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SNOWSHOE HARE AND FOREST STRUCTURE RELATIONSHIPS IN WESTERN
WYOMING

by

Nathan Daniel Berg

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Wildlife Biology

Approved:

Dr. Eric M. Gese
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ABSTRACT

Snowshoe Hare and Forest Structure Relationships in Western Wyoming

by

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Utah State University, 2009

Major Professor: Dr. Eric M. Gese
Department: Wildland Sciences

Snowshoe hares (*Lepus americanus*) are a critically important prey species for Canada lynx (*Lynx canadensis*). Determination of snowshoe hare distribution and abundance is needed in western Wyoming for lynx conservation. We used linear regression to examine the correlations between snowshoe hare density, as determined by mark-recapture estimates, and fecal pellet plot counts on both uncleared and annually cleared plots on the Bridger-Teton National Forest, western Wyoming. We found significant correlations between hare density estimates and fecal pellet counts for both uncleared and annually cleared pellet counts; however the relationship was much stronger for annually cleared pellet counts. Adjusting the buffer size by omitting hard habitat edges (not used by hares) around the trapping grids improved correlations between hare density and fecal pellet counts further. We recommend pellet counts from annually cleared plots be used when precise estimates of snowshoe hare abundance are required. Though precision is sacrificed when using uncleared plots, they are useful as a coarse index of habitat use by hares. The derived regression equations should be used to identify foraging habitat for lynx in western Wyoming.

In addition to snowshoe hares, in western Wyoming red squirrels (*Tamiasciurus*

hudsonicus) and grouse (*Bonasa umbellus* and *Dendragapus obscurus*) are used by Canada lynx. Whether young forests or older multi-storied forests contain more snowshoe hares, red squirrels, and grouse in western Wyoming is currently unknown. We estimated snowshoe hare density, and indexed red squirrel and forest grouse abundance in 3 classes of 30-70-year-old lodgepole pine (*Pinus contorta*) and 4 classes of mature multi-storied forest with a spruce (*Picea engelmannii*)-fir (*Abies lasiocarpa*) component. We recorded landscape and forest structure characteristics to understand how these influence lynx prey abundance. Overall, snowshoe hares, red squirrels, and forest grouse were more abundant in multi-storied forests than young forests. Forest attributes that predicted prey abundance were often more prevalent in multi-storied forests. Results from this study suggest that multi-storied forests with a spruce-fir component were disproportionately important to snowshoe hares, red squirrels, and forest grouse in western Wyoming. Canada lynx conservation efforts should focus on maintaining, enhancing, and promoting multi-storied forests in this region.

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Nathan Daniel Berg

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CHAPTER 1

INTRODUCTION

Snowshoe hares (*Lepus americanus*) are found in the montane and sub-boreal forests of the continental United States, including much of western Wyoming, as well as the boreal forests of Canada and Alaska (Ruggiero et al. 2000). In North America, the distribution of Canada lynx (*Lynx canadensis*) is similar to snowshoe hares (Bittner and Rongstad 1982, McCord and Cardoza 1982). During the past century the distribution of Canada lynx has contracted along the southern periphery of its range (Ruggiero et al. 2000, Mowat and Slough 2003). A lack of regulatory mechanisms for lynx was the reason conservation efforts were initiated in this region. Snowshoe hares are the primary prey for lynx throughout North America (Saunders 1963, Nellis and Keith 1968, Brand and Keith 1979, Parker et al. 1983, Mowat et al. 2000, McKelvey et al. 2000, Ruggiero et al. 2000), with hares comprising 35-97% of lynx diets (Koehler and Aubry 1994, Squires and Ruggiero 2007). Depending on hare density, on average a lynx kills 1-2 hares every three days (Quinn and Parker 1987). Understanding snowshoe hare distribution and abundance is one of the most critical elements of conservation planning for the lynx, a threatened species under the Endangered Species Act (U.S. Fish and Wildlife Service 2000).

Canada lynx currently inhabit western Wyoming (Squires et al. 2003, Murphy et al. 2006) and were recorded in the state both prehistorically (Kurten and Anderson 1980) and historically (Reeve et al. 1986, McKelvey et al. 2000). Lynx in western Wyoming may comprise the southernmost, natural population in North America and are particularly important because minor impacts could potentially eliminate this population (Squires et al. 2003). The lack of regionally specific snowshoe hare data, coupled with the need for a better understanding of Canada lynx ecology near the southern periphery of their range, was the motivating factor for conducting this study.

Canada lynx are specialist hare hunters and minimum thresholds of 0.3 hares/ha (Mills et al. 2005), 0.5 hares/ha (Mowat et al. 2000, Ruggiero et al. 2000), and >1.0 hares/ha have been suggested (Ward and Krebs 1985, Steury and Murray 2004) for lynx persistence. Actual critical hare thresholds for lynx are unknown and we believe such thresholds likely differ based on a variety of temporal, spatial and regional factors. Though hare populations are cyclic in Canada and Alaska, with amplitudes reaching 5 to 25 fold in abundance (Hodges 2000a), hare populations in the contiguous United States are at most only slightly cyclic to randomly fluctuating (Hodges 2000b). In the western United States, hare densities of >0.5 hares/ha are found in relatively small to medium size patches of suitable habitat (Ellsworth and Reynolds 2006). A patchy distribution of hares is consistent with the findings of two recent studies conducted in the Greater Yellowstone Area (GYA) using mark-recapture techniques and fecal pellet plots to estimate hare abundance at various locations and within a variety of forest types (McKelvey and McDaniel 2001, Hodges and Mills 2005).

In Yellowstone National Park (YNP), Wyoming, fecal pellet counts and mark-recapture techniques indicated that snowshoe hares were not present in many of the stands surveyed (Hodges and Mills 2005, Hodges et al. 2009). On a separate study conducted nearby in Island Park, Idaho, 11 hares were captured on one 9-ha trapping grid, while other trapping grids had much lower densities (McKelvey and McDaniel 2001). Interestingly, lynx with kittens have been documented in YNP over consecutive winters in recent years (Murphy et al. 2006). Additional research is needed to better understand what may constitute an appropriate hare threshold for lynx in the GYA.

In northern latitudes, lynx select habitats where hares are most abundant and this is often within young regenerating forest types (Aubry et al. 2000, Mowat et al. 2000, O'Donoghue et al. 2001, Mowat and Slough 2003). However, towards the southern periphery of their range, mature stands with a dense understory are also used by lynx and hares (Koehler 1990, Mowat et al. 2000,

Walker 2005, Fuller et al. 2007, Koehler et al. 2007). Lynx in Washington selected mature spruce-fir forests over other forest types due to increased hare density (Maletzke et al. 2008). Ongoing research in northwestern Montana suggests that lynx preferentially select multi-storied spruce-fir forests with a dense understory over younger forest types when hunting for snowshoe hares (Squires, unpublished data). These findings are significant since to date much of the emphasis for Canada lynx conservation in southern latitudes has been steered by studies conducted in more northerly latitudes which often focus on cycling a certain percentage of older forests into dense young regenerating stands in order to increase foraging habitat and associated snowshoe hare densities. It is unknown whether older mixed age multi-storied stands or young even-age regenerating stands provide more optimal habitat conditions for hares in this region. A mismatch in management strategy in the southern periphery of the snowshoe hare's range could prove detrimental to lynx conservation and recovery efforts in the Rocky Mountains. For this reason additional research of hare abundance and preferred habitat structure is warranted in this geographic region.

The overarching objective of this study was to compare snowshoe hare, red squirrel, and forest grouse abundance in mixed age multi-storied stands with young even-age stands regenerating after a fire or harvest event to understand patterns of potential lynx prey abundance in western Wyoming.

Specific project objectives included:

1. Create a hare density-fecal pellet regression equation by contrasting mark-recapture density estimates with associated fecal pellet counts.
2. Index snowshoe hare abundance within seven forest stand types, and examine the influence of forest structural characteristics on relative hare abundance.

3. Compare older multi-storied stands to young regenerating even-age forest types with estimates of hare density, relative abundance of red squirrels, and indices of grouse abundance.

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CHAPTER 2
RELATIONSHIP BETWEEN FECAL PELLETT COUNTS AND SNOWSHOE HARE
DENSITY IN WESTERN WYOMING

INTRODUCTION

Snowshoe hares (*Lepus americanus*) are the primary prey for Canada lynx (*Lynx canadensis*) throughout North America (e.g., Brand and Keith 1979, McKelvey et al. 2000, Murray et al. 2008) and are an important food source for many mammalian and avian predators (Zimmer 2004, Hodges and Mills 2008, McCann et al. 2008). The Canada lynx in the Greater Yellowstone Area (GYA) likely comprise the southernmost, natural population in North America and are particularly important because even minor impacts could potentially eliminate this population (Squires et al. 2003). Understanding snowshoe hare distribution and abundance is one of the most critical elements of conservation planning for the lynx, a threatened species under the Endangered Species Act (U.S. Fish and Wildlife Service 2000).

The relationship between fecal pellet counts and snowshoe hare density has been described for several regions of North America in the form of locally developed regression equations (Krebs et al. 1987, 2001; Murray et al. 2002, Mills et al. 2005, McCann et al. 2008). The correlative relationship between fecal pellet counts and snowshoe hare density holds true across the entire range of the snowshoe hare, but varies from region to region (Krebs et al. 1987, 2001, Murray et al. 2002, Homyack 2003, Mills et al. 2005, McCann et al. 2008). When concise estimates are needed for local management actions, the hare density-fecal pellet relationship should be rigorously tested for each geographic area to appropriately account for strong site-specific effects on pellet degradation (Krebs et al. 1987, Murray et al. 2002, Mills et al. 2005, Hodges and Mills 2008).

The relationship between pellet counts and snowshoe hare density in the northern GYA has not been developed due to low hare density (McKelvey and McDaniel 2001, Hodges and Mills 2005). Therefore, we evaluated this relationship in an area of the southern GYA that we believed supported high hare densities. Our goal was to investigate the hare density-fecal pellet relationship on the B-TNF by developing local regression equations for this region and then compare our equations with those equations developed beyond the GYA that utilized similar methods (Murray et al. 2002, McCann et al. 2008). Regionally specific snowshoe hare studies are needed because the GYA is important to the conservation of Canada lynx (U.S. Fish and Wildlife Service 2000, 2008; Squires et al. 2003, Murphy et al. 2006). As such, there is much interest in obtaining reliable data on snowshoe hare distribution and abundance among federal and state agencies mandated to protect and enhance local lynx populations.

Researchers recommend that regionally specific formal double-sampling studies be performed (Murray et al. 2002, Mills et al. 2005) because hare defecation rates, pellet loss, and pellet decomposition rates vary with climate, habitat, and diet (Prugh and Krebs 2004, Murray et al. 2005). As recommended, we examined the relationship between snowshoe hare density and fecal pellet counts using both uncleared plots and annually cleared plots (Hodges and Mills 2008). In addition, we investigated the relationship between the total number of individuals captured and the associated pellet counts on uncleared and annually cleared plots. Because some of the sites were bordered in part by non-forested habitat, we also investigated how estimating the buffer area around the trapping grid influenced the pellet-density relationship.

STUDY AREA

Sampling sites were located in several mountain ranges (Absaroka, Gros Ventre, Wind River, Salt River, Wyoming) in the southern portion of the GYA on the Bridger-Teton National Forest (B-TNF) in western Wyoming. Summer temperatures varied by elevation, but in general

were characterized by cool nights and warm days with frequent afternoon thunderstorms. Winters on the B-TNF were characterized by cold temperatures and deep snow which consistently remained on the ground from late October through May, or later at higher elevations. Due to relatively consistent winter weather patterns in western Wyoming the snowpack was more maritime in the western ranges where it was consistently deeper, wetter and denser, whereas the eastern ranges tended to have a drier, shallower, more continental snowpack. Precipitation varied across the B-TNF but averaged 101.35 cm annually on Togwotee Pass over the past 10 years, most of which fell as snow (Western Regional Climate Center, Reno, Nevada). Temperatures often dropped below freezing and snowfall occurred during every month except July.

Forests within the B-TNF were often heterogeneous in species composition and age structure, and included subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), whitebark pine (*Pinus albicaulis*), Douglas fir (*Pseudotsuga menziesii*), limber pine (*Pinus flexilis*), and aspen (*Populus tremuloides*). Moist areas were dominated by subalpine fir, Engelmann spruce, and aspen forests mixed with conifers. Dry locations were dominated by lodgepole pine forests, occasionally intermixed with Douglas fir, limber pine, and aspen. Whitebark pine forests were found at the highest elevations and occasionally formed pure stands, but were also intermixed with subalpine fir and Engelmann spruce. Forested habitat within the study area ranged in elevation from 1,981 m to 3,353 m. Shrubs found within forested areas included buffaloberry (*Shepherdia canadensis*), current (*Ribes* spp.), snowberry (*Symphoricarpos oreophilus*), thimbleberry (*Rubus parvifloru*) and *Vaccinium* spp. Forests were often intermixed with riparian communities dominated by willow (*Salix* spp.), as well as sagebrush (*Artemisia* spp.) and wheatgrass (*Agropyron* spp.) communities on drier western and south-facing slopes. At the lowest elevations, mountain ranges were often surrounded by sage-wheatgrass communities. For over a century, trees have been harvested for

house logs, mine props, firewood, railroad ties, and lumber (Squires et al. 2003). Natural disturbances included fires, avalanches, landslides, insect and disease outbreaks, and wind throw.

METHODS

Pellet Plots and Trapping Grids

We established 18 9.0-ha trapping grids across a range of hare densities as determined by preliminary fecal pellet counts. A wide range of hare densities were desired to allow us to examine a full-spectrum of hare density-fecal pellet relationships in this region. Sampling sites were located in several habitat types including: regenerating (30-70 yr old) lodgepole pine ($n = 4$); regenerating (30-70 yr old) Engelmann spruce, sub-alpine fir and lodgepole pine with a few remnant mature trees ($n = 1$); mature lodgepole pine mixed with Engelmann spruce and sub-alpine fir ($n = 6$); aspen mixed with Engelmann spruce and sub-alpine fir ($n = 2$); mixed Douglas fir, Engelmann spruce, sub-alpine fir, lodgepole pine and limber pine ($n = 1$); and relatively pure stands of mature Engelmann spruce and sub-alpine fir ($n = 4$). We chose sites with homogeneous stand characteristics throughout the trapping grid.

Trapping grid arrays were 5 x 10 in shape and were occasionally modified ($n = 4$) to fit within the chosen stand, as recommended by Mills et al. (2005). During the summer we established 50 (Hodges and Mills 2008) 1-m² circular fecal pellet plots (McKelvey et al. 2002, Murray et al. 2002) with 50 m spacing between each pellet plot/trapping site, for each grid array. All pellet plots were permanently marked with a rebar stake and revisited each summer (June through August) for the duration of the project. During counts, all fecal pellets within the plot boundary were counted and removed. To avoid an inclusion bias, only 50% of the pellets found directly on the plot boundary were counted (McKelvey et al. 2002). Pellets incorporated into the organic layer of the forest floor were not counted (McKelvey and McDaniel 2001). Counts were conducted by rotating a string marked with the appropriate radius around the rebar stake. We

recorded pellet counts from the initial uncleared plots and then the cleared plots 1 year later. Pellet counts from uncleared plots were based on accumulations from an unknown time period (Prugh and Krebs 2004, Murray et al. 2005, Hodges and Mills 2008) and were recorded at the time of plot establishment. Pellet counts on cleared plots were based on an accumulation of pellets over a 1-year period and were compared to hare density estimates from the previous fall/winter trapping season (Mills et al. 2005).

During the fall and winter, we placed 50 single-door live traps (81.28 x 27.94 x 30.48 cm; Tru-Catch Traps, Belle Fourche, South Dakota, USA) baited with alfalfa cubes and apple slices on each grid array. Each trap was spaced by 50 m and placed ~5 m from the nearest fecal pellet plot. Trapping of hares was conducted during the late fall and early winter months (October through January) because snow usually covered many grasses and forbs at this time of year, thus leading to increased capture success. We did not trap during late winter or early spring due to personnel and logistical constraints. Traps were checked each morning and captured hares were double-tagged (Wing Band Jiffy Style 893; National Band and Tag, Newport, Kentucky, USA), sexed, measured, weighed, and released. We double-tagged each captured hare (one tag in each ear) to prevent the loss of marks during the trapping session. Individuals were handled in lightweight zipper-topped pillowcases that securely contained the hares and allowed for effective processing. Each trapping session consisted of 6-9 nights to insure a sufficient percent of the population on each grid had been marked (Seber 1982, 1992).

Density Estimation

We estimated snowshoe hare abundance using the 2-sample Lincoln-Peterson estimator (LP) adjusted for sample size (Chapman 1951, Seber 1982) to be consistent with other hare studies in the Northern Rockies (Mills et al. 2005). These estimates were divided by the effective trapping area which equaled the trapping grid area plus an appropriate buffer of one-half the

mean maximum distance moved between captures for individual hares per trapping grid and session (Mills et al. 2005, McCann et al. 2008, Zahratka and Shenk 2008). Several trapping grids ($n = 7$) were presumed to have a hard habitat edge on ≥ 1 of their 4 outside borders; during trapping sessions, we did not observe hares tracks in the snow venturing out into this less suitable habitat, which in all cases was non-forested. For this reason, we chose to test this 'hard edge' assumption by subtracting the buffer from only these portions of the trapping grids. We then compared the relationship between pellet counts and estimated hare density with and without this hard edge included in the estimated effective trapping area.

Fecal Pellet-Hare Density Relationship

We used linear regression to examine the relationships between the total number of individuals captured and estimates of hare density versus fecal pellet counts from uncleared and cleared plots on 18 separate trapping grids using SPSS (SPSS for Windows 10, Chicago, Illinois, USA). Total number of individuals captured and estimates of density were additionally regressed with annually cleared pellet counts from all 22 survey occasions from both field seasons; 4 grids were sampled in 2006-2007 and 2007-2008, but were assumed to be temporally independent because they had separate pellet counts from both years. Previous studies recommend using both linear (McCann et al. 2008) and functional regression approaches (Krebs et al. 2001, Mills et al. 2005) when comparing pellet counts with estimates of hare density, with the suggestion that functional regression be used instead of linear regression when hare densities are low (Krebs et al. 2001, Mills et al. 2005). We did not use functional regression for 3 main reasons: (1) hare densities on our sites were relatively high with density estimates between 1.08-4.82 hares/ha for 13 of the 22 trapping sessions and all sessions captured hares, (2) other researchers recommended linear regression particularly if attempts to estimate numbers are related to minimum snowshoe hare thresholds for lynx management because the differences between functional and linear

approaches are very small (McCann et al. 2008), and (3) our data was not highly skewed (skewness/SE skewness) and was normally distributed (kurtosis/SE kurtosis) (Murray et al. 2005) with normal probability plots indicating little departure from normality in all cases (Montgomery 2005, McCann et al. 2008).

RESULTS

Pellet Plots and Trapping Grids

Mean fecal pellet counts ranged from 6.2 to 109.9 pellets/plot and 2.1 to 47.7 pellets/plot on uncleared and annually cleared plots, respectively (Table 2-1). Pellet counts from uncleared plots averaged 46.2 ± 36.05 (SD) pellets/plot and were almost 3 times higher than cleared plots (mean = 16.5 ± 13.36 pellets/plot). The number of individual hares caught on the trapping grids ranged from 1 to 64 (Table 2-1) and averaged 19.9 hares/trapping grid. The proportion of hares captured each day that had been previously marked exceeded 75% by the sixth day of trapping (Figure 2-1A). Additionally, the probability of recapturing a previously marked hare exceeded 30% each day after day 6 (Figure 2-1B).

Density Estimation

Two-sample Lincoln-Petersen density estimates averaged 24.2 hares/trapping grid (range = 1-78.6 hares/trapping grid; Table 2-1). Density estimates averaged 1.57 hares/ha (range = 0.07-4.82 hares/ha; Table 2-1) across all grids when using one-half the mean maximum distance moved by individual hares to estimate the effective trapping area. Estimates of snowshoe hare density averaged 1.70 hares/ha (range = 0.07-4.82 hares/ha; Table 2-1) across all grids when using one-half the mean maximum distance moved by individual hares with hard edges subtracted from the buffer to estimate the effective trapping area.

Fecal Pellet-Hare Density Relationship

Pellet counts from both uncleared and cleared plots were correlated with the number of snowshoe hares captured on the corresponding trapping grid (Figure 2-2). Even uncleared plots correlated to the number of hares captured (Figure 2-2C), but using annually cleared plots significantly improved the correlation (Figure 2-2A, B). The relationships between pellet counts on uncleared and annually cleared plots were also highly correlated with estimates of snowshoe hare density (Figure 2-3), with pellet counts from cleared plots (Figure 2-3A, B) again having a better fit than counts from uncleared plots (Figure 2-3C). Interestingly, adjusting the buffers on the trapping grids with hard edges (Table 2-2) improved the linear relationship between annually cleared and uncleared pellet counts and estimates of hare density (Figure 2-4). As expected, there were also significant relationships between the total number of hares captured and hare density ($r = 0.969$, $P < 0.001$), the total number of hares and hare density using the effective trapping area adjusted for hard edges ($r = 0.943$, $P < 0.001$), and between pellet counts from annually cleared and uncleared plots ($r = 0.742$, $P < 0.001$).

The equations developed using annually cleared pellet counts had similar y-intercepts and slopes with both equations estimating similar hare densities throughout the range of hare densities on the B-TNF (Table 2-3). Linear equations developed in Idaho (Murray et al. 2002) and Minnesota (McCann et al. 2008) that used similar methods had notably different y-intercepts and slopes than equations developed on the B-TNF which sometimes led to large differences in hare density estimates. The difference between the Minnesota and B-TNF equations overall was quite modest with the most notable difference being the y-intercepts. The Idaho equation's estimate of hare density at the y-intercept was more conservative than the Minnesota or Wyoming equations. However, at >5 fecal pellets/plot the Idaho equation estimated higher hare densities than the Minnesota and Wyoming equations due to the steeper slope in the equation.

DISCUSSION

We found a broad range of pellet counts and snowshoe hare densities in western Wyoming, which included some of the highest observed hare densities in recent years in the continental U.S., British Columbia, Labrador, and Quebec (de Bellefeuille et al. 2001, McKelvey et al. 2002, Murray et al. 2002, Ausband and Baty 2005, Newbury and Simon 2005, Potvin et al. 2005, Homyack et al. 2006, Sullivan et al. 2006, Hodges and Mills 2008, McCann et al. 2008, Zahratka and Shenk 2008). Prior studies based on pellet counts showed low snowshoe hare densities in the northern GYA (McKelvey and McDaniel 2001, Hodges and Mills 2005) and no regression equations relating hare density and pellet counts had been developed. Therefore, the equations we developed here provide an important reference point for future pellet count surveys to estimate hare density in the southern GYA.

The significant relationships between snowshoe hare density and pellet counts in western Wyoming were consistent with other studies throughout North America (Krebs et al. 1987, 2001, Murray et al. 2002, 2005, Mills et al. 2005, Homyack et al. 2006, McCann et al. 2008). Similar to other geographic areas where they have been implemented, pellet counts from 1-m² circular plots were highly correlated to hare density estimates obtained from associated mark-recapture studies (Murray et al. 2002, Mills et al. 2005, McCann et al. 2008). The relationship between pellet counts and mark-recapture density estimates in Wyoming on the B-TNF was similar to that observed in Minnesota but was markedly different from observations in northern Idaho. For this reason, we concur with those who have argued for the development of regionally specific regressions relating hare density to fecal pellet counts (Krebs et al. 2001, Murray et al. 2002, McKelvey et al. 2002) especially when accurate density estimates are required for the purpose of identifying important foraging habitat for Canada lynx. It remains unknown whether equations developed in other geographic areas that utilized different pellet plot sizes and shapes from the

1-m² circular plots could appropriately estimate hare abundance in Wyoming; from our observations we suspect the relationships may be different.

There have been discussions of the utility of counting fecal pellets from uncleared plots mainly due to the effects of multiple years of pellet accumulation, temporal changes in hare abundance, the difficulty in correctly aging pellets, and the influence of varying rates of pellet decomposition due to diet and climate (Murray et al. 2002, 2005, Prugh and Krebs 2004, Mills et al. 2005, Hodges and Mills 2008). Our results concurred with findings that pellet counts from cleared and uncleared plots were correlated with snowshoe hare density (Mills et al. 2005, Hodges and Mills 2008). However, the relationship between pellet counts from uncleared plots and hare density was less significant for uncleared plots than cleared plots in Wyoming. For this reason, and as suggested by Hodges and Mills (2008), we developed separate regression equations for cleared and uncleared plots. When a precise estimate of hare abundance and habitat use is required, we recommend using annually cleared pellet plots (Prugh and Krebs 2004, Murray et al. 2005). When only a coarse indication of hare abundance is needed (Hodges and Mills 2008), uncleared pellet counts likely provide insight; however, due to a lack of observed precision at low hare densities (Hodges and Mills 2008), their utility may be limited.

Suitable habitat for snowshoe hares in the GYA is naturally fragmented due to changes in elevation, topography, aspect, soils, and climate. For this reason, we found that hares tended to use disjunct patches of mesic boreal forest that have the appropriate understory characteristics (Hodges and Mills 2005, Murphy et al. 2006). Several of our survey sites, particularly in the Wyoming Range, were located in such disjunct patches of boreal forest. Such sites were partially or completely surrounded by matrix habitat composed of sagebrush-wheatgrass and/or riparian willow-meadow plant communities. On these sites, sign of hares (live animals and fecal pellets), were observed beyond the forest edge in the matrix habitat during snow-free periods but were noticeably absent from these same areas during the winter. Though beyond the scope of this

study, we believed there was a seasonal shift in habitat use by hares at these sites. Such seasonal shifts in snowshoe hare habitat use have been noted elsewhere (Wolff 1980, J. Ivan, unpublished data). Naturally fragmented landscapes increase the edge to forest ratio and further study is warranted to identify if this positively or negatively influences hare abundance. Interestingly, the relationship between pellet counts and estimates of hare density that included the buffer modification for hard edges on the grid boundaries generated a slightly higher regression coefficient than the correlations that did not consider these hard edges. A telemetry study in the GYA would be useful to elucidate whether the hard edges surrounding disjunct patches of boreal forest influences hare movements and whether there is a seasonal shift in habitat use by hares.

Documentation of high snowshoe hare density in the southern GYA provided important information with regards to the potential for lynx occupancy and habitat quality in this region. Even though hare density was high in some areas on the B-TNF, lynx numbers were low in western Wyoming (Squires and Oakleaf 2005, Murphy et al. 2006) suggesting that additional factors other than hare density may be limiting lynx population size. Other possible factors include competition with other predators, amount and spatial arrangement of suitable habitat on the landscape, climate change, historic trapping and current incidental trapping of lynx, habitat connectivity, or a lack of propagules from nearby source populations in northwest Montana and Canada.

Because snowshoe hares are the primary prey for lynx throughout their range, and because these cats are often too rare to adequately investigate their spatial use patterns, hares are often used as a surrogate for identifying potential lynx habitat. Various investigators have reported >0.3 hares/ha (Mills et al. 2005), >0.5 hares/ha (Mowat et al. 2000, Ruggiero et al. 2000), and >1.0 hares/ha (Ward and Krebs 1985, Steury and Murray 2004) as thresholds of hare density needed for lynx. None of these thresholds have been substantiated for the GYA (Hodges et al. 2009). Thus, researchers should exercise caution when using hare density-fecal pellet

equations developed from this study or any other study for the purpose of identifying potential habitat for lynx in this region until our understanding of lynx prey requirements in the GYA is more complete. Furthermore, both pellet counts and mark-recapture estimates of hare numbers have been found to be compromised at very low hare densities (<0.3 hares/ha; Mills et al. 2005), which could lead to an inability to accurately predict a proposed minimum hare threshold for lynx. Despite these shortcomings, there is value in using fecal pellet counts to identify areas of low, medium, and high hare densities for the purpose of lynx management due to the high correlation between pellet counts and density estimates; for this reason pellet counts could also be used to identify areas of very low hare density (<0.3 hares/ha; Mills et al. 2005).

MANAGEMENT IMPLICATIONS

Densities of snowshoe hares varied greatly across the patchily distributed fragmented forest landscape of western Wyoming. Mark-recapture trapping sessions for hares should be of sufficient length to ensure an adequate portion of the population has been captured for accurate density estimation. Even though the differences were small on the B-TNF, we recommend researchers construct regression equations both with and without buffer adjustments for hard forest edges when determining estimates of hare density in similarly fragmented landscapes. The correlation coefficient, when using buffer adjustments, between pellet counts and hare density for cleared and uncleared plots was greater than the alternative in all cases and may have been a better fit due to the high degree of habitat fragmentation found in the GYA; this relationship deserves to be investigated further. If needed, land managers can use equations developed with and without trapping grid buffer adjustments in order to make comparisons with other regions that may or may not have implemented similar adjustments.

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Table 2-1. Fecal pellet counts from annually cleared and uncleared plots with corresponding population estimates of snowshoe hares from 18 trapping grids, Bridger-Teton National Forest, Wyoming, 2006-2008.

Stand type	Fecal Pellet Counts		N hares captured	Population Estimate		
	\bar{x} Cleared	\bar{x} Uncleared		N	Lower CI	Upper CI
30-70 yr old LPP	16.7	32.76	31	39.6	27.5	41.6
30-70 yr old LPP	9.54	^a	25	29	21.9	34.0
30-70 yr old LPP	47.68	103.24	64	78.6	62.6	83.6
30-70 yr old LPP	35.84	^a	40	50.6	37.5	59.8
30-70 yr old LPP	8.78	18.5	12	14.75	8.5	24.1
30-70 yr old LPP	35.84	42.02	53	54.91	49.5	61.7
30-70 yr LPP/SF	16.96	65.88	16	21.3	12.1	26.6
Multi-story LPP/SF	35.28	83.04	31	32.6	28.4	38.8
Multi-story LPP/SF	12.02	109.92	9	11	6.3	16.4
Multi-story LPP/SF	14.68	^a	13	17	10.3	18.0
Multi-story LPP/SF	18.08	^a	17	18.5	13.6	37.9
Multi-story LPP/SF	3.64	25.92	6	7	4.8	14.8
Multi-story LPP/SF	3.64	12.1	5	8	4.3	8.7
Multi-story LPP/SF	25.34	78.96	23	23.9	20.5	31.3
Multi-story LPP/SF	2.06	6.2	1	1	n.a.	n.a.
Multi-story LPP/SF	8.26	39.32	10	13	7.1	18.9
Multi-story Aspen/SF	31.12	106.44	33	47	31.0	48.3
Multi-story Aspen/SF	20.7	47.6	30	41	28.6	43.7
Multi-story SF	2.38	28.58	2	2	n.a.	n.a.
Multi-story SF	3.9	11.98	8	8.8	5.0	24.9
Multi-story SF	3.9	10.24	2	2	n.a.	n.a.
Multi-story DF/LPP/SF	6.2	9.2	8	11.5	5.0	24.9

^a Trapping grid was cleared and sampled over multiple years, therefore an uncleared count was available for the first year only.

Table 2-2. Estimates of snowshoe hare density using the entire buffer included in the effective trapping area, and the buffer of the effective trapping area adjusted for hard edges, Bridger-Teton National Forest, Wyoming, 2006-2008.

Stand Type	Density (hares/ha)	
	Full buffer	Adjusted buffer
30-70 yr old LPP	2.37	2.37 ^a
30-70 yr old LPP	1.85	1.85 ^a
30-70 yr old LPP	4.82	4.82 ^a
30-70 yr old LPP	3.14	3.14 ^a
30-70 yr old LPP	0.72	0.72 ^a
30-70 yr old LPP	3.14	3.14 ^a
30-70 yr LPP/SF	1.58	1.58 ^a
Multi-story LPP/SF	2.54	3.19
Multi-story LPP/SF	0.84	1.08
Multi-story LPP/SF	1.17	1.67
Multi-story LPP/SF	1.3	1.77
Multi-story LPP/SF	0.41	0.41 ^a
Multi-story LPP/SF	0.57	0.57 ^a
Multi-story LPP/SF	0.07	0.07 ^a
Multi-story LPP/SF	1.58	1.58 ^a
Multi-story LPP/SF	0.81	1.19
Multi-story Aspen/SF	3.23	3.72
Multi-story Aspen/SF	2.90	2.90 ^a
Multi-story SF	0.14	0.16
Multi-story SF	0.48	0.58
Multi-story SF	0.14	0.16
Multi-story DF/LPP/SF	0.79	0.79 ^a

^a Trapping grid had no presumed hard edge(s), therefore no buffer adjustments were made.

Table 2-3. Regression equations for 3 studies examining the linear relationship between annually cleared fecal pellet counts and associated hare densities (hares/ha) calculated for counts of 1-30 pellets/plot.

Source	Equation	<i>r</i>	y-intercept	1 pellet	5 pellets	10 pellets	20 pellets	30 pellets
Murray et al. 2002	$y = 1.112 + 1.047x$	0.85	0.02	0.26	1.27	2.60	5.33	8.13
McCann et al. 2008	$y = 0.398 + 0.060x$	0.89	0.36	0.45	0.70	1.00	1.60	2.20
This study (adjusted buffer)	$y = 0.174 + 0.093x$	0.94	0.17	0.27	0.64	1.10	2.03	2.95
This study (full buffer)	$y = 0.102 + 0.089x$	0.93	0.10	0.19	0.55	0.99	1.89	2.78

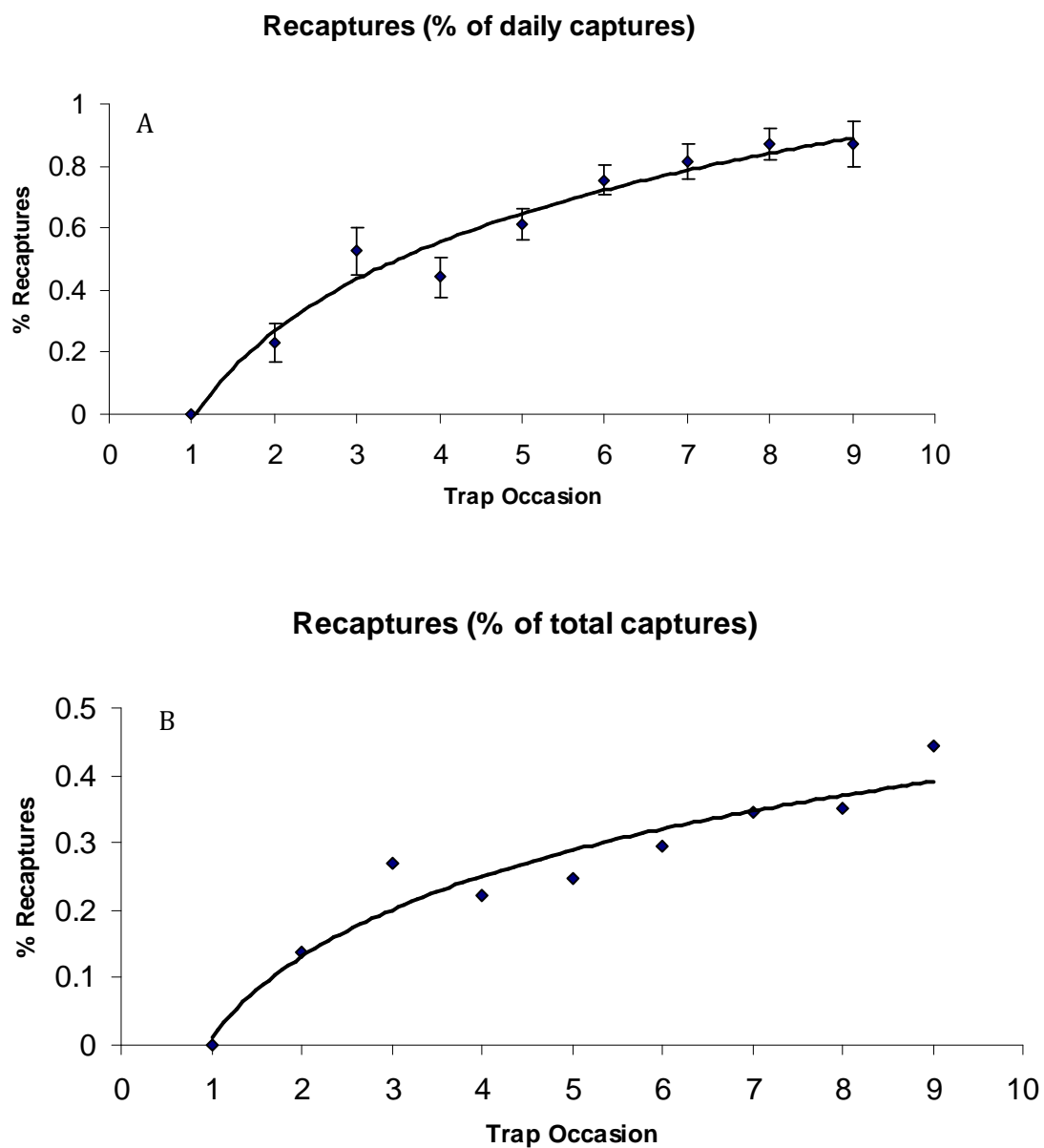


Figure 2-1. The percent of (a) daily captures that was a recapture of a marked snowshoe hare, and (b) total cumulative captures that were a marked snowshoe hare, Bridger-Teton National Forest, Wyoming, 2006-08.

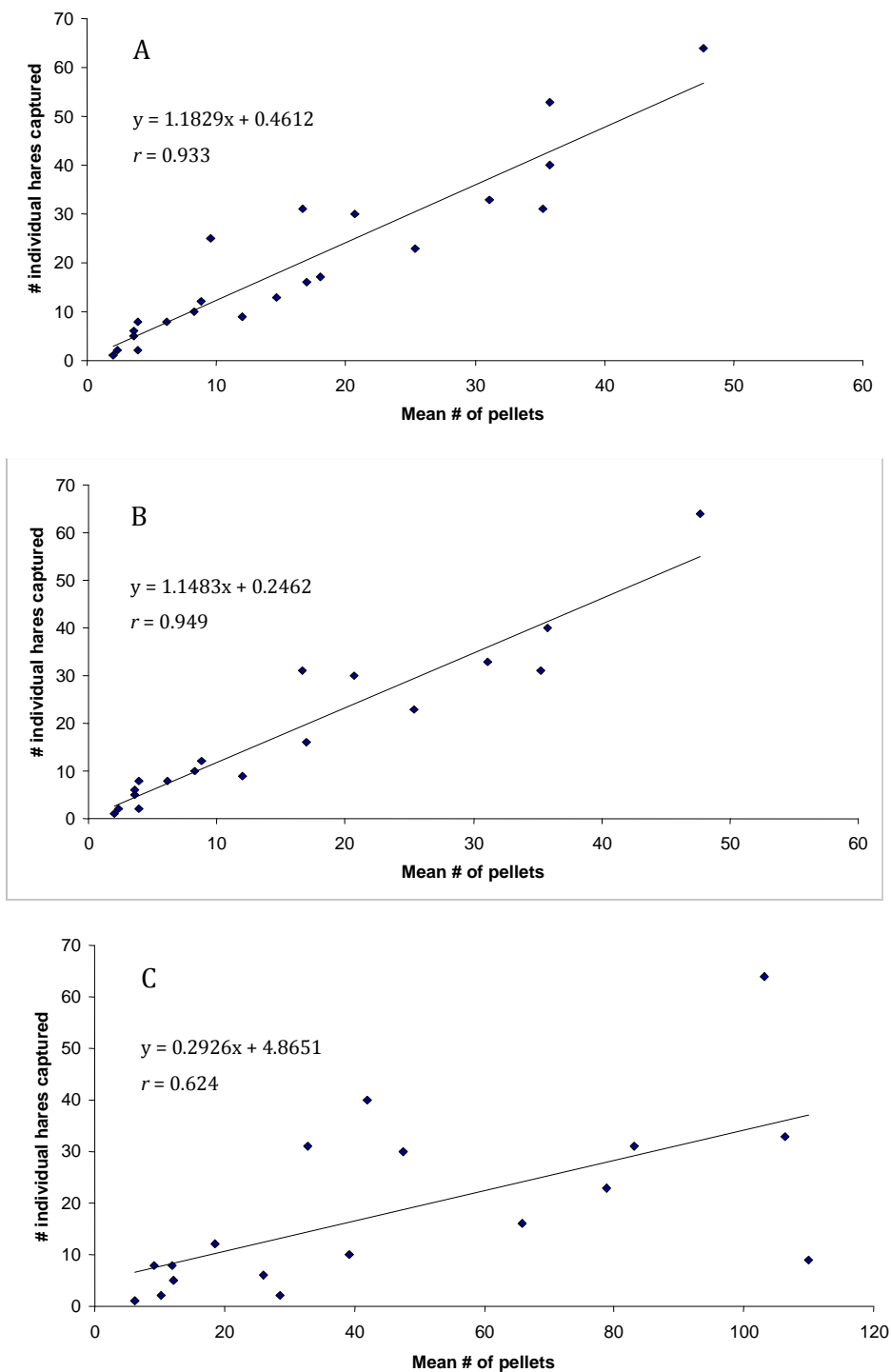


Figure 2-2. Relationships between the total number of hares captured and the mean number of pellets counted on the (a) 22 annually cleared trapping grids (4 grids repeated), (b) 18 annually cleared trapping grids (no grids repeated), and (c) 18 uncleared trapping grids, Bridger-Teton National Forest, Wyoming, 2006-2008.

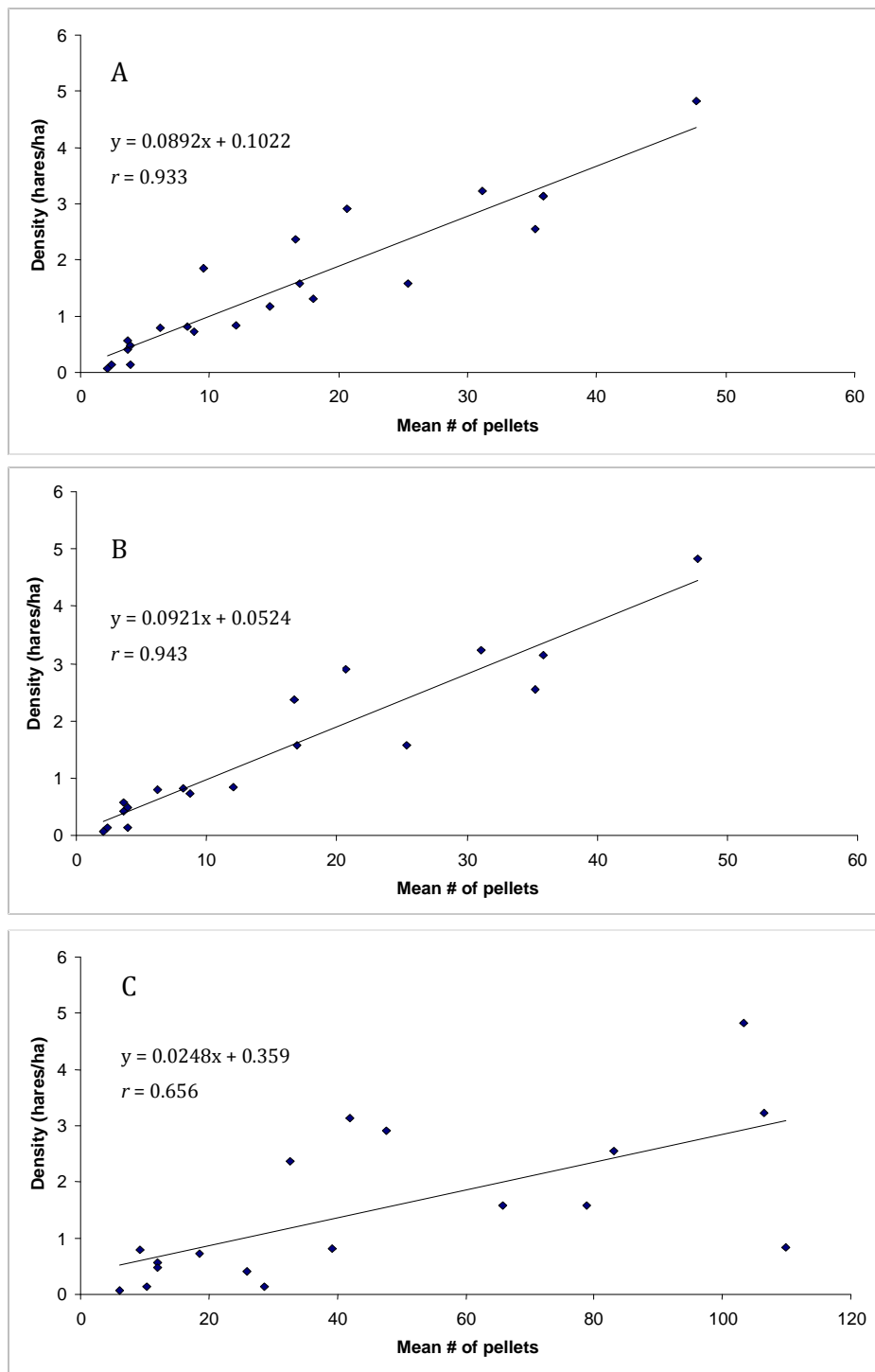


Figure 2-3. Relationships between estimates of snowshoe hare density using the full buffer around the grid and the associated pellet counts on (a) 22 annually cleared trapping grids (4 grids repeated), (b) 18 annually cleared trapping grids (no grids repeated), and (c) 18 uncleared trapping grids, Bridger-Teton National Forest, Wyoming, 2006-2008.

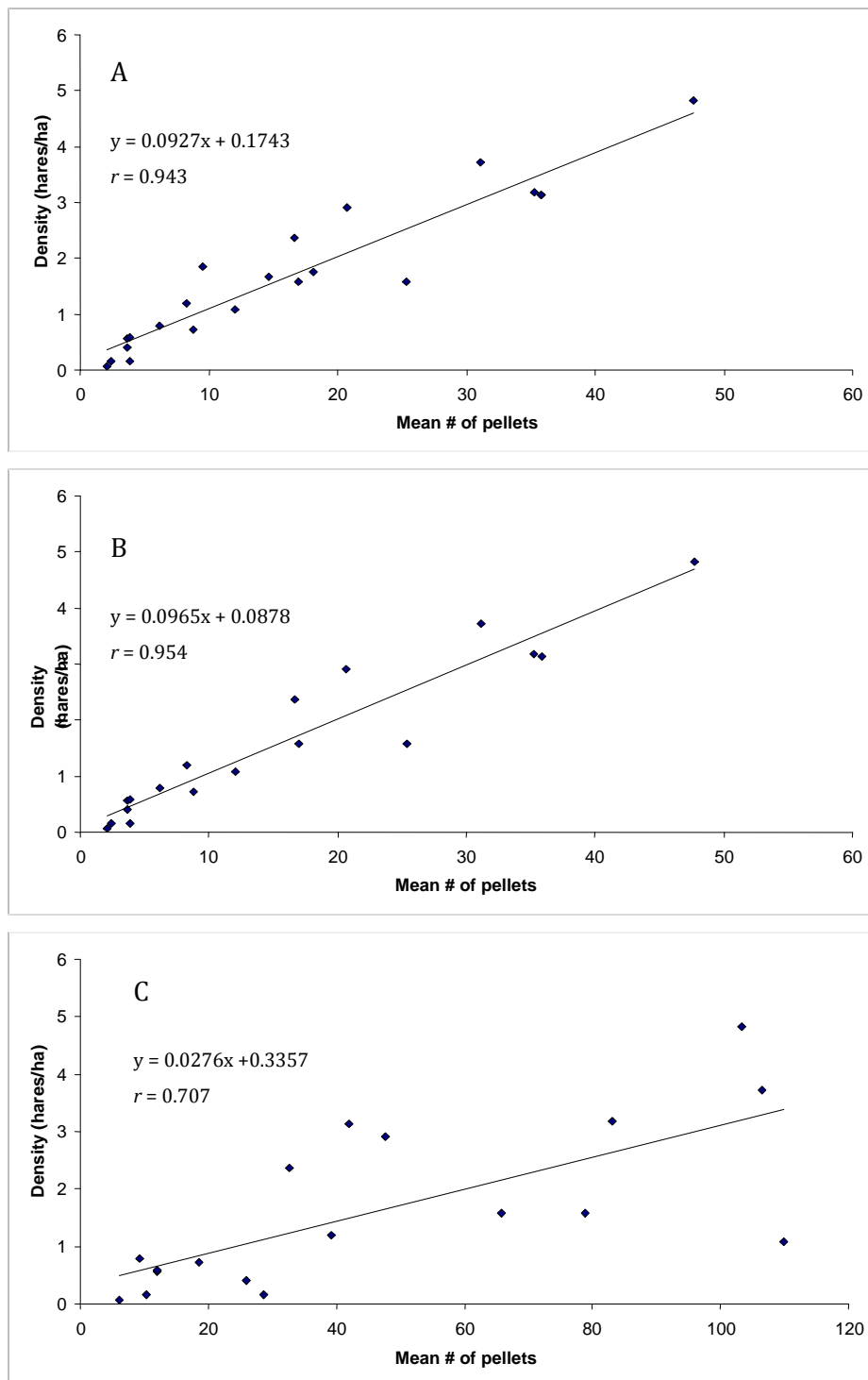


Figure 2-4. Relationships between estimates of snowshoe hare density using the adjusted buffer for hard edges and pellet counts on (a) 22 cleared trapping grids (4 grids repeated), (b) 18 cleared trapping grids (no grids repeated), and (c) 18 uncleared trapping grids, Bridger-Teton National Forest, Wyoming, 2006-2008.

CHAPTER 3

RELATIONSHIPS BETWEEN FOREST STRUCTURE AND ABUNDANCE OF LYNX PREY
SPECIES IN WESTERN WYOMING**INTRODUCTION**

Snowshoe hares (*Lepus americanus*) occur in the montane and sub-boreal forests of the continental United States, as well as the boreal forests of Canada and Alaska (Ruggiero et al. 2000). In North America, the distribution of Canada lynx (*Lynx canadensis*) occurs within the range of the snowshoe hare (Bittner and Rongstad 1982, McCord and Cardoza 1982). Snowshoe hares are the primary prey for lynx throughout North America (Saunders 1963, Nellis and Keith 1968, Brand and Keith 1979, Parker et al. 1983, McKelvey et al. 2000, Mowat et al. 2000, Ruggiero et al. 2000), with hares comprising 35-97% of lynx diets (Koehler and Aubry 1994, Squires and Ruggiero 2006). Depending on hare density, on average a lynx kills 1-2 hares every 3 days (Quinn and Parker 1987). When snowshoe hares are scarce, red squirrels (*Tamiasciurus hudsonicus*) and grouse (*Bonasa umbellus* and *Dendragapus obscurus*), are important secondary prey items (O'Donoghue et al. 1998, Aubry et al. 2000).

Canada lynx are specialist hare hunters and minimum thresholds of 0.3 hares/ha (Mills et al. 2005), 0.5 hares/ha (Mowat et al. 2000, Ruggiero et al. 2000), and >1.0 hares/ha (Ward and Krebs 1985, Steury and Murray 2004) have been suggested for lynx persistence. Actual critical hare thresholds for lynx in this region are unknown and such thresholds likely differ based on a variety of temporal, spatial and regional factors. Though snowshoe hare populations are cyclic in Canada and Alaska (Hodges 2000a), hare populations in the contiguous United States are believed to be at most only slightly cyclic to randomly fluctuating (Hodges 2000b); with recent research providing no indication of a cycle (Hodges et al. 2009). In the western United States, hare densities >0.5 hares/ha are found in relatively small to medium size patches of suitable

habitat (Ellsworth and Reynolds 2006). A patchy distribution of hares is consistent with findings from recent studies conducted in the Greater Yellowstone Area (GYA) that utilized mark-recapture techniques and fecal pellet plots to estimate hare abundance within a variety of forest types (McKelvey and McDaniel 2001, Hodges and Mills 2005, Hodges et al. 2009).

In Yellowstone National Park, Wyoming, both live-trapping data and fecal pellet count surveys indicated that snowshoe hares were not present in many of the stands surveyed and that hares are rare in the Park (Hodges and Mills 2005, Hodges et al. 2009). Nearby in Island Park, Idaho, 11 hares were captured on one 9-ha trapping grid, while other trapping grids were indicative of much lower densities (McKelvey and McDaniel 2001).

In northern latitudes, lynx select habitats where hares are most abundant which is often within young regenerating forest types (Aubry et al. 2000, Mowat et al. 2000, O'Donoghue et al. 2001, Mowat and Slough 2003). However, towards the southern periphery of their range, mature stands with a dense understory are also used by lynx, snowshoe hares, and secondary prey species (Koehler 1990, Buskirk et al. 2000, Mowat et al. 2000, Walker 2005, Fuller et al. 2007, Koehler et al. 2007, Hodges et al. 2009). Lynx in Washington selected mature spruce/fir forests over other forest types due to increased hare density (Maletzke et al. 2008). Ongoing research in northwestern Montana suggests that lynx preferentially select multi-storied spruce-fir forests with a dense understory over younger forest types when hunting for snowshoe hares (Squires, unpublished data). These findings are significant since much of the emphasis for lynx conservation in southern latitudes has been steered by studies from more northern latitudes which focus on cycling a certain percentage of older forests into dense young regenerating stands in order to increase foraging habitat and associated hare density. There is currently a lack of understanding as to whether older multi-storied stands or young even-age regenerating stands provide more optimal habitat conditions for hares in this region and whether this relationship changes among a variety of environmental factors. Lynx in Wyoming are a conservation priority

(USFWS 2008), are disjunct from the Canadian border, represent what is likely the southernmost natural population in the Continental United States (Squires et al. 2003), and may provide future propagules to a reintroduced lynx population in the Southern Rockies. A misconceived management strategy in the southern periphery could prove detrimental to lynx conservation and recovery efforts in this region. For this reason, research on lynx prey abundance and their relationship to forest structure in both young regenerating and older multi-storied forests in western Wyoming was warranted.

STUDY AREA

Study sites were located in several mountain ranges (Absaroka, Gros Ventre, Wind River, Salt River, Wyoming) in the southern portion of the GYA on the Bridger-Teton National Forest (B-TNF), western Wyoming (Fig. 1). Summer temperatures varied by elevation, but were characterized by cool nights and warm days with frequent afternoon thunderstorms. Winters on the B-TNF were characterized by cold temperatures and deep snow which remained on the ground from late October through May, or later at higher elevations. The snowpack was often maritime in the western ranges where it was consistently more abundant, wetter and denser, whereas the eastern ranges tended to have a drier shallower more continental snowpack. Precipitation varied across the B-TNF but averaged 101.3 cm annually on Togwotee Pass over the past 10 years, most of which fell as snow (Western Regional Climate Center 2008). Temperatures can dip below freezing and snows occur during any month of the year.

Forests within the study area were often heterogeneous in species composition and age structure, and included subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), whitebark pine (*Pinus albicaulis*), Douglas fir (*Pseudotsuga menziesii*), limber pine (*Pinus flexilis*), and aspen (*Populus tremuloides*). Moist areas were dominated by subalpine fir, Engelmann spruce, and aspen forests encroached by conifer. Dry

locations were dominated by lodgepole pine forests, which were occasionally intermixed with Douglas fir, limber pine, and aspen. Whitebark pine forests were found at the highest elevations and occasionally formed pure stands but were also intermixed with subalpine fir and Engelmann spruce. Forested habitat within the study area ranged in elevation from 1,981 to 3,353 m. The primary shrubs found within forested areas included buffaloberry (*Shepherdia canadensis*), current (*Ribes* spp.), snowberry (*Symphoricarpos oreophilus*), thimbleberry (*Rubus parvifloru*) and *Vaccinium* spp. Forests were often intermixed with riparian communities dominated by willow (*Salix* spp.) as well as sagebrush (*Artemisia* spp.) and wheatgrass (*Agropyron* spp.) communities on drier west and south facing slopes. At the lowest elevations, mountain ranges were often surrounded by sage-wheatgrass plant communities. For more than a century, forests within the survey area have been harvested for house logs, mine props, firewood, railroad ties, and lumber (Squires et al. 2003). Natural disturbances included forest fires, avalanches, landslides, insect and disease outbreaks, wind throw, and climate change.

METHODS

During preliminary reconnaissance surveys for snowshoe hare pellets within all forested cover types, we identified 7 principal stand types on the B-TNF that consistently contained snowshoe hare pellets and were therefore chosen for further study. These forest stand types included 3 structural classes of young regenerating lodgepole pine and 4 structural classes of older multi-storied forest with a significant spruce-fir component. The 3 young forest types surveyed were predominately 30-70-year-old even-aged lodgepole pine regenerating after timber harvest or fire. We grouped these three young forest types by stem density at 724.54 ± 51.73 , 1317.60 ± 50.42 , and 3194.16 ± 553.05 stems/ha (stems ≥ 2.54 cm diameter at breast height, DBH), respectively. The 4 older multi-storied forest types surveyed included lodgepole pine, aspen, and whitebark pine stands mixed with spruce-fir in both the overstory and understory as

well as relatively pure stands of spruce-fir. Preliminary reconnaissance surveys for hare pellets allowed us to focus our efforts on stand types with the potential to support snowshoe hares and lynx.

Forest Stand Identification

We initially planned to use an existing Geographic Information System (GIS) database to randomly place survey transects within our 7 principal stand types forest-wide. As we began visiting these computer-generated sites it was apparent that fine-scale habitat identification was not feasible using the existing GIS database; all of the first 12 sites visited were misidentified to stand type. For this reason we decided on a broader spatial approach by identifying large blocks of forest matrix that the GIS database predicted might contain our principal stand types. These sites were then visited and the appropriate stand types, if present, were identified within the forest matrix. We then conducted a walk-through assessment of the stands to ensure they were of sufficient size to contain an entire transect and composed of the appropriate species and age structure throughout (Tart et al. 2005). Transect placement was then implemented following strict establishment protocols (D. Murray, and K. Hodges, personal comm.) In order to obtain a representative sample of the 7 principal forest stand types, transects were distributed widely on the B-TNF (Figure 1).

Snowshoe Hare Pellet Counts and Density Estimation

There is a strong relationship between fecal pellet counts and snowshoe hare density (Krebs et al. 1987, 2001, Murray et al. 2002, Mills et al. 2005, Hodges and Mills 2008, McCann et al. 2008). In order to study patterns of hare abundance, we established 180 snowshoe hare pellet count transects totaling 900 individual plots on the B-TNF within the 7 predetermined forest stand types; a minimum of 20 transects totaling 100 fecal pellet plots were established in each forest stand type (Hodges and Mills 2008). Yukon rectangular plots (Krebs et al. 1987,

2001) and circular plots have been used to estimate hare abundance (McKelvey et al. 2002, Murray et al. 2002, Mills et al. 2005, Hodges and Mills 2008). We chose circular plots for 3 reasons: (a) they have a lower perimeter:area ratio than do rectangular plots, thus observers make fewer potentially biased decisions about counting pellets near the edge of the plot (Murray et al. 2002), (b) circular plots likely intersect fecal pellets more often than do the smaller rectangular plots due to their greater surface area (Murray et al. 2002), and (c) we wanted to utilize local regression equations that we developed on the B-TNF using 1-m² circular plots (Chapter 2).

We established linear transects that consisted of five 1-m² circular plots placed 50 m apart, perpendicular to roads and trails, and spaced ≥ 1 km apart (D. Murray, personal comm.). The starting point for transects was randomly placed within selected stands and located ≥ 50 m from any road. The position of an individual plot on a transect was only altered for one of the following reasons: (a) the entire plot was located within a meadow, (b) the plot was in water, (c) the plot would sample a large rock, large tree trunk, or big downed log, or (d) access to the plot was hazardous to personnel safety (K. Hodges, personal comm.). If a plot was moved, we followed a specific ordered procedure: (a) move 5 m forward along the transect and establish the plot, (b) move 5 m to the left of center and establish the new plot, or (c) move 5 m to the right of center and establish the new plot. If none of these adjustments could be performed, the plot was omitted (K. Hodges, personal comm.). All plots were permanently marked with a rebar stake and revisited each summer for the duration of the project (McCann et al. 2008). During counts, all fecal pellets within the plot boundary were tallied and removed. To avoid an inclusion bias, only 50% of the pellets found directly on the plot boundary were tallied (McKelvey et al. 2002) and only intact pellets were counted (K. Hodges, personal comm.). Vegetation and surface litter obscuring pellets was moved as needed but pellets deeply incorporated into the organic layer of the forest floor were not counted (McKelvey and McDaniel 2001). Pellet counts were conducted by rotating a string marked with the appropriate radius around the rebar stake. We recorded

pellet counts annually over the course of 2 years. Pellet counts recorded during the first year were considered uncleared counts and were based on accumulations from an unknown time period (Prugh and Krebs 2004, Murray et al. 2005, Hodges and Mills 2008). Annually cleared pellet counts, recorded during the second year, had been cleared 12 months prior and were an accumulation of pellets over a 1-year period (Prugh and Krebs 2004, Murray et al. 2005, Hodges and Mills 2008, McCann et al. 2008). Only annually cleared pellet counts were used for further analysis (Chapter 2). We then converted mean pellet counts to an estimate of hare density using the equation $y = 0.0927x + 0.1743$ (Chapter 2); hare density was estimated as hares/ha. Both pellet counts and corresponding hare density estimates were used in the analyses.

Indices of Secondary Prey Abundance

Counts of scats produced by forest grouse and counts of middens constructed by red squirrels have been used as an index of relative abundance for these species (Ball et al. 2000, Côté and Ferron 2001). Scats of forest grouse were tallied on the same 1-m² circular plots used for snowshoe hare fecal pellet counts. Grouse scats were only counted at the time of plot establishment and thus likely consisted of multiple years of fecal accumulation. Counts of grouse scats were standardized to scats/m² for analysis. Red squirrel middens that showed evidence of recent activity (i.e. within the past 12 months) were counted on a larger 0.02-ha plot (8.02 m radius circle) established directly over the 1-m² circular plots. Red squirrel middens likewise were only counted at the time of initial plot establishment. Counts of red squirrel middens were standardized to middens/ ha.

Forest Composition Surveys

We established a 0.02-ha vegetation plot (8.02 m radius circle) directly over the prey sample plots to collect data on the associated forest structure at these locations. Our sampling effort was balanced by establishing vegetation plots on ≥ 65 prey sample plots within each forest

stand type (Table 3-1). All plots were located on sites with at least one tree ≥ 3 m tall. The dominant and co-dominant stand cover type was recorded by categorizing tree species into 5 diameter at breast height (DBH) size classes: 2.54-7.37, 7.62-12.45, 12.7-22.61, 22.86-40.39, and >40.39 cm (Doerr 2004). In order for a tree species to be recorded as co-dominant in the stand that species had to contribute $\geq 20\%$ of the dominant tree species overstory canopy (Doerr 2004). Two layers of canopy cover were recorded separately for each plot and included: (a) tree canopy cover which measured cover from live stems with a DBH ≥ 2.54 cm, and (b) shrub canopy cover which measured cover from live stems with a DBH ≤ 2.54 cm and a height ≥ 15.24 cm. Sapling trees with a DBH ≤ 2.54 cm and height ≥ 15.24 cm were considered shrubs and tallied as shrub canopy cover. Tree canopy cover and shrub canopy cover were categorized and recorded to the nearest 10% for each plot (Doerr 2004). A walk-through assessment of each plot was conducted and canopy cover was then measured by imagining a top-down perspective or bird's eye view of the vegetation plot (Tart et al. 2005). When measuring tree canopy cover, only canopy in the open that was not directly overtopped by another tree was recorded. Likewise, when measuring shrub canopy cover, only the canopy that was not directly overtopped by another shrub was recorded.

Horizontal cover attributed to tree and shrub stems, branches, leaves, needles, large woody debris, and topography was recorded for each plot. Percent horizontal cover was measured by having one observer stand at the center of the plot holding the top of a 0.305 m wide x 1.83 m long cover board with the bottom of the cover board 15 cm above the ground and 8.02 m distance from the second observer (Doerr 2004). The cover board was divided into 0.305 m segments and the second observer recorded the percent of each segment to the nearest 10% that was obscured by cover (Doerr 2004). Cover readings were recorded from the 4 cardinal directions (Doerr 2004). The cover readings were then averaged to obtain one estimate of horizontal cover for each plot.

Stems with a DBH ≥ 2.54 cm were tallied on plots to calculate stem density (stems/ha). All trees with a DBH ≥ 2.54 cm were categorized within 5 DBH size classes: 2.54-7.37, 7.62-12.45, 12.7-22.61, 22.86-40.39, and >40.39 cm (Doerr 2004) and then the DBH for trees within these 5 classes were averaged to 4.95, 10.03, 17.65, 31.62, and 40.64 cm, respectively. We then converted tree stems with a DBH ≥ 2.54 cm to basal area (m^2/ha) (Fuwape et al. 2001). The density of large woody debris with a diameter ≥ 12.7 cm and length ≥ 3 m was recorded as were the density of standing dead trees with a DBH ≥ 12.7 cm because dead wood of this size might provide hiding cover and thermal protection for snowshoe hares.

To examine edge effects on potential prey abundance, we measured the distance from the outside edge of each vegetation plot to the transition (edge) of a different habitat type nearest the plot and categorized the edge distance into 4 classes: 5, 10, 20, or 30 m. Locations (Universal Transverse Mercator) were recorded at the start of each transect and the elevation determined to the nearest 10 m using U.S. Geological Survey digital elevation models (DEM; Carlile 2002) (U.S. Forest Service Geospatial Data Clearinghouse, Geospatial Service and Technology Center, Sioux Falls, South Dakota). Percent slope was recorded for each plot using a clinometer by measuring 8 m uphill and 8 m downhill and then averaging these 2 measurements.

Statistical Analysis

Individually measured forest structural attributes (i.e. canopy cover, horizontal cover, percent slope, etc.) from across the 5 plots on each transect were averaged in order to obtain one measurement of each attribute per transect. Using SPSS (SPSS for Windows 10, Chicago, Illinois USA) we compared prey abundance and forest structure attributes at the transect scale among the 7 stand types using a one-way analysis of variance (ANOVA) combined with a Duncan's multiple-contrast (Zar 1996). We performed zero inflated count regressions (Cameron and Trevedi 1998) using the 'zeroinfl' procedure in package 'pscl' in program R (R version 2.6.0,

Development Core Team, R Foundation for statistical computing, Vienna, Austria) to model the influence of the 12 independent forest stand characteristics on the dependent variables of snowshoe hare fecal pellet counts, red squirrel midden counts, and grouse scat counts. We used a negative binomial distribution to account for the excess zeros and overdispersed nature of our dataset. We used an E-M (Expectation Maximization) algorithm to maximize the likelihood underlying each model that we tested. For model selection, we used Akaike's Information Criterion (AICc) corrected for small sample size (Akaike 1973) to compare models and determine which model(s) served as the best approximation(s) to the data. We started with a global model testing for additive effects of the 12 independent variables on snowshoe hare pellet counts, red squirrel midden counts, and grouse scat counts, respectively. We then removed all covariates with P-values >0.10. We then examined whether the AIC value diminished, thereby indicating an improved model fit, and whether the covariates were still significant; if not we removed them from the model. We then used regression curve estimation to identify relationship patterns between dependent (i.e., hares/ha, squirrel middens/ha, and grouse scat/m²) and independent (i.e., forest stand characteristics) variables using SPSS. In order to investigate whether relationships at the transect scale remained significant at larger landscape scales, transects were combined by forest stand type and the means of the dependent and independent variables were calculated and regressed.

RESULTS

Forest Site and Structural Attributes

When comparing site and structural attributes as well as prey abundance between the 7 forest stand types, most attributes were significantly different between types; the exception being percent slope (Table 3-1). Snowshoe hare density (hares/ha) was lowest in young lodgepole/low density and highest in young lodgepole/high density, but overall was greater in the multi-storied

forest types than the young even-aged lodgepole pine types (Table 3-1, Figure 3-4). Red squirrel midden counts (middens/ha) were lowest in young lodgepole/low density and highest in mixed lodgepole spruce-fir, and overall were greater in multi-storied forest types (Table 3-1, Figure 3-4). Grouse scat counts (scat/m²) were lowest in young lodgepole/low density and highest in mixed whitebark spruce-fir, and overall were greater in multi-storied forest types (Table 3-1, Figure 3-4). Basal area (m²/ha) was lowest in young lodgepole/low density and highest in mixed whitebark spruce-fir, and overall was greater in multi-storied forest types (Table 3-1). Distance to edge (m) was lowest in mixed spruce-fir and greatest in young lodgepole/medium density, but overall quite similar amongst all forest types (Table 3-1). Elevation (m) was lowest in mixed lodgepole spruce-fir and highest in mixed whitebark spruce-fir (Table 3-1). Horizontal cover (%) was lowest in young lodgepole/low density and highest in mixed spruce-fir, and overall was greater in multi-storied forest types (Table 3-1). Large woody debris (logs/ha) was lowest in young lodgepole/medium density and highest in mixed lodgepole spruce-fir, and overall was greater in multi-storied forest types (Table 3-1). Shrub canopy cover (%) was lowest in young lodgepole/low density and highest in mixed aspen spruce-fir, and overall was greater in multi-storied forest types (Table 3-1). Standing dead trees (trees/ha) were lowest in young lodgepole/high density and highest in mixed whitebark spruce-fir, and overall were greater in multi-storied forest types (Table 3-1). Stem density (stems/ha) was lowest in young lodgepole/low density and highest in young lodgepole/high density, and overall was similar in both young regenerating lodgepole and older multi-storied forest types (Table 3-1). Tree canopy cover (%) was lowest in young lodgepole/low density and highest in young lodgepole/high density, but overall was higher in older multi-storied forest types (Table 3-1). Not surprisingly, basal area, horizontal cover, and tree canopy cover increased as stem density increased in the 30-70-year-old lodgepole pine stands (Table 3-1). Shrub canopy cover also increased as stem density increased in 30-70-year-old lodgepole pine stands (Table 3-1).

Snowshoe Hare Pellet Counts and Density Estimates

Results from the saturated global model (AIC: 1058.977) utilizing zero inflated count regressions indicated horizontal cover and tree canopy cover were highly significant ($P < 0.01$) predictors of increasing snowshoe hare pellet counts; soil type, percent slope, distance from the edge, and stem density were less significant ($P < 0.15$) predictors (Table 3-2). The minimized model (AIC: 1058.213) which only included horizontal cover and tree canopy cover, while excluding all variables with a P-value >0.10 , did not outperform the saturated global model (Table 3-3). The over-dispersion parameter $\text{Log}(\theta)$ from the saturated global model ($P < 0.001$) and from the minimized model ($P < 0.001$) indicated the negative binomial model using the zero inflated count regression was more appropriate than a Poisson model and appropriately fit our snowshoe hare pellet count data.

Regressions of all 112 transects, as well as the mean values for the 7 individual forest structure types, showed significant positive relationships (logistic curves were the best fit for the data) between increasing snowshoe hare density and increasing horizontal cover (Figures 3-2a,b), and between increasing snowshoe hare density and increasing tree canopy cover (Figures 3-3a,b). Regressions of the mean collapsed values of the 7 forest structure types (i.e., the 112 transects collapsed into the 7 forest types) also revealed significant ($P < 0.10$) positive relationships between increasing snowshoe hare density and increasing horizontal cover, tree canopy cover, shrub canopy cover, and stem density, but a negative relationship between hare density and elevation (Table 3-4).

Red Squirrel Midden Counts

The saturated global model (AIC: 608.921) utilizing zero inflated count regressions comparing the dependent variable of red squirrel midden counts with associated independent forest structure variables indicated that habitat type, shrub canopy cover, and standing dead trees

significantly influenced counts of red squirrel middens (Table 3-2). However, the global model was outperformed by our first minimized model (AIC: 599.695) which included the variables of habitat type, shrub canopy cover, and standing dead trees. Our second minimized model (AIC: 598.701) which only included the significant variables of habitat type and standing dead trees was similar to the first minimized model, therefore our model of choice was the first minimized model. Log(theta) values from the saturated global model ($P = 0.260$) and from our model of choice ($P = 0.690$) were not significantly different from zero ($P < 0.001$) indicating that a Poisson model could be used for the squirrel midden counts. However, we choose to use the negative binomial model to be consistent with the models for snowshoe hare pellet and grouse scat counts and because results using this model or a Poisson model should be the same. When we collapsed the transects into the 7 forest structure types, regression analyses revealed significant relationships ($P < 0.10$) between increasing red squirrel middens and increasing basal area, standing dead trees, large woody debris, and shrub canopy cover (Table 3-4).

Forest Grouse Scat Counts

The saturated global model (AIC: 585.604) utilizing zero inflated count regressions comparing the dependent variable of grouse scat counts with independent forest stand characteristics indicated that basal area, habitat type, and tree canopy cover significantly influenced counts of grouse scats among the transects (Table 3-2). Our first minimized model outperformed (AIC: 571.703) the global model and included basal area, habitat type, and tree canopy cover (Table 3-3). The over-dispersion parameter Log(theta) from the saturated global model ($P < 0.001$) and from the minimized model ($P < 0.001$) indicated that a negative binomial model such as zero inflated count regressions was more appropriate than a Poisson model and appropriately fit our grouse scat count data. Regression analyses using transect data collapsed into the 7 forest structure types revealed significant positive relationships ($P < 0.10$) between

increasing grouse scat counts and increasing basal area, standing dead trees, and percent slope (Table 3-4).

Comparisons of Young versus Old Forests

We used the prey abundance data from all 180 transects (900 plots) to compare prey abundance in young regenerating lodgepole pine stands versus older multi-storied stands with a spruce/fir component. There was an overall increase in snowshoe hare density and indices of forest grouse abundance in the three young lodgepole pine forest types as stem density increased from low to high; while indices of red squirrel abundance were similar within these three forest types (Table 3-1). When contrasted amongst the seven stand types surveyed, snowshoe hare densities were high in all categories of multi-storied stands, the one exception being whitebark pine-spruce-fir where hare densities were lower than other multi-storied forest types (Table 3-1). Indices of red squirrel abundance were similar in all multi-storied types surveyed (Table 3-1). Within multi-storied stands indices of grouse abundance were highest in whitebark pine-spruce-fir and lowest in spruce-fir, with aspen-spruce-fir and lodgepole pine-spruce-fir falling between respectively (Table 3-1). Overall hare densities were slightly higher in older multi-storied forests than they were in young lodgepole pine forests (Figure 3-4). Indices of red squirrel and forest grouse abundance were several-fold higher in older multi-storied forests than in young lodgepole pine forests (Figure 3-4).

DISCUSSION

In certain portions of their geographical range snowshoe hare's prefer young regenerating forest stands to mature forest types (Koehler et al. 1979, Wolff 1980, Bittner and Rongstad 1982, Monthey 1986, Koehler 1991) and as expected, snowshoe hares used these young forest types on the B-TNF. However, within the southern portion of their range hares also use mature late successional forest types (Buskirk et al. 2000, Walker 2005, Murphy et al. 2006, Fuller et al.

2007, Koehler et al. 2007, Maletzke et al. 2008, Hodges et al. 2009) which was evident on the B-TNF. Results from this study suggest snowshoe hares preferred dense, structurally diverse stands and these characteristics were most consistently found in older multi-storied forests with a spruce-fir component on the B-TNF. Overall, multi-storied stands had higher hare densities than 30-70-year-old lodgepole pine stands (Figure 3-4). Moreover, because hare habitat in young regenerating stands is short-lived in the GYA (Zimmer et al. 2008), older multi-storied stands will often have higher hare density than young lodgepole pine stands 70+ years post-disturbance. In addition, abundance indices for red squirrels and forest grouse, prey items for lynx when hares are sparse (Aubry et al. 2000), were several-fold higher in multi-storied forests than 30-70-year-old lodgepole pine stands (Figure 3-4). Moreover, habitat characteristics that significantly predicted grouse and squirrel abundance were usually more prevalent in multi-storied forests. This suggests that older multi-storied forests with a spruce-fir component that contained high horizontal cover and tree canopy cover, an abundant shrubby understory with plentiful large woody debris, as well as standing dead trees, play a disproportionately important role in providing primary and secondary foraging habitat for lynx in this region.

Overall horizontal cover and tree canopy respectively were the most significant predictors of hare density on the B-TNF. Stem density and shrub canopy cover which are components of horizontal cover also predicted hare density; however the relationship was less significant in both cases. A reduction in understory horizontal cover is known to negatively affect hares and Canada lynx in forested habitat (Squires and Ruggiero 2005) and our results were indicative of a similar relationship between hares and horizontal cover. A horizontal cover-hare density equation (Figure 3-2a) developed here is a valid tool that can be used to convert horizontal cover measurements in to an accurate estimate of hare density. For example, horizontal cover measurements recorded during the summer months of 24% and 32% predict hare densities of 0.3 and 0.5 hares/ha, respectively (Figure 3-2a). We recommend the use of this

equation on the B-TNF and perhaps elsewhere in the GYA for the purpose of identifying potentially important foraging habitat for lynx.

There was a weak relationship between increasing distance from a habitat edge and increasing hare density (Table 3-2); snowshoe hares may have been exhibiting a slight preference for the interior portions of surveyed stands. Future studies should investigate the hare-habitat edge relationship further to determine what may constitute the optimal patch size for sustaining abundant snowshoe hare populations in this region.

Within the past century many older multi-storied stands have been mechanically harvested on the B-TNF and a number of these sites were not regenerating adequately to provide the horizontal cover required for abundant hare populations 30-70-years post-harvest. This lack of regeneration contributes to increased habitat fragmentation, smaller patch sizes of important multi-storied stands, and consequently a temporal reduction in primary and secondary prey at such sites. The naturally fragmented spatial arrangement of habitat in the GYA has been identified as a limiting factor for lynx in this area (U.S. Fish and Wildlife Service 2008) and past, present, and future human-caused fragmentation may further reduce habitat suitability for hares and lynx in this region. Further research is warranted to better understand the role silviculture, prescribed and natural fire events, disease and insect infestation, and climate change plays in snowshoe hare and lynx population and habitat dynamics in this region.

Timber harvest and wildfire significantly modify forested landscapes in southern boreal forests and can be used as an instrument for improving snowshoe hare habitat (Peet 2000, Veblen 2000, Zimmer 2004, Hodges and Mills 2005). However, the effects of fire and timber harvest on hare abundance depend on a variety of site-specific environmental factors and range from beneficial to damaging to snowshoe hares (Turner et al. 1997, Buskirk et al. 2000, Anderson et al. 2004, Ellsworth and Reynolds 2006, Murphy et al. 2006).

Within older predominately even-aged lodgepole pine forests timber harvest or stand replacing fire and the subsequent regeneration of young stands of small trees can create hare habitat post-disturbance if adequate cover develops (Agee 2000, Hodges 2000a, Hodges and Mills 2005, Murphy et al. 2006, Zimmer et al. 2008, Hodges et al. 2009). We found, as have others, that after natural or mechanical disturbance, snowshoe hares prefer medium to densely stocked stands of small trees and shrubs (Brocke 1975, Wolff 1980, Parker 1984, Litvaitis et al. 1985, Koehler 1990, Griffin 2004, Zimmer et al. 2008, Hodges et al. 2009) because these stands provide abundant horizontal cover (Hodges 2000a, Hodges and Mills 2005, Murphy et al. 2006). From our observations 30-70-year-old lodgepole pine stands containing abundant large woody debris, a tall (≥ 1 m) shrubby understory, and a significant sub-alpine fir-Engelmann spruce component, structurally mimic older multi-storied forest types and often harbor higher snowshoe hare, red squirrel, and forest grouse numbers than do similarly aged lodgepole pine stands that lack these important horizontal cover components. Additionally, the temporal window of use for lynx prey species was likely lengthened in these more structurally diverse young stands because of increased horizontal cover (Figures 3-5a,b). For this reason, we encourage the use of harvest techniques that mimic and promote the structural assortment and species diversity that are found in older multi-storied stands. Our research suggests that in this region, management techniques that promote the structural and species diversity found in multi-storied forests are likely of more benefit to hares and lynx than traditional even-aged management.

Dissimilar from mature even-aged lodgepole pine forests, there are likely to be few short-term temporal and/or spatial benefits to hares from fire and timber harvest in multi-storied stands that contain a significant spruce-fir component, because these forest types tend to retain live branches to the forest floor, and often already have a well developed understory of young trees and shrubs (Despain 1990); thus providing hares with food and cover over a longer period of time than do even-aged forests (Wolfe et al. 1982, Buskirk et al. 2000, Koehler et al. 2008, Zimmer et

al. 2008). Within multi-storied stands, large-scale timber harvest or fire disturbance is likely more often detrimental to hares because these forests are very slow growing and regeneration can take several decades under the best circumstances before young trees and shrubs have grown tall and thick enough to provide winter cover and food for snowshoe hares (Wolfe et al. 1982, Buskirk et al. 2000, Zimmer et al. 2008).

Net primary productivity on forested sites varies considerably in the GYA and is driven by site-specific environmental factors that are known to influence species abundance (Whittaker 1975, Perry 1994, Hansen et al. 2000). Accordingly, we observed noteworthy dissimilarities in hare use of habitats across the forest that may have reflected underlying distinctions in net primary productivity at these sites. At certain locations on the B-TNF hare densities were highest in older multi-storied forests, while in contrast, hare densities were highest in 30-70-year-old lodgepole pine at other sites. Hansen et al. (2000) observed higher net primary productivity in forests at low elevations and we observed a similar pattern of hare abundance on the B-TNF (Table 3-4). Snowshoe hare management in the GYA should explicitly consider variations in site quality such as differences in soils, species composition, stand age structure, and seed production, as well as environmental and climatic variability.

The restoration of whitebark pine and aspen stands are a management priority for a variety of ecological reasons (McKinney et al. 2009, Hollenbeck and Ripple 2007) and when these stands are mixed with spruce and fir they are often a vital component of lynx habitat in the GYA. Whitebark pine and aspen stands that are mixed with spruce and fir are structurally similar to other multi-storied forest types and often support moderate to high numbers of snowshoe hares, red squirrels, and forest grouse (Table 3-1). Because foraging habitat is believed to be a major limiting factor for the federally listed Canada lynx in the GYA we recommend that whitebark pine and aspen that are currently and/or naturally mix with spruce and fir on the landscape be

managed as long-term foraging habitat for lynx; thus ensuring that both valuable lynx habitat and valuable aspen and whitebark pine are maintained across the landscape.

MANAGEMENT IMPLICATIONS

Overall, multi-storied stands with a spruce-fir component had higher snowshoe hare density than did 30-70 year old even-aged lodgepole pine forests; additionally, abundance indices for red squirrels and forest grouse were much higher in these same multi-storied stands. For this reason, and until our understanding of hare and lynx habitat patch size preferences are better understood in this region, management should focus on maintaining, enhancing, and promoting increased acreage and connectivity of multi-storied forests in the GYA. We concur with Buskirk et al. (2000) and Zimmer et al. (2008) that the preservation and enhancement of extensive tracts of dense multi-storied forests likely are of greatest benefit to snowshoe hares and lynx in this region.

Of all the forest structural components that we measured, in both young even-aged and older multi-storied forests, horizontal cover, which was composed of both living and dead tree stems, branches, leaves, needles, shrubs, and large woody debris, was the most significant predictor of snowshoe hare density on the B-TNF. For this reason, and similar to highly predictive fecal pellet-hare density equations that have been developed for the B-TNF (Chapter 2) and elsewhere in North America (Krebs et al. 1987, 2001, Murray et al. 2002, Mills et al. 2005, McCann et al. 2008), the horizontal cover-hare density equation developed here (Figure 3-2a) is a useful and accurate tool for identifying potential lynx foraging habitat on the B-TNF. However, due to observed differences in vegetative species structure within lynx habitat from region to region, we do not recommend the use of the B-TNF horizontal cover-hare density equation beyond the GYA without thorough field verification. For this same reason horizontal cover-hare availability relationships that have been developed elsewhere should be thoroughly tested in this

region before being used to identify valuable snowshoe hare or lynx habitat in the GYA. We observed on this study, as have others (Squires et al. 2003), that lynx habitat in Wyoming tends to have fewer deciduous shrubs in the understory than lynx habitat in Montana; and this, along with other possible factors, could significantly alter the horizontal cover-hare density relationship. Regionally specific horizontal cover-hare density relationships should be developed and tested that incorporate local habitat and environmental conditions because the use of an inappropriate equation could prove detrimental to lynx conservation efforts.

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Table 3-1. Forest structure characteristics among the 7 forest types surveyed with ANOVA values and corresponding Duncan's statistical contrasts, Bridger-Teton National Forest, Wyoming, 2006-2008. Means \pm 1 SE are presented, number of transects sampled in parentheses. Letters following mean values denote values not significantly different from one another (Duncan's contrast).

	Young lodgepole low (16)	Young lodgepole medium (16)	Young lodgepole high (16)	Mixed whitebark spruce-fir (13)	Mixed aspen spruce-fir (20)	Mixed lodgepole spruce-fir (17)	Mixed spruce- fir (14)	<i>F</i>	<i>P</i>
Hare density (hares/ha)	0.48 _A ± 0.07	0.85 _{AB} ± 0.16	1.69 _C ± 0.24	0.56 _A ± 0.09	1.46 _C ± 0.25	1.24 _{BC} ± 0.19	1.58 _C ± 0.26	5.58	<0.001
Squirrel counts (middens/ha)	0.29 _A ± 0.20	0.30 _A ± 0.12	0.33 _A ± 0.13	1.75 _B ± 0.29	1.85 _B ± 0.27	2.12 _B ± 0.44	1.68 _B ± 0.37	8.78	<0.001
Grouse counts (scat/m ²)	0 _A ± 0	0.05 _A ± 0.03	1.46 _A ± 0.94	7.23 _B ± 4.14	4.66 _{AB} ± 1.51	4.26 _{AB} ± 1.62	0.93 _A ± 0.39	2.70	0.018
Basal area (m ² /ha)	9.74 _A ± 1.02	17.71 _B ± 0.48	30.58 _D ± 2.25	46.40 _{CD} ± 4.82	31.74 _{BC} ± 2.12	39.14 _{BCD} ± 4.37	39.89 _{CD} ± 4.28	9.79	<0.001
Distance to edge (m)	26.1 _{BC} ± 0.85	27.3 _C ± 0.78	26.4 _{BC} ± 1.02	24.2 _{ABC} ± 1.03	23.5 _{AB} ± 1.10	26.9 _{BC} ± 0.79	22.7 _A ± 1.52	2.92	0.011
Elevation (m)	2562 _B ± 22	2535 _B ± 39	2497 _{AB} ± 41	2831 _C ± 28	2449 _{AB} ± 33	2392 _A ± 49	2487 _{AB} ± 63	11.20	<0.001
Horizontal cover (%)	31.1 _A ± 1.94	42.1 _{BC} ± 3.01	52.3 _D ± 4.86	36.6 _{AB} ± 2.45	55.6 _D ± 3.45	46.3 _{CD} ± 3.06	55.8 _D ± 3.00	8.85	<0.001
Large woody debris (logs/ha)	25.79 _A ± 8.53	24.85 _A ± 5.47	69.80 _{AB} ± 35.11	64.38 _{AB} ± 12.05	49.29 _A ± 9.47	113.12 _B ± 11.79	104.18 _B ± 8.84	4.71	<0.001
Shrub canopy (%)	5.8 _A ± 1.29	10.9 _{AB} ± 2.22	15.5 _{BC} ± 4.13	10.4 _{ABD} ± 1.49	27.5 _D ± 3.40	22.2 _{CD} ± 2.53	21.5 _C ± 3.28	8.44	<0.001
Slope (%)	10.2 _{AB} ± 1.66	9.5 _A ± 1.39	12.5 _{AB} ± 1.66	13.9 _{AB} ± 1.02	14.4 _B ± 1.19	11.1 _{AB} ± 1.78	12.1 _{AB} ± 1.61	1.71	0.126
Standing dead trees (trees/ha)	1.94 _A ± 1.32	4.75 _A ± 2.04	1.43 _A ± 0.53	38.85 _B ± 7.10	34.72 _B ± 6.06	28.38 _B ± 7.52	26.71 _B ± 7.53	9.78	<0.001
Stem density (stems/ha)	724.5 _A ± 51.73	1317.6 _{AB} ± 50.42	3194.2 _C ± 553.05	1724.6 _B ± 171.14	1508.7 _B ± 144.95	1693.3 _B ± 163.77	1679.4 _B ± 125.47	10.08	<0.001
Tree canopy (%)	27.9 _A ± 1.59	39.2 _{BC} ± 2.27	49.1 _{CD} ± 2.42	37.1 _B ± 1.90	46.1 _{CD} ± 2.36	42.6 _{BCD} ± 2.47	44.6 _{CD} ± 1.50	11.31	<0.001

Table 3-2. Results from the saturated global models utilizing zero inflated count regressions for the dependent variables of snowshoe hare pellet counts, red squirrel midden counts, and forest grouse scat counts and the 12 independent forest structure characteristics, Bridger-Teton National Forest, Wyoming, 2006-2008.

Variable	<u>Snowshoe hare</u>		<u>Red squirrel</u>		<u>Forest grouse</u>	
	<i>Z</i>	<i>P</i>	<i>Z</i>	<i>P</i>	<i>Z</i>	<i>P</i>
Basal area	-0.612	0.540	0.782	0.434	1.780	0.075
Distance from edge	1.465	0.143	0.083	0.933	-0.768	0.442
Elevation	-1.167	0.243	0.575	0.565	-0.577	0.564
Habitat type	0.007	0.994	3.768	<0.001	2.333	0.019
Horizontal cover	2.669	0.008	-1.520	0.128	0.364	0.715
Large woody debris	1.402	0.161	-0.276	0.782	-0.408	0.683
Shrub canopy	0.649	0.516	2.599	0.009	-0.812	0.416
Slope	-1.617	0.105	-1.416	0.156	-0.082	0.934
Soil type	1.549	0.121	-1.453	0.146	0.163	0.870
Standing dead trees	0.858	0.391	2.892	0.003	-0.101	0.919
Stem density	1.621	0.105	-0.789	0.430	-1.513	0.130
Tree canopy	2.722	0.006	0.933	0.350	3.100	0.002

Table 3-3. Results from the preferred minimized models utilizing zero inflated count regressions for the dependent variables of snowshoe hare pellet counts, red squirrel midden counts, and forest grouse scat counts and the significant forest structure characteristics, Bridger-Teton National Forest, Wyoming, 2006-2008.

Variable	<u>Snowshoe hare</u>		<u>Red squirrel</u>		<u>Forest grouse</u>	
	<i>Z</i>	<i>P</i>	<i>Z</i>	<i>P</i>	<i>Z</i>	<i>P</i>
Basal area	ns ^a	ns	ns	ns	3.439	<0.001
Habitat type	ns	ns	5.385	<0.001	3.631	<0.001
Horizontal cover	5.487	<0.001	ns	ns	ns	ns
Standing dead trees	ns	ns	3.191	0.001	ns	ns
Tree canopy	3.971	<0.001	ns	ns	2.836	0.004

^a ns: not significant.

Table 3-4. Regression curve estimation models using logistic equations for the dependent variables of snowshoe hare pellet counts, red squirrel midden counts, and forest grouse scat counts and 10 forest structure characteristics, Bridger-Teton National Forest, Wyoming, 2006-2008.

Variable	<u>Snowshoe hare</u>			<u>Red squirrel</u>			<u>Forest grouse</u>		
	Relationship	R^2	P	Relationship	R^2	P	Relationship	R^2	P
Basal area	S	0.178	<0.001	Cubic	0.120	0.003	Logarithmic	0.029	0.074
Distance from edge	Linear	0.026	0.091	Logarithmic	-0.019	0.148	Cubic	0.029	0.198
Elevation	Linear	-0.105	<0.001	Cubic	0.028	0.208	Linear	<0.001	0.875
Horizontal cover	Logistic	0.455	<0.001	Logarithmic	0.054	0.014	Linear	0.008	0.352
Large woody debris	Logistic	0.123	<0.001	Cubic	0.212	<0.001	Quadratic	0.013	0.492
Shrub canopy	Linear	0.266	<0.001	Linear	0.165	<0.001	Linear	0.005	0.447
Slope	Quadratic	0.007	0.694	Cubic	0.037	0.255	Logarithmic	0.002	0.626
Standing dead trees	Cubic	0.042	0.199	Cubic	0.311	<0.001	Linear	0.043	0.030
Stem density	Power	0.233	<0.001	Cubic	0.078	0.032	Cubic	0.027	0.398
Tree canopy	Logistic	0.344	<0.001	Logarithmic	0.066	0.006	Logarithmic	0.030	0.067

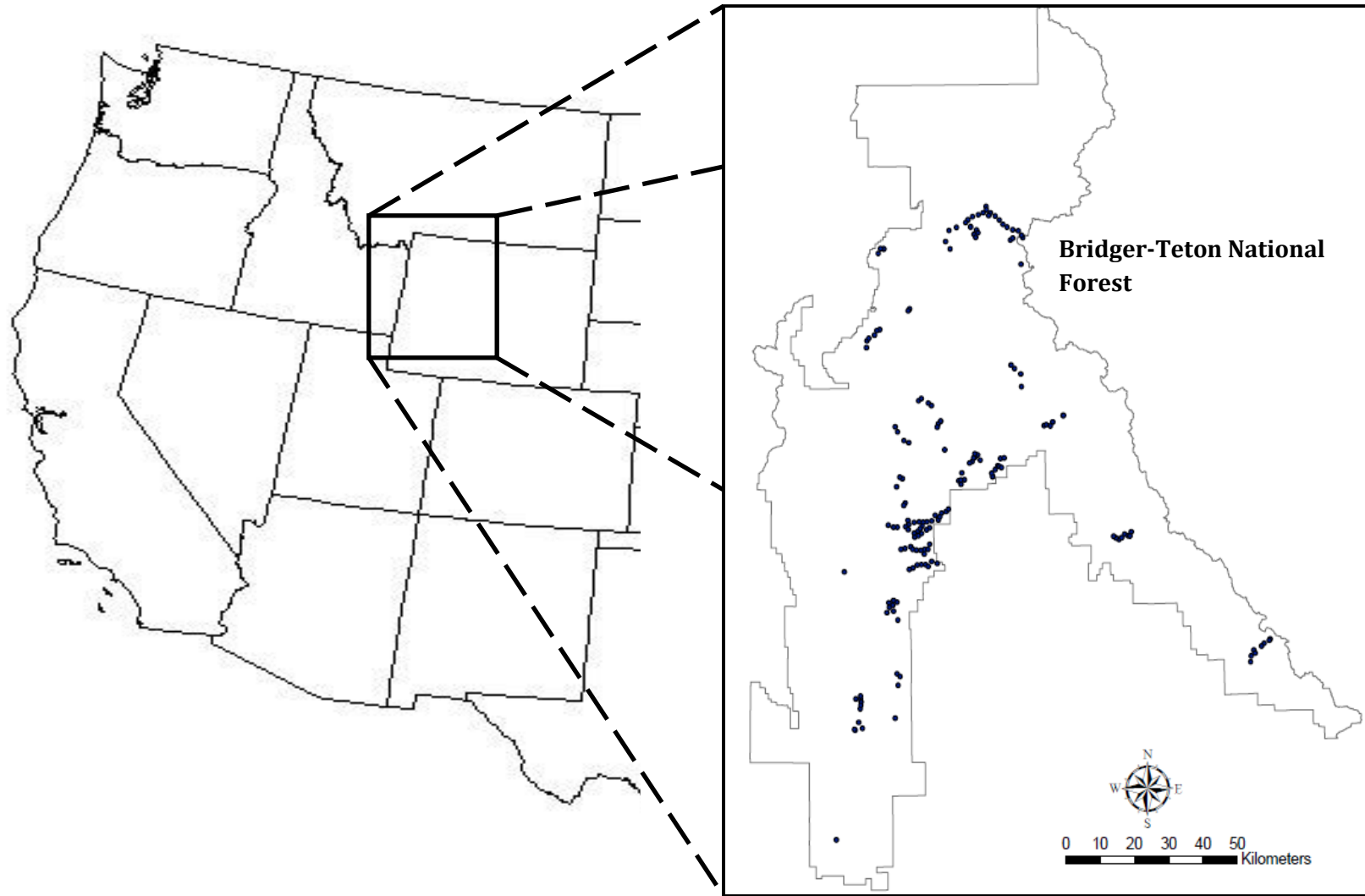


Figure 3-1. Location of the Bridger-Teton National Forest Study Area and prey survey transects in western Wyoming.

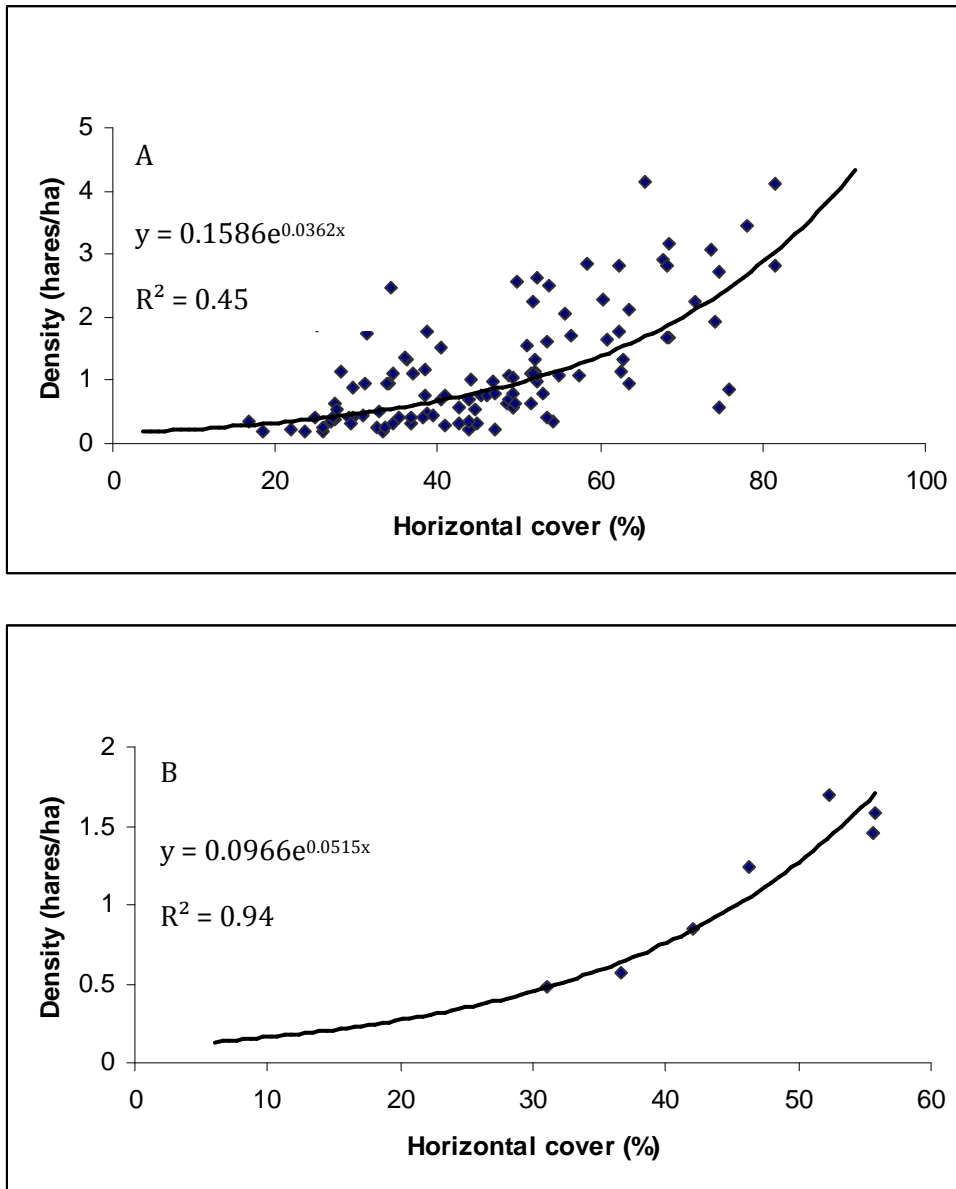


Figure 3-2. Relationship between horizontal cover and snowshoe hare density for (a) all 112 transects, and (b) by 7 forest structure types, Bridger-Teton National Forest, Wyoming, 2006-2008.

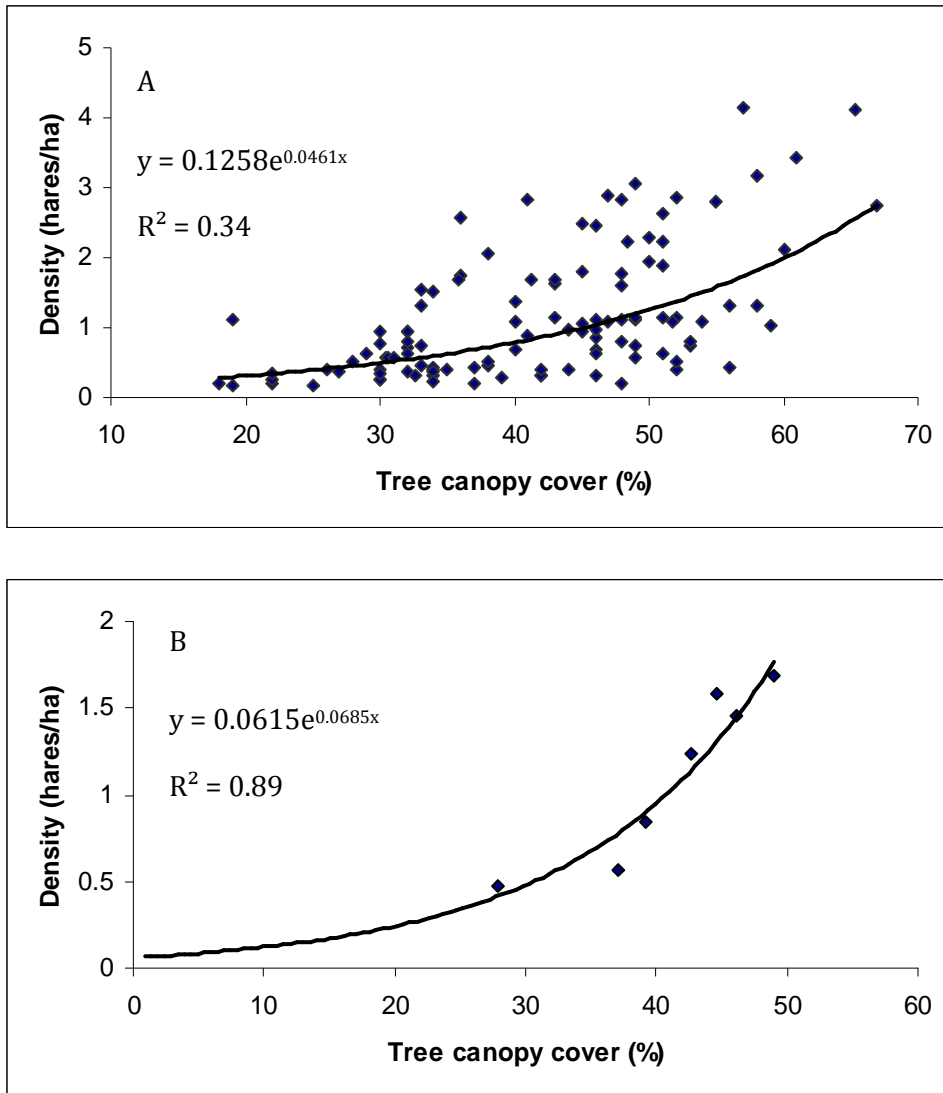


Figure 3-3. Relationship between percent tree canopy cover and snowshoe hare density for (a) all 112 transects and (b) by 7 forest structure types, Bridger-Teton National Forest, Wyoming, 2006-2008.

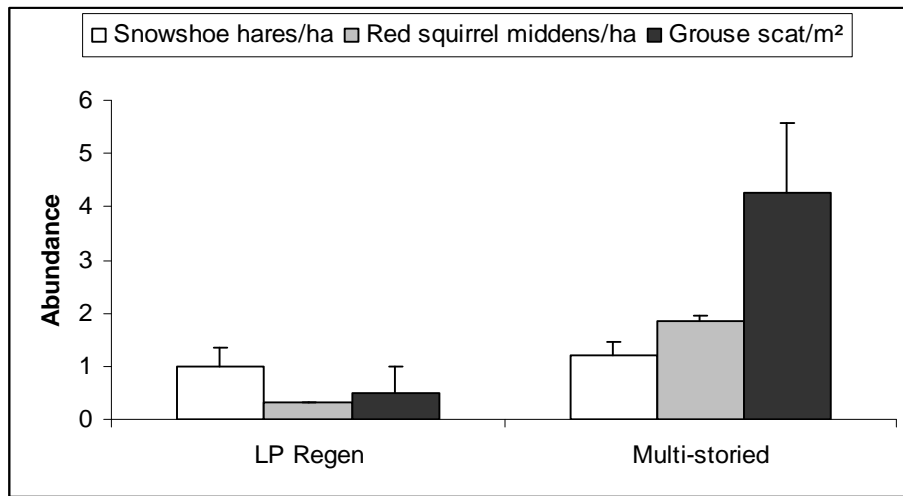
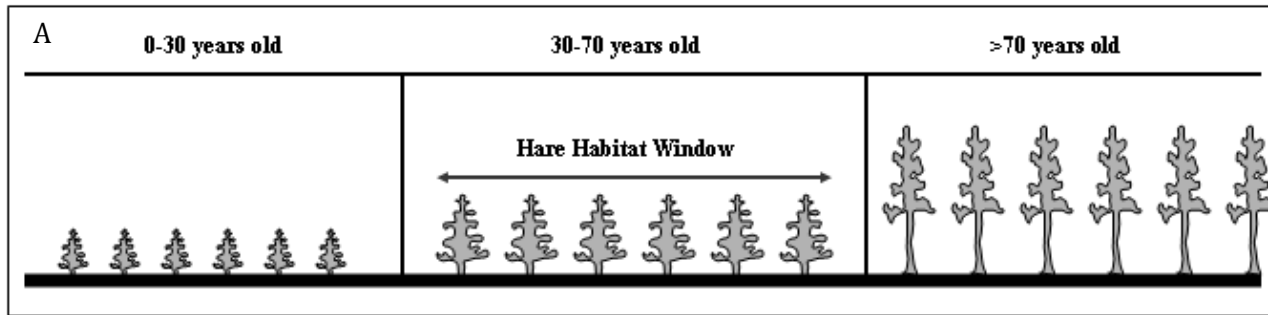


Figure 3-4. Prey abundance estimates (means \pm 1 *SE*) for LP regen (combined 30-70-year-old lodgepole forest types) and Multi-storied (combined multi-storied forest types), Bridger-Teton National Forest, Wyoming, 2006-2008.

Lodgepole Pine Regeneration (Typical Even-aged)



Lodgepole Pine Regeneration (Lynx/Hare Alternative)

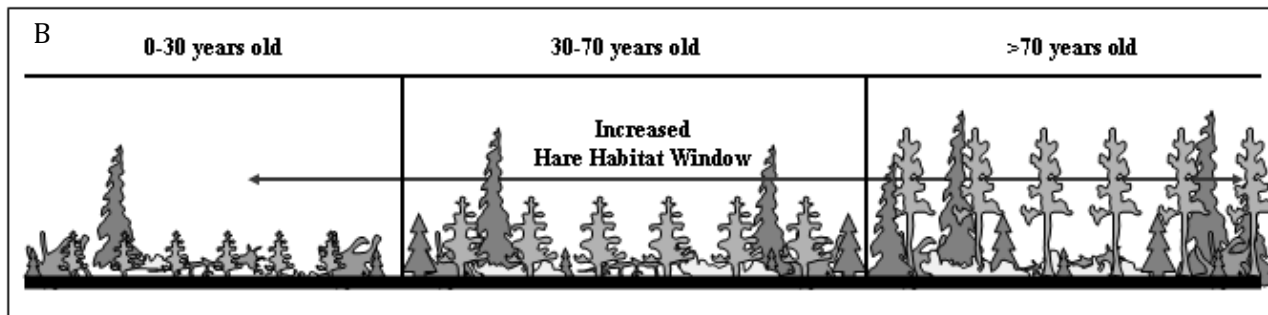


Figure 3-5. Silviculture schematic depicting (a) typical even-aged lodgepole pine regeneration and (b) a preferred lynx/hare alternative for even-aged lodgepole pine regeneration that lengthens the hare habitat window and mimics multi-storied stand conditions by leaving residual spruce and fir seed trees, large woody debris, and by promoting a shrubby understory.

CHAPTER 4

CONCLUSIONS

This research focused on 2 main objectives: (a) elucidating the correlation between snowshoe hare density (*Lepus americanus*) and fecal pellet counts, and (b) examining the relationships between forest structure characteristics and abundance of snowshoe hares, red squirrels (*Tamiasciurus hudsonicus*), and forest grouse (*Bonasa umbellus* and *Dendragapus obscurus*). For the first objective, we found significant correlations between snowshoe hare density and pellet counts in western Wyoming that were consistent with other studies throughout North America (Krebs et al. 1987, 2001, Murray et al. 2002, Mills et al. 2005, Murray et al. 2005, Homyack et al. 2006, McCann et al. 2008). Before the initiation of this study, no regression equations relating hare density and pellet counts had been developed for this region due to low observed hare numbers. Therefore, the equations developed on the Bridger-Teton National Forest (B-TNF), where there were a range of hare densities, provided an important reference point and can be used by researchers and managers to estimate snowshoe hare density in this region. Additionally, the correlation coefficient between hare density and pellet counts was greater when using equations that utilized a buffer adjustment for hard forest edges and may be a better fit due to the high degree of habitat fragmentation found in the region.

There have been discussions of the utility of counting fecal pellets from uncleared plots due to the effects of multiple years of pellet accumulation, temporal changes in hare abundance, the difficulty in correctly aging pellets, and the influence of varying rates of pellet decomposition due to diet and climate (Murray et al. 2002, Prugh and Krebs 2004, Mills et al. 2005, Murray et al. 2005, Hodges and Mills 2008). Our results suggest that when a precise estimate of hare abundance and habitat use is required, annually cleared pellet plots are preferred (Prugh and Krebs 2004, Murray et al. 2005). When only a coarse indication of hare abundance or habitat use

is needed (Hodges and Mills 2008), uncleared pellet counts can provide insight; however, due to a lack of observed precision, we believe their utility is limited.

Second, we examined the influence of forest stand characteristics on snowshoe hare fecal pellet counts, as well as density estimates of snowshoe hares, red squirrel midden counts, and forest grouse scat counts, to investigate prey abundance in 3 young even-aged and 4 older multi-storied forest types. Older multi-storied forest types with a thick understory, as well as moderate to densely stocked 30-70-year-old lodgepole pine stands, showed moderate to high levels of hare abundance (Zimmer 2004, Hodges and Mills 2005). Overall, multi-storied forest types had higher hare densities and likewise higher red squirrel and forest grouse abundance indices than did the 30-70-year-old even-aged lodgepole pine stands. Correspondingly, forest structure attributes that were significant predictors of snowshoe hare, red squirrel, and grouse abundance were more prevalent in multi-storied stands than 30-70-year-old lodgepole pine stands. These findings suggest that multi-storied forests play a disproportionately important role in providing Canada lynx (*Lynx canadensis*) with adequate primary and secondary prey in western Wyoming. We found that older multi-storied forests outscored younger forest types in importance to hares both in the short-term (30-70 years post harvest) and long-term (70+ years post harvest).

In all forest types, horizontal cover was the most significant predictor of snowshoe hare density on the B-TNF. Similar to findings in Yellowstone National Park where hare abundance was highest on andesitic soils (Murphy et al. 2006), multi-storied stands in the Wyoming Range on the moisture and nutrient rich Wasatch Formation had higher hare densities than similar stands located on different parent material found elsewhere on the B-TNF.

RESEARCH AND MANAGEMENT RECOMMENDATIONS

We recommend the construction of regional-specific regression equations using a buffer adjustment for hard forest edges when determining estimates of snowshoe hare density in highly

fragmented landscapes. If needed, managers could also use equations developed without such adjustments to the buffer area in order to make direct comparisons with regions that did not implement similar adjustments. Further research is needed to better understand the influence of habitat fragmentation on hare abundance at varying scales.

Snowshoe hare habitat is considered to be a significant limiting factor for lynx in the Greater Yellowstone area (U.S. Fish and Wildlife Service 2008), and until this study, only low hare densities had been observed (McKelvey and McDaniel 2001, Hodges and Mills 2005, Hodges et al. 2009). We found a broad range of snowshoe hare densities in western Wyoming, which included some of the highest observed densities in recent years in the continental U.S., British Columbia, Labrador, and Quebec (de Bellefeuille et al. 2001, McKelvey et al. 2002, Murray et al. 2002, Ausband and Baty 2005, Newbury and Simon 2005, Potvin et al. 2005, Homyack et al. 2006, Sullivan et al. 2006, Hodges and Mills 2008, McCann et al. 2008, Zahratka and Shenk 2008). Documentation of high snowshoe hare density in the southern Greater Yellowstone Area (GYA) provided important insights with regards to the potential for lynx occupancy and habitat quality in this region. Even though hare density was high in some areas on the B-TNF, lynx numbers were low in western Wyoming (Squires and Oakleaf 2005, Murphy et al. 2006), strongly suggesting that additional factors other than hare density may be limiting lynx population size and recovery. Future research should focus on pinpointing these additional limiting factors so managers can appropriately focus their conservation and recovery efforts for lynx in the GYA.

While indices of red squirrel and forest grouse abundance remained relatively constant among forest types across the B-TNF, snowshoe hare abundance varied considerably by forest type across the landscape. While multi-storied forests had greater hare densities as well as red squirrel and grouse abundance indices than even-aged 30-70-year-old lodgepole pine, there were noteworthy areas where snowshoe hare densities were much greater in even-aged 30-70-year-old

lodgepole pine. Even though horizontal cover was significantly linked to snowshoe hare abundance in all forest types across the landscape we believe there were also other site-specific attributes including environmental and climate variability, soils, and overall net primary productivity that were strong underlying drivers of hare abundance.

Due to the dissimilarities in forest types used by hares across the landscape, management decisions for the purpose of lynx conservation should be site specific. Lynx conservation is complex and managers and researchers must gain a comprehensive understanding of individual landscapes and their specific attributes and abilities to sustain prey populations if they are to appropriately implement policy to conserve and/or promote habitat for the species. Without an in-depth understanding of the complexities of a specific site it is unlikely management will be appropriately implemented on that landscape which may then inadvertently lead to short-term and long-term detrimental consequences to lynx and their prey. When considering lynx prey requirements there is no one management prescription that fits all lynx habitat appropriately; regional-specific strategies need to be thoroughly researched and properly implemented. Future studies should focus on deciphering which site-specific attributes give rise to prey rich and prey poor landscapes and at which forest structural stage and spatial scale this is most likely to occur on each different landscape. On the B-TNF the appropriate scale for observing these differences in hare abundance and associated forest structural relationships was at the mountain range scale; the Absaroka, Gros Ventre, Salt River, Wind River, and Wyoming mountain ranges were all quite unique in their overall soils, climate, forest structure and species composition, and associated prey abundances. Future lynx conservation efforts in this region would benefit most from the development of conservation strategies at the individual mountain range scale; this would allow for appropriate flexibility in understanding individual systems.

The U.S. Forest Service is currently using horizontal cover threshold guidelines developed in northwestern Montana to determine what constitutes important multi-storied lynx

and snowshoe hare habitat throughout the Northern Rocky Mountains (Bertram and Claar 2008). From our observations, the Montana thresholds likely put many stands with high hare densities at risk in this region and for this reason we suggest locally developed horizontal cover thresholds be used that take into account regional differences in hare habitat structure and use patterns.

Timber harvest and wildfire significantly alter forested landscapes in southern boreal forests and can be used as tools for improving snowshoe hare habitat (Peet 2000, Veblen 2000, Hodges and Mills 2005, Ellsworth and Reynolds 2006, Zimmer et al. 2008). However, the effects of fire and timber harvest on hare abundance depend on a variety of site-specific environmental factors and range from highly beneficial to highly detrimental to snowshoe hares (Turner et al. 1997, Buskirk et al. 2000, Anderson et al. 2004, Ellsworth and Reynolds 2006, Murphy et al. 2006). In the recent past, many older multi-storied stands have been mechanically harvested or burned on the B-TNF and a number of these sites are not regenerating adequately to provide horizontal cover required for abundant hare populations 30-70 years post-harvest. No doubt this lack of regeneration contributes to increased habitat fragmentation, smaller patch sizes in important multi-storied stands, and consequently a temporal reduction in primary and secondary prey numbers on these sites. The naturally fragmented spatial arrangement of habitat in the GYA has been identified as a limiting factor for lynx in this area (U.S. Fish and Wildlife Service 2008) and additional human-caused and natural fragmentation in important foraging nodes that are found in multi-storied forests likely further reduces habitat suitability for hares and lynx in this region.

Our study, as well as other recent studies, suggests that multi-storied forests with a spruce-fir component are disproportionately important to snowshoe hares, red squirrels, grouse and lynx in the GYA (Buskirk et al. 2000, Hodges and Mills 2005, Murphy et al. 2006). For this reason, management in this region should focus on maintaining, enhancing, and promoting increased acreage and connectivity of multi-storied forests in the GYA. We concur with Buskirk

et al. (2000) that the preservation of extensive tracts of mature multi-storied forests likely will be of greatest benefit to snowshoe hares and lynx in this region.

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