



Management and Conservation Article

Relationship Between Fecal Pellet Counts and Snowshoe Hare Density in Western Wyoming

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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 estimates, and pellet plot counts on both uncleared plots and annually cleared plots on 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 coarse 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

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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°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 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 5×10 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-m² 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,

Table 1. Mean fecal pellet counts (\pm SD) from annually cleared and uncleared plots with corresponding population estimates with upper and lower 95% confidence intervals of snowshoe hares from 18 trapping grids, Bridger-Teton National Forest, Wyoming, USA, 2006–2008.

Stand type ^a	Fecal pellet counts				Population estimate			
	Cleared		Uncleared		No. hares captured	N	Lower 95% CI	Upper 95% CI
	\bar{x}	SD	\bar{x}	SD				
30–60-yr-old LPP	16.7	14.0	32.8	30.8	31	39.6	27.5	41.6
30–60-yr-old LPP	47.7	33.2	103.2	85.7	64	78.6	62.6	83.6
30–60-yr-old LPP	8.8	11.7	18.5	18.6	12	14.8	8.5	24.1
30–60-yr-old LPP	35.8	23.3	42.0	37.3	53	54.9	49.5	61.7
30–60-yr-old LPP–SF	17.0	13.0	65.9	57.6	16	21.3	12.1	26.6
Multistory LPP–SF	35.3	22.8	83.0	93.2	31	32.6	28.4	38.8
Multistory LPP–SF	12.0	9.0	109.9	108.7	9	11.0	6.3	16.4
Multistory LPP–SF	3.6	3.3	25.9	24.1	6	7.0	4.8	14.8
Multistory LPP–SF	3.6	5.1	12.1	15.8	5	8.0	4.3	8.7
Multistory LPP–SF	25.3	16.7	79.0	87.6	23	23.9	20.5	31.3
Multistory LPP–SF	2.1	2.9	6.2	8.3	1	1.0	NA ^b	NA
Multistory LPP–SF	8.3	9.9	39.3	45.4	10	13.0	7.1	18.9
Multistory aspen–SF	31.1	25.8	106.4	88.4	33	47.0	31.0	48.3
Multistory aspen–SF	20.7	22.2	47.6	43.6	30	41.0	28.6	43.7
Multistory SF	2.4	2.9	28.6	28.2	2	2.0	NA	NA
Multistory SF	3.9	5.2	12.0	16.8	8	8.8	5.0	24.9
Multistory SF	3.9	5.7	10.2	14.8	2	2.0	NA	NA
Multistory DF–LPP–SF	6.2	8.5	9.2	8.5	8	11.5	5.0	24.9

^a LPP: lodgepole pine; SF: spruce–fir; DF: Douglas fir.

^b NA: not available.

measured, weighed, and released them. We double-tagged each captured hare (one tag in each ear) to prevent loss of marks during the trapping session. We handled individuals in lightweight zipper-topped pillowcases that securely contained hares and allowed for effective processing. Each trapping session consisted of 6–9 nights to ensure we marked a sufficient percent of the population on each grid (Seber 1982, 1992).

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 area, which was 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 (Wilson and Anderson 1985, Karanth and Nichols 1998, Mills et al. 2005, McCann et al. 2008, Zahratka and Shenk 2008). We presumed several trapping grids ($n = 7$) to have a hard habitat edge on ≥ 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

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 we captured hares on all trapping grids; 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 ($\bar{x} = 15.8 \pm 13.4$ pellets/plot). Number of individual hares caught on the trapping grids ranged from 1 to 64 (Table 1) and averaged

Table 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, USA, 2006–2008.

Stand type ^a	Estimated density (hares/ha)	
	Full buffer	Adjusted buffer
30–60-yr-old LPP	2.37	2.37 ^b
30–60-yr-old LPP	4.82	4.82 ^b
30–60-yr-old LPP	0.72	0.72 ^b
30–60-yr-old LPP	3.14	3.14 ^b
30–60-yr-old LPP–SF	1.58	1.58 ^b
Multistory LPP–SF	2.54	3.19
Multistory LPP–SF	0.84	1.08
Multistory LPP–SF	0.41	0.41 ^b
Multistory LPP–SF	0.57	0.57 ^b
Multistory LPP–SF	0.07	0.07 ^b
Multistory LPP–SF	1.58	1.58 ^b
Multistory LPP–SF	0.81	1.19
Multistory aspen–SF	3.23	3.72
Multistory aspen–SF	2.90	2.90 ^b
Multistory SF	0.14	0.16
Multistory SF	0.48	0.58
Multistory SF	0.14	0.16
Multistory DF–LPP–SF	0.79	0.79 ^b

^a LPP: lodgepole pine; SF: spruce–fir; DF: Douglas fir.

^b Trapping grid had no presumed hard edge(s); therefore, we made no buffer adjustments.

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 = 1.0–78.6 hares/trapping grid; Table 1). Density estimates for snowshoe hares averaged 1.51 hares/ha (range = 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 = 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

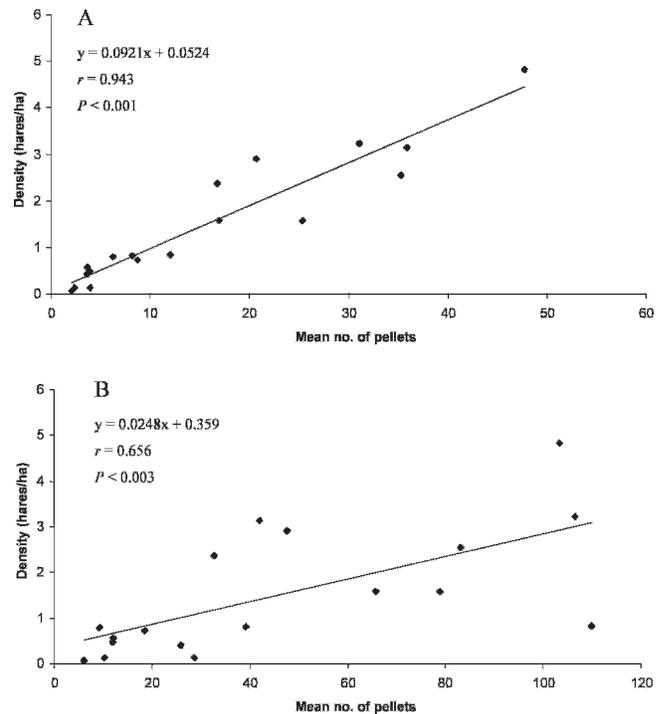


Figure 1. Relationships between estimates of snowshoe hare density using the full buffer around the grid and associated pellet counts on (A) 18 annually cleared trapping grids, and (B) 18 uncleared trapping grids, Bridger-Teton National Forest, Wyoming, USA, 2006–2008.

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

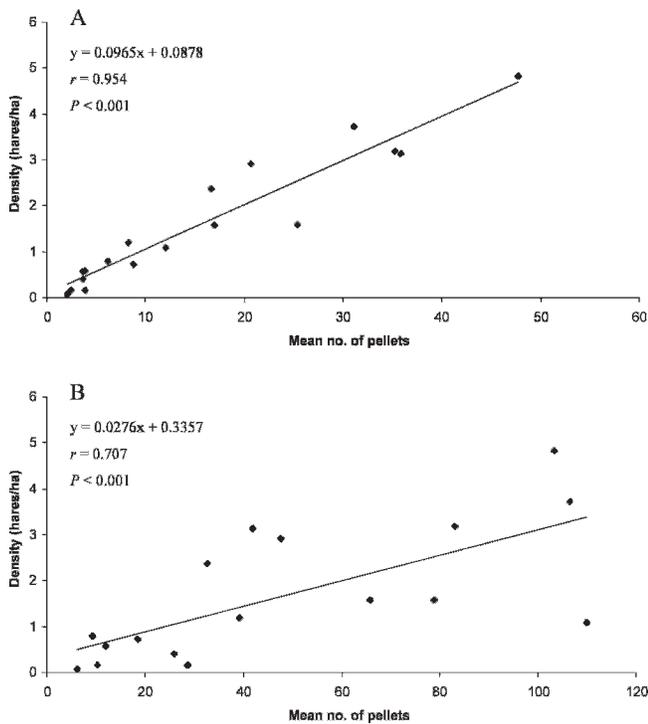


Figure 2. Relationships between estimates of snowshoe hare density using the adjusted buffer for hard edges and pellet counts on (A) 18 cleared trapping grids, and (B) 18 uncleared trapping grids, Bridger-Teton National Forest, Wyoming, USA, 2006–2008.

pellet counts showed low snowshoe hare densities in the northern GYE (Hodges and Mills 2005, Hodges et al. 2009) and no regression equations relating hare density and pellet counts were developed. Therefore, equations we developed provided an important reference point for future pellet count surveys to estimate hare density in the southern GYE.

Significant relationships between snowshoe hare density and pellet counts in western Wyoming were consistent with other studies throughout North America (e.g., Murray et al. 2002, 2005; Mills et al. 2005; Homyack et al. 2006). Similar to other geographic areas where they were 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 and Montana. We therefore concur with those who argued for 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 to identify important foraging habitat for Canada lynx.

Equations developed in other geographic areas that used 1-m² circular plots apparently were not synonymous or interchangeable for estimating snowshoe hare abundance in Wyoming. Our simple example of using other equations produced vastly different hare densities. We caution that

Table 3. 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.

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

how equations were developed varied among studies and, therefore, direct comparison is limited. Although all studies used 1-m² circular pellet plots to count pellet numbers, Murray et al. (2002) and Mills et al. (2005) transformed their data set prior to developing regression equations. In contrast, neither we nor McCann et al. (2008) transformed data to develop equations. In addition, differences in size of the buffer area around the trapping grid (i.e., determination of the effective trapping area) varied among studies, as did inclusion of correction factors in determining estimates of snowshoe hare density (Murray et al. 2002).

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

- Ausband, D. E., and G. R. Baty. 2005. Effects of precommercial thinning on snowshoe hare habitat use during winter in low-elevation montane forests. *Canadian Journal of Forestry Resources* 35:206–210.
- Brand C. J., and L. B. Keith. 1979. Lynx demography during a snowshoe hare decline in Alberta. *Journal of Wildlife Management* 43:827–849.
- Brand, C. J., L. B. Keith, and C. A. Fischer. 1976. Lynx responses to changing snowshoe hare densities in central Alberta. *Journal of Wildlife Management* 40:416–428.
- Chapman, D. G. 1951. Some properties of the hypergeometric distribution with applications to zoological censuses. *University of California Publications on Statistics* 1:131–160.
- de Bellefeuille, S., L. Belanger, J. Huot, and A. Cimon. 2001. Clear-cutting and regeneration practices in Quebec boreal balsam fir forest: effects on snowshoe hare. *Canadian Journal of Forestry Resources* 31:41–51.
- Hodges, K. E., and L. S. Mills. 2005. Snowshoe hares in Yellowstone. *Yellowstone Science* 13:3–6.
- Hodges, K. E., and L. S. Mills. 2008. Designing fecal pellet surveys for snowshoe hares. *Forest Ecology and Management* 256:1918–1926.
- Hodges, K. E., L. S. Mills, and K. M. Murphy. 2009. Distribution and abundance of snowshoe hares in Yellowstone National Park. *Journal of Mammalogy* 90:870–878.
- Homyack, J. A. 2003. Effects of precommercial thinning on snowshoe hares, small mammals, and forest structure in northern Maine. Thesis, University of Maine, Orono, USA.

- Homyack, J. A., D. J. Harrison, J. A. Litvaitis, and W. B. Krohn. 2006. Quantifying densities of snowshoe hares in Maine using pellet plots. *Wildlife Society Bulletin* 34:74–80.
- Karanth, K. U., and J. D. Nichols. 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* 79:2852–2862.
- Keith, L. B., J. R. Cary, O. J. Rongstad, and M. C. Brittingham. 1984. Demography and ecology of a declining snowshoe hare population. *Wildlife Monographs* 90.
- Krebs, C. J., R. Boonstra, V. Nams, M. O'Donoghue, K. E. Hodges, and S. Boutin. 2001. Estimating snowshoe hare population density from pellet counts: a further evaluation. *Canadian Journal of Zoology* 79:1–4.
- Krebs, C. J., B. S. Gilbert, S. Boutin, and R. Boonstra. 1987. Estimation of snowshoe hare population density from turd transects. *Canadian Journal of Zoology* 65:565–567.
- McCann, N. P., R. A. Moen, and G. J. Niemi. 2008. Using pellet counts to estimate snowshoe hare numbers in Minnesota. *Journal of Wildlife Management* 72:955–958.
- McKelvey, K. S., K. B. Aubry, and Y. K. Ortega. 2000. History and distribution of lynx in the contiguous United States. Pages 207–267 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. *Ecology and conservation of lynx in the United States*. University Press of Colorado, Boulder, USA.
- McKelvey, K. S., G. W. McDaniel, L. S. Mills, and P. C. Griffin. 2002. Effects of plot size and shape on pellet density estimates for snowshoe hares. *Wildlife Society Bulletin* 30:751–755.
- Mills, L. S., P. C. Griffin, K. E. Hodges, K. McKelvey, L. Ruggiero, and T. Ulizio. 2005. Pellet count indices compared to mark-recapture estimates for evaluating snowshoe hare density. *Journal of Wildlife Management* 69:1053–1062.
- Montgomery, D. C. 2005. *Design and analysis of experiments*. Sixth edition. John Wiley and Sons, Hoboken, New Jersey, USA.
- Murphy, K. M., T. M. Potter, J. C. Halfpenny, K. A. Gunther, M. T. Jones, P. A. Lundberg, and N. D. Berg. 2006. Distribution of Canada lynx in Yellowstone National Park. *Northwest Science* 80:199–206.
- Murray, D. L., E. Ellsworth, and A. Zack. 2005. Assessment of potential bias with snowshoe hare fecal pellet-plot counts. *Journal of Wildlife Management* 69:385–395.
- Murray, D. L., J. D. Roth, E. Ellsworth, A. J. Wirsing, and T. D. Steury. 2002. Estimating low-density snowshoe hare populations using fecal pellet counts. *Canadian Journal of Zoology* 80:771–781.
- Murray, D. L., T. D. Steury, and J. D. Roth. 2008. Assessment of Canada lynx research and conservation needs in the southern range: another kick at the cat. *Journal of Wildlife Management* 72:1463–1472.
- National Oceanic and Atmospheric Administration. 2009. Western Regional Climate Center, Reno, Nevada. <<http://www.wrcc.dri.edu/clisum.html>>. Accessed: 12 Feb 2010.
- Newbury, T. L., and N. P. P. Simon. 2005. The effects of clearcutting on snowshoe hare (*Lepus americanus*) relative abundance in central Labrador. *Forest Ecology and Management* 210:131–142.
- Potvin, F., L. Breton, and R. Courtois. 2005. Response of beaver, moose, and snowshoe hare to clear-cutting in a Quebec boreal forest: a reassessment 10 years after cut. *Canadian Journal of Forestry Resources* 35:151–160.
- Prugh, L. R., and C. J. Krebs. 2004. Snowshoe hare pellet-decay rates and aging in different habitats. *Wildlife Society Bulletin* 32:386–393.
- Seber, G. A. F. 1982. *The estimation of animal abundance and related parameters*. Second edition. MacMillan, New York, New York, USA.
- Seber, G. A. F. 1992. A review of estimating animal abundance, II. *International Statistical Review* 60:129–166.
- Squires, J. R., N. J. DeCesare, S. Tomson, L. F. Ruggiero, and B. Oakleaf. 2003. Distribution of lynx and other forest carnivores in the Wyoming Range, south-central Wyoming. U.S. Forest Service, Rocky Mountain Research Station, Final Report, Missoula, Montana, USA.
- Squires, J. R., and R. Oakleaf. 2005. Movements of a male Canada lynx crossing the Greater Yellowstone Area, including highways. *Northwest Science* 79:196–201.
- Squires, J. R., and L. F. Ruggiero. 2007. Winter prey selection of Canada lynx in northwestern Montana. *Journal of Wildlife Management* 71:310–315.
- Sullivan, T. P., D. S. Sullivan, P. M. F. Lindgren, and D. B. Ransome. 2006. Influence of repeated fertilization on forest ecosystems: relative habitat use by snowshoe hares (*Lepus americanus*). *Canadian Journal of Forest Research* 36:2080–2089.
- U.S. Fish and Wildlife Service. 2000. Endangered and threatened wildlife and plants; determination of threatened status of the contiguous USA distinct population segment of the Canada lynx and related rule. *Federal Register* 65:16051–16086.
- U.S. Fish and Wildlife Service. 2008. Endangered and threatened wildlife and plants; revised critical habitat for the contiguous USA distinct population segment of the Canada lynx; proposed rule. *Federal Register* 73:10860–10896.
- Wilson, K. R., and D. R. Anderson. 1985. Evaluation of 2 density estimators of small mammal population size. *Journal of Mammalogy* 66:13–21.
- Wolff, J. O. 1980. The role of habitat patchiness in the population dynamics of snowshoe hares. *Ecological Monographs* 50:111–130.
- Zahratka, J. L., and T. M. Shenk. 2008. Population estimates of snowshoe hares in the Southern Rocky Mountains. *Journal of Wildlife Management* 72:906–912.

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