the disparity of snowshoe hare use within our study area. We attribute the differences that we observed to the timing and specific locations that

sampling occurred. Overall, our findings from each index of snowshoe hare use were similar and we concluded that snowshoe hares showed a preference for lodgepole pine stands that were approximately 30–60 years post-disturbance.

We hypothesize that our results may be related to forage preferences of snowshoe hares. Other research related to snowshoe hare diet in this region observed that lodgepole pine is was a preferred food source for snowshoe hares during winter months due to higher nutritional quality (Zimmer et al. 2008a, Ellsworth et al. 2013, Holbrook et al. 2017). Our findings are likely reflective of the preference for lodgepole pine as a food source when adequate cover is available within the same stand or in a nearby stand. However, the mature forest stands in our study area had slightly less horizontal cover than the young regenerating lodgepole pine stands (Table 1). Thus, our findings may also be correlated to the structural density of horizontal cover in the younger lodgepole pine stands. 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, thus providing snowshoe hares with low hanging branches for cover and forage.

Forest stand size and connection to other stands are factors that may influence snowshoe hare use. Our mark-recapture data indicated that snowshoe hares used multiple stands possibly because the intense timber management in our study area produced a mosaic of relatively small varied forest stands. Hodges et al. (2009) recorded a lack of use in the vast, homogeneous, young regenerating lodgepole pine stands in Yellowstone

National Park, resulting from the 1988 wildfires. We reason that these stands may not have been able to provide yearlong cover and browse. Due to their size, snowshoe hares could not travel the required distances to other stands types when seasonal changes occurred, thus they could not utilize these stand at all. Holbrook et al. (2017) noted the importance of multi-use lands for snowshoe hares, such as National Forests, which may be a reflection of the potential positive effects silviculture and a mosaic of smaller stands can have on snowshoe hare habitat.

Previous research within the GYE has emphasized the importance of mature multi-storied forests for snowshoe hares (Hodges et al. 2009, Berg et al. 2012). Silvicultural practices have been restricted to maintain these older seral classes of forests (US Forest Service 2007). However, our results indicate that the two youngest regenerating lodgepole pine forests were preferred by snowshoe hares. This highlights that mature forest types may not be the only important forest type for snowshoe hares in the GYE as previously suggested (Hodges et al. 2009). Snowshoe hares may benefit from the silvicultural practices of clear-cutting and pre-commercial thinning that created these younger stand types. Therefore, silviculture may ultimately have an important role in improving forest structure to the benefit of snowshoe hares. Our results may also suggest that there can be different snowshoe hare use patterns based on location even within the GYE. This intra-regional variation may be overlooked in snowshoe hare habitat management directives.

Restrictions have been placed on pre-commercial thinning in lynx recovery areas because snowshoe hare research in the western United States has indicated that reducing

cover in dense conifer stands with pre-commercial thinning is detrimental to snowshoe hare habitat (Griffin and Mills 2007, US Forest Service 2007, Berg et al. 2012, Abele et al. 2013). However, our results suggest that middle-aged regenerating lodgepole pine stands which had been thinned were among the greatest used cover types, with even greater use than many 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. While pre-commercial thinning may immediately remove cover, over time pre-commercial thinning likely limits self-pruning, maintains a lower live crown, and potentially promotes understory growth of other suitable browse species (Anhold et al. 1996). We advocate for more research on pre-commercial thinning based on the relatively high use of middle-aged regenerating stands (LP1) within our study area, all of which had been pre-commercially thinned.

Short-term studies on snowshoe hare use may not be taking into account the trends in use that occur as forests progress through succession. We found evidence of an upward trend in snowshoe hare use in young regenerating lodgepole pine stand (LP0) that becomes apparent around 30 years post-disturbance and a decreasing trend in the middle-aged lodgepole pine stand (LP1; Figure 11). 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 which we attributed to the structural maturity in the younger stand and the onset of self-pruning in the middle-aged stands. Short term

studies would likely not have been able to document this shift in use and conclusion could have misrepresented what is occurring over time.

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 result among method suggests 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 stand are providing the cover and forage that snowshoe hares need to survive the crucial winter months and thus are a main component of quality snowshoe hare habitat.

Management Implications

We agree with previous research that found similar result using three snowshoe hare use indices (Litvaitis et al. 1985a, Griffin and Mills 2007). Since indirect indices, such as pellet plots and tracks counts, are less costly and time demanding to implement, we were able to repeat these methods for over 10 years. Live-capture of snowshoe hares

is a useful tool. However, due to the high cost to researchers, replication may be difficult and can even be detrimental to the studied population (Silvy 2012). Low densities of snowshoe hares in the southern portion of their range also make it difficult to capture a large enough sample size to effectively estimate populations (Murray et al. 2002).

Replication and long-term data likely reveal more information regarding snowshoe hare preferences and changes over time, thus we encourage researchers to continue to utilize indirect indices such as pellet plots and track counts.

In our study area, snowshoe hares preferred 30–60 year old regenerating lodgepole pine stands, leading us to suggest that clear-cutting and pre-commercial thinning have the potential to benefit snowshoe hares. The mosaic of small and differing age class stands that can result from these silvicultural practices may provide snowshoe hares with the opportunity to relocate and find the cover and forage that they need to survive ground and avian predators and changing environmental conditions. We reiterate that regional and intra-regional differences should be considered as our findings are translated by managers outside of our study area. Resource managers must also take into consideration the specific needs of Canada lynx. The focus may be to improve snowshoe hare habitat to provide more prey for lynx, however, denning habitat requirements and other prey species should be considered as well as the density of cover which could affect lynx hunting success (Ruggiero et al. 2000). 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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