Effects of plot size and shape on pellet density estimates for snowshoe hares

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Abstract   A variety of plot shapes and sizes have been used to estimate pellet densities of snowshoe hares (*Lepus americanus*), but we lack a clear understanding of whether plot shape and size affect measured pellet density. Snowshoe hare pellet densities associated with several plot designs were compared at 2 locations in the Rocky Mountains. Plot designs and pellet-inclusion rules were identical on both sites, but crews were independent. Density estimates were systematically biased by plot size and shape, with smaller plots and higher edge-to-area ratios leading to higher density estimates. In particular, the plot size and dimensions suggested by Krebs et al. (1987, 2001) produced the highest density estimates on both sites. Thus, we caution against using the regression equations developed by Krebs et al. (1987, 2001) if plot dimensions differ from theirs. Similarly, we believe that direct comparison of hare pellet densities (and, by inference, hares) between studies using different plot designs is not valid. Within the pellet density range associated with our study areas, we suggest using large circular plots except where comparison with other studies using Krebs et al.'s (1987, 2001) methodologies is vital. Large circular plots minimize potential inclusion bias associated with pellets on the plot boundary, are easy to implement, and are common in the literature.

Key words   density estimates, *Lepus americanus*, pellets, snowshoe hare

Snowshoe hares (*Lepus americanus*) are the primary winter diet for Canada lynx (*Lynx canadensis*; Quinn and Parker 1987, Koehler and Aubry 1994, O'Donoghue et al. 1998), and because the lynx was recently listed as threatened under the federal Endangered Species Act (Federal Register, Vol. 63, No. 130), interest in estimating snowshoe hare densities has increased. Counting pellets is an appealing method for obtaining relative population density estimates because it is easier to count pellets than to count organisms. Krebs et al. (1987, 2001) suggested that snowshoe hare pellet densities were highly correlated with snowshoe hare densities throughout their cycle in Yukon, Canada and that pellets could therefore serve as a robust index of hare densities.

Pellet counts have been used in many studies to infer lagomorph densities, and many different plot designs have been used to assess snowshoe hare densities. The most common are circular plots of various sizes: 0.4 m² (Adams 1959), 1.0 m² (Rogowitz 1988, Koehler 1990, Litvaitis et al. 1985, Ferron et al. 1998, Malloy 2000), 1.8 m² (Wolfe et al. 1982), or 2.0 m² (Ball et al. 2000). Additionally, various rectangular plots have been used (Fuller and Heisey 1986, Krebs et al. 1987, Nams et al. 1996, Darveau et al. 1998).

Krebs et al. (1987, 2001) developed regressions between pellet and snowshoe hare densities using long, thin plots (0.0508 × 3.0800 m) for pellet counts. The relationship between estimated hare density and pellet counts was good (*r*=0.76, Krebs et al. 2001). There are, however, a number of issues associated with transferring Krebs et al.'s (1987, 2001) equations to southern montane ecosystems

(Krebs et al. 2001). One of these is whether the plot design that Krebs et al. (1987) found optimal is ideal in areas with much lower densities of snowshoe hares. To our knowledge, no direct comparison of the relative efficacy of plot shapes at low hare densities has been published. We tested a variety of pellet-plot designs in southern boreal forests to determine whether density estimates were affected by plot size and shape and whether certain combinations of size and shape were preferable for density estimation.
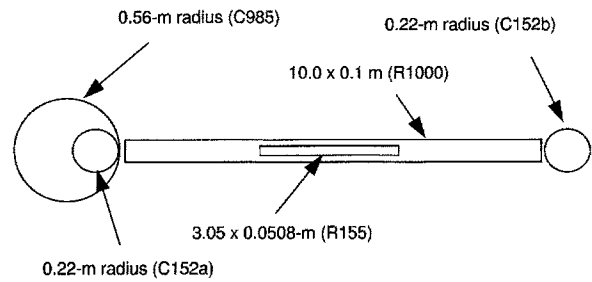

Figure 1. Representation of the plot arrays used to estimate snowshoe hare pellets at Seeley Lake, Montana and Island Park, Idaho. Plots are not drawn to scale.

Study area

We estimated hare pellet densities in 2 areas within the Rocky Mountains from May to September 2000. The first study area was located in Seeley Lake in the Clearwater drainage of west-central Montana (47°20′N, 113°50′W). Average annual precipitation was 55 cm, with heaviest precipitation occurring in December, January, and June. Average temperature varied from -6.5°C in January to 16.6°C in July. Elevations at the Seeley Lake study area ranged from approximately 1,200 to 2,100 m. Lower elevations within the area were dominated by forests of Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*), and ponderosa pine (*P. ponderosa*). Subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and lodgepole pine covered higher elevations.

The second study area was located in Island Park, Idaho on the northwestern corner of the Greater Yellowstone Ecosystem (44°20′N, 111°20′W). This area was located in a large caldera, which is approximately 1,800 m elevation on the floor and 2,400 m on the rim. Average precipitation at the Island Park Ranger Station was 74 cm per year, but precipitation varied widely across the area. Precipitation for the area was heaviest in winter. Temperatures varied from a daily mean temperature of -10°C in January to 16°C in July. Forests in the Island Park study area were almost exclusively composed of lodgepole pine, with local areas of Engelmann spruce and subalpine fir. Douglas-fir forests were found on the steep slopes between the rim and caldera floor.

Methods

Within Seeley Lake and Island Park we counted pellets at 23 and 52 grids, respectively, located in a variety of forest types and age classes. Each grid consisted of 25 pellet-plot arrays. To determine the efficacy of various plot designs, each array consisted of 4 types of pellet-plots (Figure 1). Two enclosed an area of approximately 1 m²: a 10 × 1,000-cm rectangle (R1000) and a 56-cm-radius circle (0.985 m²; C985). Two enclosed an area of approximately 0.15 m²: a 5.08 × 305-cm rectangle (0.155 m²; R155) equivalent to the plots utilized by Krebs et al. (1987, 2001) and a 22-cm-radius circle (0.152 m²; C152). Two 22-cm-radius circles were sampled at each plot location to determine the benefits associated with sampling additional small plots and because we assumed that pellet counts within these plots would be highly variable. We nested the large and small circular and rectangular plots to ensure that they were sampling the same areas for purposes of comparison. We attempted to count all pellets that occurred within the plot areas, excluding pellets incorporated into the ground litter. Vegetation was moved if it obscured the ground. We counted every other pellet located on the plot borders to minimize inclusion bias. Density was estimated by dividing counted pellets by plot size. Methods for pellet collection were identical on the 2 sites, but the crews and supervisors were independent.

Because we were interested in comparing pellet densities among plot designs, we excluded from analysis all plot arrays that contained no pellets. Because the pellets were not normally distributed across plots, we used a Friedman test (Zar 1996) blocking on plot-array and treated the plot types as treatments to test for density differences between plot types. Where the Friedman test was significant ($P \leq 0.05$), we used Wilcoxon paired sample tests (Zar 1996) to test for pairwise differences between plot types. P-values associated with the Wilcoxon paired sample tests were Bonferroni-adjusted to account for experiment-wide error (Sokal and

Table 1. Descriptive statistics for pellet density (pellets per m²) of snowshoe hares using various shapes and sizes of plots at Seeley Lake, Montana and Island Park, Idaho, May–September, 2000.

	Plot type[1]					
	R155	C152a	C152b	C152	R1000	C985
Seeley Lake						
Maximum	354.84	190.79	1,039.47	519.74	105.00	80.20
Mean	11.53	7.06	13.38	10.22	8.76	4.91
Percent CV	238.99	257.61	549.10	377.77	147.43	199.33
Island Park						
Maximum	51.61	52.63	59.21	36.18	32.00	27.41
Mean	3.72	2.90	3.56	3.23	3.21	1.96
Percent CV	228.66	256.23	251.72	184.83	139.82	194.07

[1] R155 = 5- × 305-cm rectangle; C152a = first 22-cm-radius circle; C152b = second 22-cm-radius circle; C152 = combined estimates from C152a and C152b; R1000 = 10- × 1,000-cm rectangle; C985 = 56-cm-radius circle.

Rohlf 1981). We also calculated variance associated with each plot type.

Results

Hare pellets in Seeley Lake were both more common and more generally distributed than in Island Park. For this reason, even though fewer grids were sampled, Seeley Lake had 456 plot arrays containing at least 1 pellet, compared with 222 in Island Park. Hare pellets were unevenly distributed at both the grid and plot levels. At the grid level in Seeley Lake, 48% of the pellets were contained in 23% of the grids. In Island Park, where pellets were unevenly distributed across the landscape, 47% of the pellets were concentrated in 6% of the grids. At the plot level, variance was high, with CVs exceeding the means for all plot types (Table 1), indicating

a clumped distribution. Because of the high variance associated with the C152 plots, we combined data from these 2 plots for testing.

Overall, estimated pellet densities varied significantly by plot type in both Seeley Lake (Friedman test statistic=67.87, 3 df, $P \le 0.001$) and Island Park (Friedman test statistic = 39.85, 3 df, $P \le 0.001$). In both study areas, pairwise comparisons indicated that density estimates associated with the C985 plots were different from the other plot types. In Seeley Lake, C985 was significantly different from all other types (Table 2, Figure 2a), and in Island Park C985 was significantly different from C152 and R1000 (Table 2, Figure 2b). The rank order of mean density

Table 2. Results from Wilcoxon paired sample tests of average pellet density by plot type from May to September 2000. P-values associated with significance were reduced to 0.0085 to account for experimentwise error rates (Sokal and Rohlf 1981). Probabilities were 2-sided using the normal approximation (Zar 1996). Significant comparisons are in bold type.

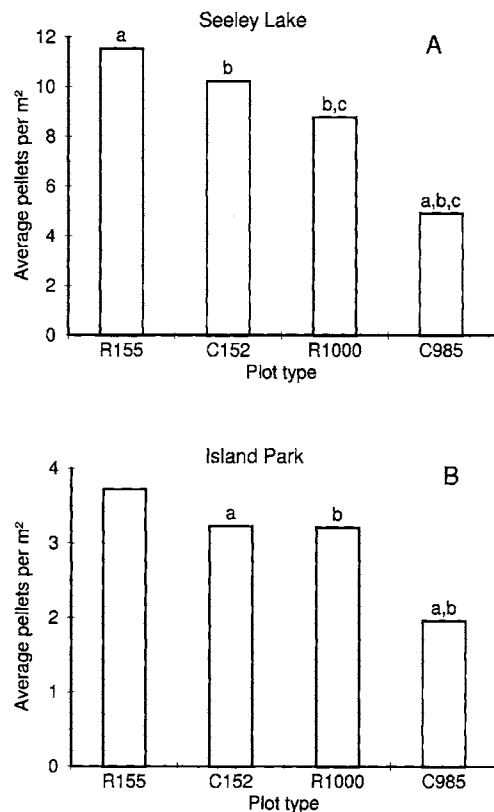|		Plot type		
Plot type		R155	C152	R1000
Seeley Lake				
	C152	0.041		
	R1000	0.756	**<0.001**	
	C985	**<0.001**	**<0.001**	**<0.001**
Island Park				
	C152	0.567		
	R1000	0.198	0.048	
	C985	0.090	**<0.001**	**<0.001**

Figure 2. Average pellet densities (pellets per m²) by plot type in Seeley Lake, Montana (A) and Island Park, Idaho (B). Plot types are ordered from those types with the highest computed pellet densities to the lowest. Groups with the same letters above the bars were significantly different ($P \le 0.0085$) based on Bonferroni-adjusted Wilcoxon paired tests (Table 2).

estimates was the same on both sites; R155 produced the highest computed densities, followed by C152, R1000, and C985. Average computed densities on R155 plots were 2.3 times and 1.8 times as high as those computed on C985 plots in Seeley Lake and Island Park, respectively.

Discussion

Krebs et al. (1987, 2001) suggested that hare and pellet densities were highly correlated and that pellets could therefore be used to estimate snowshoe hare population densities. Our studies indicated that if pellet counts were used for density estimation, plot size and shape were important. Using long, thin rectangles (R155) following Krebs et al. (1987, 2001) produced pellet density estimates (and therefore hare abundance estimates) approximately twice as high as those calculated using larger circular plots. Overall, small plots (R155, C152) produced, on average, the highest density estimates. For plots of similar size, narrow rectangular plots with high edge-to-area ratios produced higher density estimates than circular plots. There are 2 potential reasons for these differences. Either pellets were missed in the larger circular plots (Smith 1968) or inclusion bias was associated with pellets on the edge of the plots. Rules were in place to avoid inclusion bias and standardize sampling intensity, leaving us unclear as to which of these 2 factors was primarily responsible for the observed patterns. However, the differences in density estimates associated with different plots were consistent and large. It is therefore clear that comparing pellet densities between studies is not reliable unless the studies use similar plot designs.

Thin rectangular plots were chosen by Krebs et al. (1987, 2001) because they would mitigate plot-to-plot variance associated with clumped pellet distributions. Even though our pellets were clumped, the variance of R155 plots was similar to the C985 plots. While it was true that the C985 plots had 6 times the area, it was also our experience that they were easier to lay out and the boundaries were easier to define; precise placement of a plot 3.0 m long by 0.05 m wide was difficult in dense brush.

Similar to our study, Eaton (1989) found that pellet density estimates varied widely, both between plot types and between sites. Also, small rectangular plots with high edge-to-area ratios produced higher pellet estimates than large (3.14 m²) circular plots. Eaton's (1989) study plots, similar to those

suggested by Krebs et al. (1987, 2001), produced estimates approximately 2.6 times higher than those obtained using the large circular plots. Pellet distribution was clearly different in Seeley Lake and Island Park (Table 1), and undoubtedly differed from Eaton's (1989) study areas in Nova Scotia. The consistent differences in pellet density estimates associated with large circular plots versus thin rectangular plots across these studies suggest that plot geometry rather than site-specific factors, such as crew training or pellet density, are the primary cause. Although we do not know the precise causes of these patterns, we believe that larger circular plots are preferable, at least at low hare densities similar to those that occurred within our study areas. Circular plots were easier to lay out, plot boundaries were more precisely defined, and their use was more prevalent in the literature compared to other plot types.
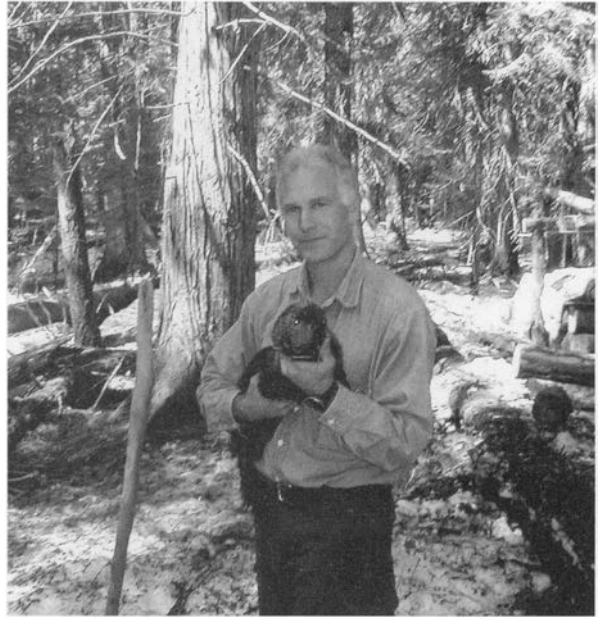
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