ABSTRACT Snowshoe hares \((Lepus americanus)\) are an important prey species for Canada lynx \((Lynx canadensis)\) and are considered critical for lynx population persistence. Determination of snowshoe hare distribution and abundance is needed by land management agencies for lynx conservation. An accepted approach for estimating snowshoe hare abundance is the use of fecal-pellet plot counts. Locally derived regression equations are preferred for accurate calibration of pellet counts to snowshoe hare density due to local differences in pellet deposition and decomposition. We used linear regression to examine correlations between snowshoe hare density, as determined by mark–recapture, and fecal pellet counts on both uncleared plots and annually cleared plots from the Bridger-Teton National Forest, western Wyoming, USA. We found significant correlations between snowshoe hare density estimates and fecal pellet counts for both uncleared and annually cleared pellet counts; however, the relationship was stronger (higher \(r\)) when using pellet counts from annually cleared plots. In addition, we found that adjusting the buffer size by omitting hard habitat edges (not used by hares) around trapping grids improved correlations between snowshoe hare density and fecal pellet counts for both uncleared plots and annually cleared plots. Though precision is sacrificed when using uncleared plots, they may be useful as a course index of habitat use by snowshoe hares. Our derived regression equations may be useful to identify important foraging habitat for Canada lynx in western Wyoming. Land managers responsible for conserving snowshoe hare habitat in western Wyoming may use these equations to monitor changes in hare populations among habitats and during prescribed management actions.

KEY WORDS density, fecal pellet, \(Lepus americanus\), mark–recapture, snowshoe hare, Wyoming.

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 (Brand et al. 1976, Keith et al. 1984, Squires and Ruggiero 2007). The Canada lynx in the Greater Yellowstone Ecosystem (GYE) likely are 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 as 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, Murray et al. 2002, Homyack 2003, Mills et al. 2005, McCann et al. 2008). When precise 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 rates of pellet deposition and degradation due to varying forage and microclimate (Krebs et al. 1987, Murray et al. 2002, Hodges and Mills 2008).

The relationship between pellet counts and snowshoe hare density in the northern GYE has not been developed due to low hare density (Hodges and Mills 2005, Hodges et al. 2009). Therefore, we evaluated this relationship in an area of the southern GYE that we believed supported high hare densities. Our goal was to investigate the hare density–fecal pellet relationship on the Bridger–Teton National Forest (B-TNF) by developing local regression equations for this region and then to compare our equations with those developed beyond the GYE using similar methods (Murray et al. 2002, Mills et al. 2005, McCann et al. 2008). Regionally, specific snowshoe hare studies are needed because the GYE is important to 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 because hare defecation rates, pellet loss, and pellet decomposition rates vary with climate, habitat, and diet (Murray et al. 2002, Prugh and Krebs 2004, Mills et al. 2005, 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). Because some sites were bordered in part by nonforested habitat, we also investigated how estimating the buffer area around the trapping grid influenced the pellet-density relationship. In addition, we examined the utility of using fecal pellet–snowshoe hare
equations determined from other study areas by comparing the equations and estimated hare density with results from our study area.

STUDY AREA

Sampling sites were located in several mountain ranges (Absaroka, Gros Ventre, Wind River, Salt River, WY) in the southern portion of the GYE on the B-TNF in western Wyoming, USA. Summer temperatures varied by elevation but were generally characterized by cool nights and warm days with frequent afternoon thunderstorms. From 1974 to 2009, mean maximum and minimum temperatures in January were $-3.3^\circ$ C and $-22.0^\circ$ C, respectively; July maximum and minimum temperatures averaged $22.3^\circ$ C and $1.7^\circ$ C, respectively (National Oceanic and Atmospheric Administration 2009). Winters on B-TNF were characterized by cold temperatures and deep snow that consistently remained on the ground from late October through May, or later at higher elevations. Mean annual precipitation was 75–115 cm across the study area, but due to consistent winter weather patterns in western Wyoming, the snow pack was more maritime in western ranges where it was consistently deeper, wetter, and denser, whereas eastern ranges tended to have a drier, shallower, more continental snow pack. Precipitation varied across the study area 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 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 encroached by 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 within forested areas 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 western and south-facing slopes. At the lowest elevations, mountain ranges were often surrounded by sage–wheatgrass communities. For over a century, trees were harvested (Squires et al. 2003). Natural disturbances included fires, avalanches, landslides, insect and disease outbreaks, and wind throw.

METHODS

We established 18 9.0-ha trapping grids across a range of snowshoe hare densities as determined by preliminary fecal pellet counts. We wanted a wide range of hare densities to allow us to examine a full-spectrum of hare density–fecal pellet relationships in this region. We located sampling sites in several habitat types including regenerating (30–60 yr old) lodgepole pine ($n = 4$); regenerating (30–60 yr old) Engelmann spruce, subalpine fir, and lodgepole pine with a few remnant mature trees ($n = 1$); mature lodgepole pine mixed with Engelmann spruce and subalpine fir ($n = 7$); aspen mixed with Engelmann spruce and subalpine fir ($n = 2$); mixed Douglas fir, Engelmann spruce, subalpine fir, lodgepole pine, and limber pine ($n = 1$); and pure stands of mature Engelmann spruce and subalpine fir ($n = 3$). We chose sites with homogeneous stand characteristics throughout the trapping grid.

Trapping grid arrays were $5 \times 10$ in shape and we occasionally modified them ($n = 4$) to fit within the chosen stand, as recommended by Mills et al. (2005). We established 50 1-m$^2$ circular fecal pellet plots with 50-m spacing between each pellet plot and trapping site, for each grid array (McKelvey et al. 2002, Murray et al. 2002, Hodges and Mills 2008). We permanently marked all pellet plots with a rebar stake and cleared them of pellets in June through August; then we revisited and counted them the following summer (Jun–Aug), approximately 1 year later. During counts, we counted and removed all fecal pellets within the plot boundary. To avoid an inclusion bias, we counted only 50% of pellets found directly on the plot boundary (McKelvey et al. 2002). We did not count pellets incorporated into the organic layer of the forest floor. We conducted counts by rotating a string marked with the appropriate radius around the rebar stake (Murray et al. 2002). We recorded pellet counts from initial uncleared plots and then cleared plots 1 year later. We based pellet counts from uncleared plots on accumulations from an unknown time period (Prugh and Krebs 2004, Murray et al. 2005, Hodges and Mills 2008) and we recorded them at the time of plot establishment. We compared pellet counts from uncleared plots to snowshoe hare density estimates from the subsequent winter trapping season. We based pellet counts on cleared plots on an accumulation of pellets over a 1-year period and compared them to hare density estimates from the previous autumn–winter trapping season (Mills et al. 2005).

During autumn and winter, we placed 50 single-door live traps ($81.28 \times 27.94 \times 30.48$ cm; Tru-Catch Traps, Belle Fourche, SD) baited with alfalfa cubes and apple slices on each grid array. We spaced traps 50 m apart and placed them approximately 5 m from the nearest fecal pellet plot. We conducted trapping of hares during late autumn and early winter (Oct–Jan) because snow usually covered many grasses and forbs at this time of year, thus leading to increased capture success. We checked traps each morning and double-tagged captured hares (Wing Band Jiffy Style 893; National Band and Tag, Newport, KY) and sexed,
Pellet Counts and Snowshoe Hares

To mean fecal pellet counts (L Na: not available. ion estimates with upper and lower 95%eton National Forest, Wyoming, USA, 2006–2008. Population estimate

N pellets/plot and were NA 1747 x 36.1 (SD) pellets/plot and were

have a hard habitat edge on

buffer of one-half the mean maximum distance moved

area, which was the trapping grid area plus an appropriate

We estimated snowshoe hare abundance using the 2-

sample Lincoln–Peterson estimator adjusted for sample size (Chapman 1951, Seber 1982) to be consistent with other hare studies in the Northern Rocky Mountains (Mills et al. 2005). We divided these estimates by the effective trapping

We used linear regression to examine relationships between estimates of hare density from uncorrected and cleared plots on 16 trapping grids using SPSS (SPSS for Windows 10, Chicago, IL). Previous studies recommend using both linear and functional

regression approaches 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, McCann et al. 2008). We did not use functional regression for 3 main reasons: 1) hare densities on our sites were high, with density estimates between 0.70 hares/ha and 4.82 hares/ha for 12 of 18 trapping sessions; and 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 small (McCann et al. 2008); and 3) our snowshoe hare capture data were not highly skewed (skewness/SE skewness) and were 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

Fecal pellet plots were cleared in the summers of 2006 and 2007, while cleared plots were counted in the summers of 2007 and 2008; cleared plots were always counted 12 months after clearing. Grids were trapped in the winters of 2006–2007 and 2007–2008. Mean fecal pellet counts ranged from 6.2 pellets/plot to 109.9 pellets/plot and from 2.1 pellets/plot to 47.7 pellets/plot on uncleared and annually cleared plots, respectively (Table 1). Pellet counts from uncleared plots averaged 46.2 ± 36.1 (SD) pellets/plot and were almost 3 times higher than cleared plots (x = 15.8 ± 13.4 pellets/plot). Number of individual hares caught on the trapping grids ranged from 1 to 64 (Table 1) and averaged

<table>
<thead>
<tr>
<th>Stand typea</th>
<th>Fecal pellet counts</th>
<th>Population estimate</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Cleared</td>
<td>Uncleared</td>
</tr>
<tr>
<td></td>
<td>x</td>
<td>SD</td>
</tr>
<tr>
<td>30–60-yr-old LPP</td>
<td>16.7</td>
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<td>30–60-yr-old LPP</td>
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<td>33.2</td>
</tr>
<tr>
<td>30–60-yr-old LPP</td>
<td>8.8</td>
<td>11.7</td>
</tr>
<tr>
<td>30–60-yr-old LPP</td>
<td>35.8</td>
<td>23.3</td>
</tr>
<tr>
<td>30–60-yr-old LPP–SF</td>
<td>17.0</td>
<td>13.0</td>
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<tr>
<td>Multistory LPP–SF</td>
<td>35.3</td>
<td>22.8</td>
</tr>
<tr>
<td>Multistory LPP–SF</td>
<td>12.0</td>
<td>9.0</td>
</tr>
<tr>
<td>Multistory LPP–SF</td>
<td>3.6</td>
<td>3.3</td>
</tr>
<tr>
<td>Multistory LPP–SF</td>
<td>3.6</td>
<td>5.1</td>
</tr>
<tr>
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<td>16.7</td>
</tr>
<tr>
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<td>2.1</td>
<td>2.9</td>
</tr>
<tr>
<td>Multistory LPP–SF</td>
<td>8.3</td>
<td>9.9</td>
</tr>
<tr>
<td>Multistory aspen–SF</td>
<td>31.1</td>
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<td>22.2</td>
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<td>2.9</td>
</tr>
<tr>
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<td>Multistory SF</td>
<td>3.9</td>
<td>5.7</td>
</tr>
<tr>
<td>Multistory DF–LPP–SF</td>
<td>6.2</td>
<td>8.5</td>
</tr>
</tbody>
</table>

a LPP: lodgepole pine; SF: spruce–fir; DF: Douglas fir.
b NA: not available.

1 of their 4 outside borders; during trapping sessions, we did not observe hare tracks in the snow venturing out into this less suitable habitat, which in all cases was nonforested. For this reason, we chose to test this hard edge assumption by subtracting the buffer from only these portions of trapping grids. We then compared the relationship between pellet counts and estimated snowshoe hare density with and without this hard edge included in the estimated effective trapping area.

We used linear regression to examine relationships between estimates of hare density versus fecal pellet counts from uncleared and cleared plots on 18 trapping grids using SPSS (SPSS for Windows 10, Chicago, IL). Previous studies recommend using both linear and functional
19.1 hares/trapping grid. The proportion of hares captured each day that were previously marked exceeded 75% by the sixth day of trapping.

Two-sample Lincoln–Petersen population estimates averaged 23.2 hares/trapping grid (range 5 1.0–78.6 hares/trapping grid; Table 1). Density estimates for snowshoe hares averaged 1.51 hares/ha (range 5 0.07–4.82 hares/ha; Table 2) across all grids when using one-half the mean maximum distance moved by individual hares as a buffer to estimate effective trapping area for each site. Estimates of snowshoe hare density averaged 1.61 hares/ha (range 5 0.07–4.82 hares/ha; Table 2) across all grids when using the same buffer with hard edges subtracted to estimate the effective trapping area.

Relationships between pellet counts on uncleared and annually cleared plots were highly correlated with estimates of snowshoe hare density, with pellet counts from cleared plots (Fig. 1A) having a better fit (i.e., higher r) than counts from uncleared plots (Fig. 1B). Interestingly, adjusting buffers on trapping grids with hard edges (Table 2) improved the linear relationship (i.e., higher r) between annually cleared and uncleared pellet counts and estimates of snowshoe hare density (Fig. 2).

Equations we developed using annually cleared pellet counts had similar y-intercepts and slopes whether we estimated hare density with or without buffers corrected for hard edges (Table 3). Linear equations developed in Idaho (Murray et al. 2002), Montana (Mills et al. 2005), and Minnesota, USA (McCann et al. 2008) that used similar methods had different y-intercepts and slopes than equations we developed on the B-TNF, which could lead to large differences in snowshoe hare density estimates. The Minnesota and our B-TNF equations were similar in their slopes (0.060 vs. 0.089 or 0.093, respectively) but y-intercepts differed. The hare density estimate from the Idaho equation at the y-intercept was initially smaller than the Minnesota or Wyoming equations at lower pellet plot counts. However, the Idaho equation estimated higher hare densities than the Minnesota and Wyoming equations due to the steeper slope in the equation. Equations for Montana (Mills et al. 2005) had negative y-intercepts but greater slopes. If we used these equations for estimating snowshoe hare density without consideration of local environmental conditions, a variety of results would be produced. For example, plugging 30 pellets/plot into our equations would yield 2.96 hares/ha and 2.77 hares/ha using the adjusted buffer and full buffer, respectively. Using the equation from McCann et al. (2008) would produce a resulting 2.20 hares/ha. After reconfiguring the equation for Murray et al. (2002) to back-transform the data and equation (with no correction factor for zeros and root mean-square error), 30 pellets/plot would yield an estimate of 5.63 hares/ha. Using similar back-transformation on the Mills et al. (2005) equations would produce an estimate of 0.14 hares/ha.

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 contiguous United States, and British Columbia, Labrador, and Quebec, Canada (e.g., de Bellefeuille et al. 2001, Ausband and Baty 2005, Newbury and Simon 2005, Potvin et al. 2005, Sullivan et al. 2006). Prior studies based on
Circular plots were highly correlated 1.67 0.51. Circular plots apparently were not synonymous or 5 2 1.047X 0.060X N 5 circular plots and r 0.174 0.94 2 0.102 0.93 0.77X + Regression equations for studies examining the linear relationship between fecal pellet counts using 1-m² circular plots and snowshoe hare density in Idaho, Minnesota, Montana, and Wyoming, USA, 2002–2008.

<table>
<thead>
<tr>
<th>Source</th>
<th>Location</th>
<th>Eq</th>
<th>r</th>
</tr>
</thead>
<tbody>
<tr>
<td>Murray et al. 2002</td>
<td>ID</td>
<td>Y = 1.047X + 1.112</td>
<td>0.85</td>
</tr>
<tr>
<td>McCann et al. 2008</td>
<td>MN</td>
<td>Y = 0.060X + 0.398</td>
<td>0.89</td>
</tr>
<tr>
<td>Mills et al. 2005</td>
<td>MT</td>
<td>Y = 0.77X − 1.67</td>
<td>0.51</td>
</tr>
<tr>
<td>Mills et al. 2005</td>
<td>MT</td>
<td>Y = 0.63X − 1.14</td>
<td>0.68</td>
</tr>
<tr>
<td>This study (adjusted buffer)</td>
<td>WY</td>
<td>Y = 0.093X + 0.174</td>
<td>0.94</td>
</tr>
<tr>
<td>This study (full buffer)</td>
<td>WY</td>
<td>Y = 0.089X + 0.102</td>
<td>0.93</td>
</tr>
</tbody>
</table>

Possible factors influencing higher correlation coefficients between pellet counts and hare density we found (Table 3) as compared to other studies in the northern Rockies (Mills et al. 2005, Murray et al. 2005) are difficult to determine without detailed knowledge of each specific sampling protocol. Our trapping sessions lasted 6–9 days to provide an adequate (>75%) recapture rate of individually identified hares. We attempted to place live traps in optimal locations and screened the back and sides of traps with sticks, pine boughs, or logs to reduce the likelihood of a hare missing the entrance to the trap. Most trapping sessions (>95%) occurred when snow covered the ground and, therefore, food may have been less available. On days with no snow cover, capture success declined. In addition, our study area was drier than other study sites, particularly in terms of precipitation and humidity, possibly influencing pellet decomposition rates.

There have been discussions of the utility of counting fecal pellets from uncleared plots mainly due to effects of multiple years of pellet accumulation, temporal changes in hare abundance, 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 had a worse fit (lower r) 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. We recognize that the correlation between uncleared plots and snowshoe hare density used the estimated hare...
density calculated from the winter following clearing of the plots; a higher correlation may have been produced if we had estimates of snowshoe hare density before clearing plots. When a precise estimate (i.e., higher correlation) of snowshoe hare abundance and habitat use is required, we recommend using annually cleared pellet plots (Prugh and Krebs 2004, Murray et al. 2005); adjusting buffer size minimally improved precision in our study (Table 3). When only a coarse indication of snowshoe hare abundance is needed, uncleared pellet counts likely provide insight to relative abundance and distribution of snowshoe hares (Hodges and Mills 2008). However, due to a lack of observed precision at low hare densities, we believe their utility may be limited (Hodges and Mills 2008).

Suitable habitat for snowshoe hares in the GYE is naturally fragmented due to differences in elevation, topography, aspect, soils, and climate. We thus found that snowshoe hares used disjunct patches of mesic boreal forest that had appropriate understory characteristics (Hodges and Mills 2005, Murphy et al. 2006). Several of our survey sites, particularly in the Wyoming Range, were located in disjunct patches of montane forest and such sites were partially or completely surrounded by matrix habitat composed of sagebrush–wheatgrass or riparian willow–meadow plant communities. On these sites, we observed sign of hares (live animals and fecal pellets) beyond the forest edge in the matrix habitat during snow-free periods but sign was noticeably absent from these same areas during winter, suggesting seasonal shifts in habitat use by snowshoe hares at these sites (Wolff 1980).

Documentation of high snowshoe hare density in the southern GYE 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, suggesting that additional factors may also be influencing lynx population size (Squires and Oakleaf 2005, Murphy et al. 2006). Additional factors include competition with other predators (mainly coyotes, Canis latrans), amount and spatial arrangement of suitable habitat on the landscape, climate change, historic trapping and current incidental trapping of lynx, habitat connectivity, and 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, snowshoe hares are often used as a surrogate for identifying potential lynx habitat. Managers should exercise caution when using hare density–fecal pellet equations to identify potential habitat for lynx in this region until an understanding of lynx prey requirements is more complete. Furthermore, both pellet counts and mark–recapture estimates of hare numbers may be compromised at low hare densities, leading to an inability to accurately predict a proposed minimum hare threshold for lynx (Mills et al. 2005). Despite these shortcomings, there is value in using fecal pellet counts to identify areas of low, medium, and high hare densities for lynx management.

MANAGEMENT IMPLICATIONS

Densities of snowshoe hares varied across the patchily distributed fragmented forest landscape of western Wyoming. Even though 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. We found that when using buffer adjustments, the correlation coefficient 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. We recommend construction of local regression equations for precise estimates of snowshoe hare density due to the influence of local environmental conditions on the rates of pellet deposition (diet) and decomposition (climate).

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LITERATURE CITED


