



Influence of Forest Structure on the Abundance of Snowshoe Hares in Western Wyoming

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ABSTRACT Snowshoe hares (*Lepus americanus*) are a primary prey species for Canada lynx (*Lynx canadensis*) in western North America. Lynx management plans require knowledge of potential prey distribution and abundance in the western United States. Whether even-aged regenerating forests or multi-storied forests contain more snowshoe hares is currently unknown. During 2006–2008, we estimated snowshoe hare density in 3 classes of 30–70-year-old lodgepole pine (*Pinus contorta*) and 4 classes of late seral multi-storied forest with a spruce (*Picea engelmannii*)–fir (*Abies lasiocarpa*) component in the Bridger-Teton National Forest, Wyoming. We recorded physiographic variables and forest structure characteristics to understand how these factors influence abundance of snowshoe hares. In many instances, snowshoe hares were more abundant in late seral multi-storied forests than regenerating even-aged forests. Forest attributes predicting hare abundance were often more prevalent in multi-storied forests. Late seral multi-storied forests with a spruce–fir component and dense horizontal cover, as well as 30–70-year-old lodgepole pine with high stem density, were disproportionately influential in explaining snowshoe hare densities in western Wyoming. In order to promote improved habitat conditions for snowshoe hares in this region, management agencies should consider shifting their focus towards maintaining, enhancing, and promoting multi-storied forests with dense horizontal cover, as well as developing 30–70-year-old lodgepole pine stands with high stem density that structurally mimic multi-storied forests. © 2012 The Wildlife Society.

KEY WORDS forest structure, *Lepus americanus*, Poisson regression models, snowshoe hare, Wyoming.

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). Snowshoe hares are the primary prey for lynx throughout North America (Mowat et al. 2000, Ruggiero et al. 2000), with hares comprising 35–97% of lynx diets (Koehler and Aubry 1994, Squires and Ruggiero 2007).

Although snowshoe hares are more abundant in contiguous habitats with high horizontal cover (Hodges 2000, Lewis et al. 2011), they will use small patches of suitable habitat (Ellsworth and Reynolds 2006). Horizontal cover provides food and cover for hares during winter from dense lateral foliage touching the snow surface. Although lynx are consistent in their preference for forests with high horizontal

cover (Fuller et al. 2007, Koehler et al. 2007, Maletzke et al. 2008, Squires et al. 2010), considerable regional variation exists within the contiguous United States regarding the forest structures and compositions providing suitable horizontal cover for lynx and hares. In northern Maine, lynx used densely stocked stands dominated by young conifers with a lesser component of deciduous trees (Hoving et al. 2004, Fuller et al. 2007, Vashon et al. 2008). Conversely, in the western United States, lynx also selected mature multi-storied forests providing the necessary structure for hares (Malaney and Frey 2006) that sustain lynx during winter (Koehler et al. 2007, Maletzke et al. 2008, Squires et al. 2010). In the western United States, mature and late successional forests (e.g., spruce–fir forests) may provide more stable habitat for snowshoe hares over a longer period (Buskirk et al. 2000, Ellsworth and Reynolds 2006). In summer, lynx in western forests may then broaden their foraging niche to include both early and later successional forests (Squires et al. 2010); these forests provide abundant sapling and shrub thickets for hares (Wolfe et al. 1982, Koehler and Brittell 1990, Hodges 2000).

Lynx in western Wyoming occur at low densities, have apparently persisted since historic times (Murphy et al.

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2006), and are a conservation priority (U.S. Fish and Wildlife Service 2008) given these individuals represent the southernmost natural population in the continental United States (Squires et al. 2003). Because lynx are obligate predators on snowshoe hares, the distribution and abundance of their primary prey is important to this cat's continued long-term persistence in this region. Whether mature multi-storied stands, even-aged regenerating stands, or a mixture of both provide optimal habitat conditions for hares in western boreal forests is unknown. Misconceived management strategies could jeopardize recovery efforts for lynx in the western United States, particularly in the Greater Yellowstone Ecosystem (GYE). Therefore, understanding the relationships between snowshoe hare abundance and forest structure in both even-aged regenerating and older multi-storied forests in western forests are needed to make informed management decisions.

STUDY AREA

Sampling sites were located in 5 mountain ranges (Absaroka, Gros Ventre, Wind River, Salt River, Wyoming) in the southern portion of the GYE on the Bridger-Teton National Forest (BTNF), western Wyoming. Summer temperatures varied by elevation but were characterized by cool nights and warm days with frequent afternoon thunderstorms. Mean maximum and minimum temperatures in January were -3.3°C and -22.0°C , respectively; July maximum and minimum temperatures averaged 22.3°C and 1.7°C , respectively (National Oceanic and Atmospheric Administration 2009). Winters were cold with deep snow remaining on the ground from late October through May, or later at higher elevations. Mean annual precipitation was 75–115 cm, but because of weather patterns, the snowpack was more maritime (deeper, wetter, denser) in western ranges, whereas eastern ranges had a drier, shallower, more continental snowpack. Precipitation varied but averaged 101.35 cm annually on Togwotee Pass over the past 10 years, most of which fell as snow. Temperatures often dropped below freezing and snowfall occurred during every month except July (National Oceanic and Atmospheric Administration 2009).

Forests in the study area were heterogeneous in species composition and age structure, and included subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), whitebark pine (*Pinus alba-caulis*), 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 conifers. Dry areas 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 ranged in elevation from 1,981 m to 3,353 m. Shrubs found within forests included buffaloberry (*Shepherdia canadensis*), currant (*Ribes* spp.), snowberry (*Symphoricarpos oreophilus*), thimbleberry (*Rubus parviflorus*) 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 lower elevations, mountain ranges were often surrounded by sage-wheatgrass plant communities. For more than a century, forests within the area have been harvested (Squires et al. 2003). Natural disturbances included forest fires, avalanches, landslides, insect and disease outbreaks, and wind throw.

The study area contained a diverse assemblage of predators. Although wolves were extirpated from Wyoming by the 1930s, they have since re-established as a result of the 1995 reintroduction efforts in Yellowstone National Park (U.S. Fish and Wildlife Service 2006). Other carnivores aside from lynx included coyote (*Canis latrans*), cougar (*Puma concolor*), wolverine (*Gulo gulo*), grizzly bear (*Ursus arctos*), black bear (*Ursus americanus*), bobcat (*Lynx rufus*), red fox (*Vulpes vulpes*), and pine marten (*Martes americana*). The area was classified in 2008 as a lynx Critical Habitat Designation because lynx have persisted historically and recently, although in relatively low numbers. This Wyoming Distinct Population Segment (DPS) is part of the Greater Yellowstone Area designation, encompassing 110,727 km² primarily composed of federal land.

METHODS

During summer 2005, we conducted a pilot survey for snowshoe hares by establishing 18 fecal pellet transects (25 plots per transect) using the methods outlined in Krebs et al. (2001) to better understand relative abundance within a variety of high elevation forest types on the BTNF. We used the results from this pilot survey, coupled with several years of field observations of snowshoe hare habitat use, to identify 7 principle forest types that likely contained the greatest number of snowshoe hares on the BTNF. We chose these forest types because they provided habitat for the primary prey of lynx (i.e., focused on forest types with the greatest potential to support snowshoe hares) and because estimating hare density, regardless of method, when hare density is <0.3 hare/ha is not feasible (Murray et al. 2002, Mills et al. 2005). These 7 forest types included 3 classes of young, even-aged, regenerating lodgepole pine and 4 classes of older late seral, multi-storied forest containing a spruce-fir component in both the understory and overstory. We stratified the 3 young forest types, predominately 30–70-year-old even-aged lodgepole pine, by stem density: 724.54 ± 51.73 stems/ha, $1,317.60 \pm 50.42$ stems/ha, and $3,194.16 \pm 553.05$ stems/ha; all stems were greater than 2.54 cm diameter at breast height (DBH). We stratified the 4 late seral multi-storied forest types containing a spruce-fir component by overstory species including lodgepole pine, aspen, whitebark pine, and pure stands of spruce-fir. All structural stages and age classes of lodgepole pine, Engelmann spruce, subalpine fir, aspen, whitebark pine, and mixed stands of these trees comprised 55.1% of the land cover on the BTNF.

Forest Stand Identification

Our initial attempts to identify forest stands for random sampling based on existing vegetation maps were unsuccessful because of poor classifications. Therefore, we used aerial photographs (U.S. Geological Survey ortho-photo quads) along with a land cover map (WyGAP; Driese et al. 1997) to identify and spatially distribute 140 candidate survey locations (20 per surveyed forest type) throughout the BTNF. For logistical reasons, these candidate survey locations were located ≤ 1 km from designated roads and/or trails. We then visited all of these locations and identified stands large enough for a 200-m transect that were multi-storied with a spruce-fir component in the overstory and understory for mature forests, or that had appropriate stem density for regenerating lodgepole pine stands (Tart et al. 2005). To reduce potential observer bias and to obtain a robust representative sample of the 7 forest types, we surveyed all identified stands that met our selection criteria (112 stands).

Snowshoe Hare Pellet Counts and Density Estimation

We found a strong relationship between fecal pellet counts and snowshoe hare density as determined using mark-recapture estimators (Berg and Gese 2010), similar to findings from other studies (Krebs et al. 1987, 2001; Murray et al. 2002; Mills et al. 2005; McCann et al. 2008). Therefore, we established snowshoe hare pellet count plots along transects within the 7 forest types to study patterns of hare abundance (Hodges and Mills 2008). We used the 1-m² circular pellet plots to estimate hare abundance (McKelvey et al. 2002, Murray et al. 2002, Mills et al. 2005). We established 200-m linear transects consisting of 5 1-m² circular plots placed 50 m apart, perpendicular to roads and trails, and spaced ≥ 1 km apart. The starting point for transects was randomly placed within a stand and located ≥ 50 m from any road. We permanently marked all plots with a rebar stake and revisited them each summer for the duration of the project (McCann et al. 2008). During counts, we tallied and removed all fecal pellets within the plot boundary. To avoid an inclusion bias, we tallied only 50% of the pellets found directly on the plot boundary (McKelvey et al. 2002) and counted only intact pellets. We moved vegetation and surface litter that obscured pellets as needed, but did not count pellets deeply incorporated into the organic layer of the forest floor (McKelvey and McDaniel 2001). Forbs and grass ground cover that can obscure pellets from view, especially as this vegetation grows throughout the summer months, were usually sparse in the understory of our survey transects and therefore were unlikely to decrease pellet detection rates. We counted pellets on plots annually (2006–2008) by rotating a string marked with the appropriate radius around the rebar stake. We considered pellet counts recorded during the first year uncleared counts because they were based on accumulations from an unknown time period (Prugh and Krebs 2004, Murray et al. 2005, Hodges and Mills 2008). We cleared pellet plots annually, so the subsequent accumulation of pellets was for a 1-year period (Prugh and Krebs 2004, Murray et al. 2005, Hodges and Mills 2008). To alleviate concerns regarding pellet decomposition rates in various

forest types (Murray et al. 2005) and to increase precision (Berg and Gese 2010), we only analyzed annually cleared pellet counts. We estimated snowshoe hare density (hares/ha) for each plot using the equation: hare density = 0.093 (mean pellet plot count) + 0.174 (from Berg and Gese 2010).

Forest Composition Surveys

We established vegetation sample plots (0.02-ha circular plots) within each forest type centered on the prey sample plots to quantify forest structure. We recorded the dominant and co-dominant cover type by categorizing tree species into 5 size classes: 2.54–7.37 cm, 7.62–12.45 cm, 12.7–22.61 cm, 22.86–40.39 cm, and >40.39 cm DBH (Doerr 2004). We classified tree species that contributed $\geq 20\%$ to the overstory canopy as co-dominant (Doerr 2004). We recorded 2 layers of canopy cover separately for each plot and included: 1) tree canopy cover, which measured cover from live stems with a DBH ≥ 2.54 cm; and 2) shrub canopy cover, which measured cover from live stems with a DBH ≤ 2.54 cm and a height ≥ 15.24 cm. We considered sapling trees with a DBH ≤ 2.54 cm and height ≥ 15.24 cm as shrubs and tallied them as shrub canopy cover. We recorded tree canopy cover and shrub canopy cover to the nearest 10% for each plot (Doerr 2004). Canopy cover was an ocular estimate of the percentage of the plot surface covered by the periphery of the foliage of the plants (Tart et al. 2005). We quantified horizontal cover attributed to tree and shrub stems, branches, leaves, needles, large woody debris, and topography. One observer stood at the plot center holding a 0.305 m wide $\times$ 1.83 m high cover board (divided into 0.305 m segments) 15 cm above the ground (Doerr 2004). A second observer at 8.02 m distance from the plot center then estimated, to the nearest 10%, the amount of the board obscured by cover (Doerr 2004). We recorded cover readings from the 4 cardinal directions (Doerr 2004) and averaged to obtain 1 estimate of horizontal cover for each plot.

We tallied stems with a DBH ≥ 2.54 cm on plots to calculate stem density (stems/ha). We classed all trees with a DBH ≥ 2.54 cm into the 5 size classes previously defined. We then converted tree stems with a DBH ≥ 2.54 cm to basal area (m²/ha; Fuwape et al. 2001). In order to investigate the potential value of relatively large woody logs (debris) as security cover for hares, we counted those with a diameter ≥ 12.7 cm and length ≥ 3 m and converted the tally to density (logs/ha). We also counted the number of standing dead trees with a DBH ≥ 12.7 cm and converted the tally to density (dead trees/ha).

To examine edge effects on snowshoe hare abundance, we measured the distance from the outside edge of each vegetation plot to the edge of a different habitat type nearest the plot. We plotted locations using a Global Positioning System (GPS) and determined the elevation to the nearest 10 m using digital elevation models (U.S. Forest Service Geospatial Data Clearinghouse, Geospatial Service and Technology Center, Sioux Falls, SD). We recorded percent slope for each plot using a clinometer by averaging the up and down slope measurements.

Statistical Analysis

We averaged forest structural attributes (i.e., canopy cover, horizontal cover, etc.) from the 5 plots per transect for analyses. We used SPSS (SPSS for Windows 10, Chicago, IL) to compare snowshoe hare abundance and forest structure attributes among the 7 stand types using Duncan's multiple-contrasts (Zar 1996). We performed generalized linear regression models for Poisson distributed data (i.e., pellet counts) using the "glm" procedure in package "stats" in program R (version 2.13.2, R Development Core Team 2011; Cameron and Trevedi 1998) to model the influence of the 12 independent forest stand characteristics on the dependent variables of snowshoe hare fecal pellet counts. We calculated a variance inflation factor (VIF) for each variable implemented in the Poisson regression model (procedure "vif" in package "HH" in R version 2.13.2, R Development Core Team 2011). A simple diagnostic of colinearity is the variance inflation factor. The VIF for predictor i is $1/(1-R_i^2)$, where R_i^2 is the R^2 from a regression of predictor i against the remaining predictors. Values of VIF exceeding 5 are considered evidence of colinearity, meaning that the information carried by a predictor having such a VIF is contained in a subset of the remaining predictors. If, however, all of a model's regression coefficients differ significantly from 0 (P -value < 0.05), a somewhat larger VIF may be tolerable.

Since the proportion of null counts was less than 2% of the overall sample pellet counts, this approach is more appropriate than using negative binomial distribution designed to account for excess zeros in the response variables. We computed a single Poisson regression model that accounted for all 12 explanatory variables of interest, and discussed the significance (or lack thereof) of each explanatory variable in the model. Results obtained via a model selection based on Akaike's Information Criterion (AIC_c) corrected for small sample size (Akaike 1973) resulted in the exact same conclusions (results not presented here for the sake of conciseness). We also presented relationships between estimates of snowshoe hare pellets counts and significant covariates of interest from the Poisson regression model of interest. We used the "cor" procedure in R to calculate the coefficient of determination (R^2), the square of the sample correlation coefficient between the response variable (i.e., pellet counts) and the explanatory variable of interest (i.e., significant variables only).

RESULTS

Hare Abundance and Structural Attributes Among Forest Types

We found the lowest densities of snowshoe hares in young lodgepole-low density and late seral stands of mixed white-bark spruce-fir (Table 1). In contrast, we found the greatest hare densities in young lodgepole-high density, and late seral multi-storied stands of mixed spruce-fir, mixed aspen spruce-fir, and mixed lodgepole spruce-fir. Young lodgepole-medium density had intermediate hare densities when compared to the other forest stand types.

Table 1. Snowshoe hare densities and forest structure characteristics among the 7 forest types surveyed, Bridger-Teton National Forest, Wyoming, 2006–2008. We present means (± 1 SE) and show number of transects sampled in parentheses. Letters following mean values denote values not significantly different from one another (Duncan's multiple contrasts).

	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)
Hare density (hares/ha)	0.48 _A $\pm$ 0.07	0.85 _{AB} $\pm$ 0.16	1.69 _C $\pm$ 0.24	0.56 _A $\pm$ 0.09	1.46 _C $\pm$ 0.25	1.24 _{BC} $\pm$ 0.19	1.58 _C $\pm$ 0.26
Basal area (m^2 /ha)	9.74 _A $\pm$ 1.02	17.71 _B $\pm$ 0.48	30.58 _D $\pm$ 2.25	46.40 _{CD} $\pm$ 4.82	31.74 _{BC} $\pm$ 2.12	39.14 _{BCD} $\pm$ 4.37	39.89 _{CD} $\pm$ 4.28
Distance to edge (m)	26.1 _{BC} $\pm$ 0.85	27.3 _C $\pm$ 0.78	26.4 _{BC} $\pm$ 1.02	24.2 _{ABC} $\pm$ 1.03	23.5 _{AB} $\pm$ 1.10	26.9 _{BC} $\pm$ 0.79	22.7 _A $\pm$ 1.52
Elevation (m)	2562 _B $\pm$ 22	2535 _B $\pm$ 39	2497 _{AB} $\pm$ 41	2831 _C $\pm$ 28	2449 _{AB} $\pm$ 33	2392 _A $\pm$ 49	2487 _{AB} $\pm$ 63
Horizontal cover (%)	31.1 _A $\pm$ 1.94	42.1 _{BC} $\pm$ 3.01	52.3 _D $\pm$ 4.86	36.6 _{AB} $\pm$ 2.45	55.6 _D $\pm$ 3.45	46.3 _{CD} $\pm$ 3.06	55.8 _D $\pm$ 3.00
Large woody debris (logs/ha)	25.79 _A $\pm$ 8.53	24.85 _A $\pm$ 5.47	69.80 _{AB} $\pm$ 35.11	64.38 _{AB} $\pm$ 12.05	49.29 _A $\pm$ 9.47	113.12 _B $\pm$ 11.79	104.18 _B $\pm$ 8.84
Shrub canopy (%)	5.8 _A $\pm$ 1.29	10.9 _{AB} $\pm$ 2.22	15.5 _{BC} $\pm$ 4.13	10.4 _{ABD} $\pm$ 1.49	27.5 _D $\pm$ 3.40	22.2 _{CD} $\pm$ 2.53	21.5 _C $\pm$ 3.28
Slope (%)	10.2 _{AB} $\pm$ 1.66	9.5 _A $\pm$ 1.39	12.5 _{AB} $\pm$ 1.66	13.9 _{AB} $\pm$ 1.02	14.4 _B $\pm$ 1.19	11.1 _{AB} $\pm$ 1.78	12.1 _{AB} $\pm$ 1.61
Standing dead trees (dead trees/ha)	1.94 _A $\pm$ 1.32	4.75 _A $\pm$ 2.04	1.43 _A $\pm$ 0.53	38.85 _B $\pm$ 7.10	34.72 _B $\pm$ 6.06	28.38 _B $\pm$ 7.52	26.71 _B $\pm$ 7.53
Stem density (stems/ha)	724.5 _A $\pm$ 51.73	1317.6 _{AB} $\pm$ 50.42	3194.2 _C $\pm$ 553.05	1724.6 _B $\pm$ 171.14	1508.7 _B $\pm$ 144.95	1693.3 _B $\pm$ 163.77	1679.4 _B $\pm$ 125.47
Tree canopy (%)	27.9 _A $\pm$ 1.59	39.2 _{BC} $\pm$ 2.27	49.1 _{CD} $\pm$ 2.42	37.1 _B $\pm$ 1.90	46.1 _{CD} $\pm$ 2.36	42.6 _{BCD} $\pm$ 2.47	44.6 _{CD} $\pm$ 1.50

Comparing structural attributes among the forest stand types revealed most of the characteristics were different among the forest types, with the exception being percent slope (Table 1). Distance to edge was relatively similar in all 7 stand types. Elevation was lowest in mixed lodgepole spruce–fir and highest in mixed whitebark spruce–fir. Basal area was smallest in young lodgepole-low density and greatest in mixed whitebark spruce–fir. Percentage of horizontal cover was lowest in young lodgepole-low density, and greatest in mixed spruce–fir, mixed aspen spruce–fir, young lodgepole-high density, and mixed lodgepole spruce–fir. Density of large woody debris was lowest in young lodgepole-medium density and young lodgepole-low density, and highest in mixed lodgepole spruce–fir and mixed spruce–fir. Percentage of shrub canopy cover was lowest in young lodgepole-low density, and greatest in mixed aspen spruce–fir, mixed lodgepole spruce–fir, and mixed spruce–fir. Density of standing dead trees was lowest in young lodgepole-high density and highest in mixed whitebark spruce–fir. Stem density was lowest in young lodgepole-low density, and highest in young lodgepole-high density. Percentage of tree canopy cover was lowest in young lodgepole-low density, and highest in young lodgepole-high density, mixed aspen spruce–fir, mixed spruce–fir, and mixed lodgepole spruce–fir. Not surprisingly, basal area, horizontal cover, and tree canopy cover increased as stem density increased in the 30–70-year-old lodgepole pine stands. In general, shrub canopy cover also increased as stem density increased in 30–70-year-old lodgepole pine stands.

Influence of Forest Structure on Hare Abundance

To account for multi-collinearity issues, we calculated the following VIFs for each variable in the model: habitat type (2.05), soil type (1.97), slope (1.19), distance to edge (1.17), tree canopy (2.07), shrub canopy (2.43), elevation (1.94), basal area (6.56), horizontal cover (2.56), large wood debris (1.46), standing dead tree (1.96), and stem density (7.66). Only basal area and stem density ended up being redundant in our model, but since they did not have any significant effect in explaining variability in snowshoe hare pellets counts, the slight issue of collinearity for these two variables was not of any consequence.

Results from the Poisson regression model indicated that habitat type, soil type, slope (%), distance to edge (m), tree canopy (%), shrub canopy (%), horizontal cover (%), and large woody debris (logs/ha) were significant predictors of increasing snowshoe hare pellet counts (Table 2, $P < 0.05$ in all cases). Snowshoe hare pellet counts had the strongest relationships with tree canopy, shrub canopy, and horizontal cover (Fig. 1; $R^2 = 0.426, 0.392$, and 0.669 , respectively). Pellet counts were greater on soils that had developed from the Wasatch geologic formation when compared to pellet counts on other soil types ($P < 0.001$). On the other hand, slope and elevation were significant negative predictors of hare pellet counts (Table 2; $P < 0.001$ in both cases). However, the negative relationship between slope and snowshoe hare pellet counts was extremely weak (Fig. 1; $R^2 < 0.001$), whereas the negative relationship between elevation and snowshoe hare pellet counts was more clearly established (Fig. 1; $R^2 = 0.155$). Basal area (m^2/ha), standing dead trees (dead trees/ha), and stem density (stems/ha) were not significant predictors of hare pellet counts (Table 2; $P > 0.10$).

DISCUSSION

Snowshoe hares in the contiguous United States exhibit considerable regional variation in abundance relative to forest structure. In the Midwest and northeastern United States, hares are most abundant in young, regenerating forests (Bittner and Rongstad 1982, Monthey 1986, Fuller et al. 2007), whereas hares in the western United States may be most abundant in mature, multistoried forests (Malaney and Frey 2006, Koehler et al. 2007, Maletzke et al. 2008, Hodges et al. 2009). In Wyoming, we found snowshoe hare abundance, as indexed by annual pellet counts, to have a bimodal distribution in response to forest-age classes. Hares in Wyoming were most abundant in late seral multi-storied forests composed largely of thick spruce–fir as well as in high density 30–70-year-old regenerating lodgepole pine stands. Low density 30–70-year-old lodgepole pine and late seral mixed whitebark spruce–fir, the 2 stand types with the least recorded horizontal cover and tree canopy, held relatively few hares.

Table 2. Generalized linear model for Poisson distributed count data testing for the effects of 12 independent forest stand characteristics on snowshoe hare fecal pellet counts (i.e., a proxy to snowshoe hare density) in Bridger-Teton National Forest, Wyoming, 2006–2008.

	Coefficient estimate	95% CI		Z	P
		Lower	Upper		
Intercept	0.3452	−0.1586	0.8490	0.6850	0.4932
Habitat type	0.0256	0.0162	0.0351	2.7140	0.0066
Soil type	0.2197	0.1775	0.2619	5.2070	<0.001
Slope (%)	−0.0167	−0.0191	−0.0143	−6.9120	<0.001
Distance to edge (m)	0.0337	0.0302	0.0373	9.5110	<0.001
Tree canopy (%)	0.0203	0.0184	0.0222	10.5150	<0.001
Shrub canopy (%)	0.0061	0.0046	0.0075	4.1950	<0.001
Elevation (m)	−0.0009	−0.0010	−0.0008	−9.5480	<0.001
Basal area (m^2/ha)	0.0032	0.0008	0.0056	1.3420	0.1796
Horizontal cover (%)	0.0236	0.0222	0.0250	17.1560	<0.001
Large woody debris (logs/ha)	0.0008	0.0006	0.0010	4.3620	<0.001
Standing dead trees (tree/ha)	−0.0011	−0.0018	−0.0003	−1.3740	0.1695
Stem density (stems/ha)	0.1084	0.0318	0.1850	1.4150	0.1571

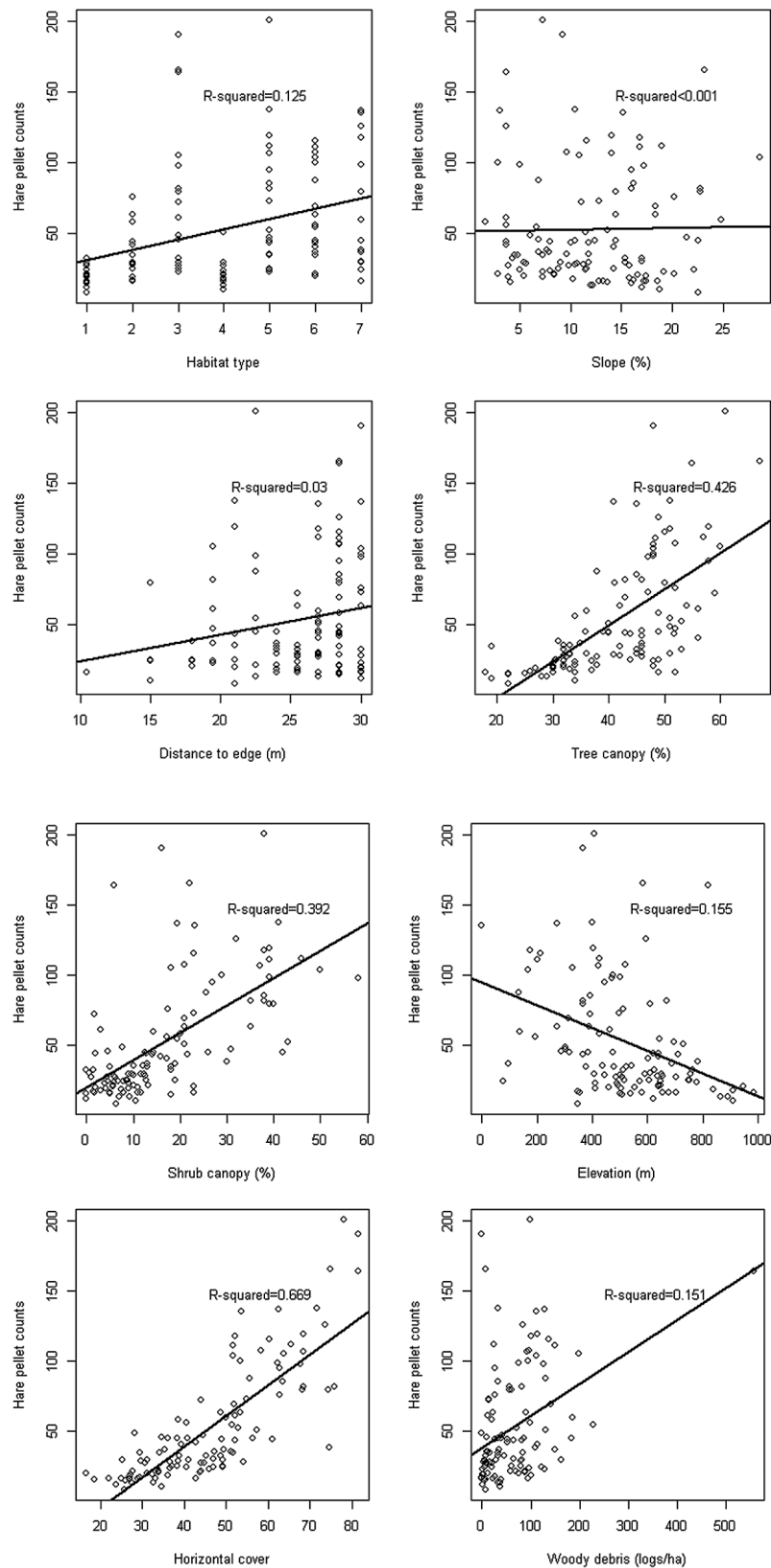


Figure 1. Relationship between snowshoe hare pellet counts and significant covariates of interest (from the Poisson regression model), including habitat type, slope, shrub canopy, elevation, distance to edge, tree canopy, horizontal cover, and large wood debris, Bridger-Teton National Forest, Wyoming, 2006–2008. Habitat type for forest stands included: 1—low density lodgepole pine, 2—medium density lodgepole pine, 3—high density lodgepole pine, 4—whitebark pine mixed with spruce and fir, 5—aspens mixed with conifers, 6—lodgepole pine mixed with spruce and fir, and 7—spruce and fir.

Hare density increased in the younger lodgepole pine types as stem density increased, but we did not observe a similar relationship in the multi-storied stands (Table 1). Biotic, abiotic, and anthropogenic factors can affect tree regeneration and corresponding stem density in young lodgepole pine stands in western Wyoming. A variety of harvest methods and silvicultural techniques, such as soil scarification and tree planting, could be used to increase the number of regenerating lodgepole pine and other conifer seedlings at disturbed (timber harvest and fire) forest sites on the BTNF. Management designed to increase stem density at disturbed sites could be used to improve conditions for snowshoe hares 30–70 years post-disturbance. However, habitat provided to hares in 30–70-year-old lodgepole pine stands can be short-lived in the GYE when compared to older multi-storied spruce–fir forests that tend to be more persistent on the landscape (Zimmer et al. 2008). In addition to containing high hare densities, mature late seral spruce–fir dominated forests supported much greater abundance of alternative prey (grouse and squirrels) compared to young lodgepole pine forests (Berg 2010).

High hunting success by lynx is not always associated with the greatest number of hares, but can be an interaction between prey density and prey accessibility (Parker et al. 1983, Murray et al. 1995). Research conducted in Maine found that lynx selected against short regenerating (11–26 years post-harvest) stands averaging $\geq 14,000$ coniferous stems/ha even though snowshoe hares were abundant (Fuller et al. 2007). The same study found lynx selected for similarly aged tall regenerating stands with 7,000–11,000 coniferous stems/ha (Fuller et al. 2007). On our study area, young lodgepole high-density stands had the greatest stem densities of any stand type surveyed but still fell well below 14,000 or even 7,000–11,000 coniferous stems/ha. For this reason, and because of the relatively patchy nature of prime snowshoe hare habitat in the GYE, we predict lynx would not likely avoid quality hare habitat in the BTNF because of excessive stem densities.

In Wyoming, horizontal cover, tree canopy, and shrub canopy were the best predictors of hare density. Horizontal cover measurements often included overlapping components of tree canopy and shrub canopy because of the physical location of these attributes within surveyed stands. Reducing horizontal cover in spruce–fir forests negatively affects lynx in the northern Rocky Mountains (Squires et al. 2008, 2010) and reduces hare densities in western forests (Griffin 2004, Griffin and Mills 2007, Lewis et al. 2011). A horizontal cover-hare density relationship may provide a useful tool for managers to predict hare densities from horizontal cover measures. Because of regional differences in the components of horizontal cover, the relationship between horizontal cover and hare density that we documented is best applied to the GYE, but we believe these results are also relevant to forests in Utah, Colorado, Wyoming, southeastern Idaho, and southern Montana. We also documented a weak relationship between hare abundance and distance to patch edges indicating snowshoe hares likely exhibited a slight avoidance of patch edges. In

Washington, landscapes in which hare habitat was more contiguous, or good patches of hare habitat surrounded by other patches of similar quality habitat, supported more hares than fragmented landscapes or matrix habitats of poor quality (Lewis et al. 2011). Future studies are needed to investigate how habitat edges affect hare density, to determine optimal patch sizes for hares in the GYE and similar ecosystems (i.e., Utah, Colorado, southern Montana, and southeastern Idaho). We found the fecal pellet to hare-density equations developed for Wyoming (Berg and Gese 2010) and elsewhere in North America (Krebs et al. 1987, 2001; Murray et al. 2002; Mills et al. 2005; McCann et al. 2008) to be useful tools for managers when identifying potential lynx habitat.

Forest management can modify southern boreal forests in ways that benefit or degrade snowshoe hare habitat depending on the type of implementation considered (Veblen 2000, Zimmer 2004, Hodges and Mills 2005). Since the 1950s, many late seral multi-storied mixed stands with a spruce–fir component have been clear-cut for even-aged timber management in western Wyoming. Many sites have not adequately regenerated to forest conditions that support snowshoe hares even 30–70 years post-harvest. Poor regeneration may contribute to habitat fragmentation of existing spruce–fir forests suitable to hares and lynx. In addition, naturally fragmented patches of forests in the GYE may already be limiting lynx habitat throughout the region (U.S. Fish and Wildlife Service 2008). Shrub canopy and large woody debris were also significant predictors of hare abundance in western Wyoming. On sites that had regenerated adequately for hares, we observed that 30–70-year-old lodgepole pine stands with abundant large woody debris, a tall (≥ 1 m) shrubby understory, and a high sub-alpine fir–Engelmann spruce component, appeared to structurally mimic older multi-storied forest types and were likely able to support abundant snowshoe hares over a longer timeframe compared to similar young stands without structural complexity (Berg 2010). Forest harvest and regeneration techniques that provide for and encourage this structural complexity will likely benefit hares over an extended timeframe.

We found limited opportunities to use forest management or fire to improve late seral multi-storied stands with a spruce–fir component for hares because these forest types already contained conditions appropriate for the species. However, management actions in mature stands, especially those dominated by lodgepole pine, that presently lack abundant horizontal cover would likely benefit hares 30–70 years post-disturbance if structural diversity were promoted. Recovery of high-elevation multi-storied spruce fir forests following harvest or thinning can be slow because of short growing seasons, cold temperatures, and high winds (Fiedler et al. 1985, Long 1995). Thus, traditional even-aged management or thinning of mature multi-storied stands could degrade hare and lynx habitat for decades (Wolfe et al. 1982, Buskirk et al. 2000, Zimmer et al. 2008).

In the early 1900s, many forests in western Wyoming were selectively harvested for railroad ties (tie-hacking). These

early foresters selectively removed lodgepole pine, but retained spruce–fir; lodgepole pine was most suitable for railroad ties. The forest structure created during this tie-hack era created spruce–fir multi-layered forests that currently support abundant hare and other prey populations. spruce–fir forests are preferred by snowshoe hares (Hodges 2000, Lewis et al. 2011). In addition, large woody debris present in tie-hacked stands may have provided additional structural complexity for snowshoe hares. Thus, tie-hacked stands with retained spruce–fir structurally mimicked late seral multi-storied spruce–fir stands without apparent harvest activity.

The restoration of whitebark pine and aspen are a management priority for forests within the GYE (Hollenbeck and Ripple 2007, McKinney et al. 2009). Hares and the structural attributes that significantly predicted hare abundance were high within mixed aspen spruce–fir stands and were low to moderate within mixed whitebark spruce–fir stands when compared to the other stand types surveyed (Table 1). Because snowshoe hares are rare in many parts of the GYE (Hodges et al. 2009), managing for whitebark pine and aspen mixed with a spruce and fir component likely provides foraging habitat for lynx. Multi-storied aspen spruce–fir stands contained some of our greatest observed hare densities.

Managers with a comprehensive understanding of a landscape's ability to sustain prey populations will be able to more appropriately implement policy to conserve or promote habitat for potential prey species for lynx. The possible influence of edge effects and fragmentation on prey abundance needs further investigation. Equally important are how these measures of prey abundance actually affect lynx distribution, abundance, and population demographics, as well as how this specialist carnivore adapts to changes in prey fluctuations at the southern extent of its natural range.

MANAGEMENT IMPLICATIONS

Forest stand types with dense horizontal cover, as well as high tree and shrub canopy measurements, such as found in late seral multi-storied stands containing abundant spruce–fir and high density 30–70-year-old even-aged lodgepole pine forests, supported the greatest snowshoe hare densities. Even though horizontal cover, tree canopy, and shrub canopy were significantly linked to hare abundance in all forest types across the landscape, we recognize that other unknown site-specific attributes may be influencing snowshoe hare abundance that we did not measure. Because of the dissimilarities in forest type use by hares across the landscape, management for the purpose of enhancing snowshoe hare abundance for lynx conservation may need to be assessed and implemented on a site-specific basis.

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