Forest Ecology and Management 256 (2008) 1918–1926

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Designing fecal pellet surveys for snowshoe hares

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ARTICLE INFO

Article history:
Received 8 February 2008
Received in revised form 15 July 2008
Accepted 15 July 2008

Keywords:
Abundance index
Fecal pellet plots
Lepus americanus
Monte Carlo simulations
Negative binomial
Snowshoe hare
Survey design

ABSTRACT

Index methods can be valuable for monitoring forest-dwelling vertebrates over broad spatial or temporal scales. Fecal pellet counts are often used as an index of density or habitat use of snowshoe hares, *Lepus americanus*, but previous surveys have used different plot types and sample sizes, leading to problems comparing results from different studies and questions about the inferential power of each study. In this paper, we use field data and simulations to examine how the precision, bias, and efficiency of four commonly used plot types vary with plot type, pellet density, and sample size. Although no one plot type was consistently superior, we recommend thin rectangles (5.08 cm × 305 cm (2 in. × 10 ft), 0.155 m^2) or 1 m^2 circles over 0.155 m^2 circles or 10 cm × 10 m (1 m^2) rectangles. We recommend that researchers explicitly address the power of their survey design to detect different pellet densities, because much larger sample sizes are needed at low pellet densities than at high pellet densities to obtain similar precision. Small sample sizes are also much more likely to be biased, which could lead to incorrect inferences about management of snowshoe hare populations. Both uncleared and cleared plots performed well and will have value in different research contexts.

1. Introduction

Many research questions about population abundances in different habitat types require data across large regions or long time frames. Although estimates based on mark-recapture data provide the highest quality estimates, logistical constraints limit their use. Furthermore, mark-recapture techniques can be inaccurate at very low densities of animals (McKelvey and Pearson, 2001; Bailey et al., 2004). Index methods are therefore attractive for ecological questions requiring broad surveys. Despite problems arising when the relationship between the index and true abundance is unknown or is variable over time and space (Anderson, 2001, 2003), some popular indices, like counts of fecal pellets, have been used to answer basic ecological questions or to inform management decisions for a wide variety of species, including lagomorphs (Forys and Humphrey, 1997; Langbein et al., 1999), ungulates (Massei et al., 1998; Campbell et al., 2004), kangaroos (Vernes, 1999), and elephants (Walsh et al., 2001).

For snowshoe hares (*Lepus americanus*), there is substantial interest in developing widely applicable survey methods. This species is an important prey species for many forest carnivores, including Canada lynx (*Lynx canadensis*), which is listed as threatened in the contiguous US under the Endangered Species Act (USFWS, 2000). Previous studies have used counts of fecal pellets to examine long-term population dynamics at individual sites (Malloy, 2000; Krebs et al., 2001), use of riparian set-asides in harvested areas (Darveau et al., 1998), relative abundance in different stand types in landscapes affected by various types of harvest (Newbury and Simon, 2005; Potvin et al., 2005; Fuller et al., 2007), and the impacts of precommercial thinning on population size (Sullivan et al., 2002; Ausband and Baty, 2005; Griffin and Mills, 2007; Homyack et al., 2007). Increasingly, forest managers in federal and state agencies are also using pellet counts as a way to determine which forest stands support enough hares to be considered as lynx foraging habitat, as that designation triggers particular management strategies.

Pellet counts are widely used for these questions relating to snowshoe hare abundances and habitat use because pellet counts have a relatively strong and repeatable relationship to mark-recapture population estimates at different times, places, and hare densities (Krebs et al., 1987, 2001; Murray et al., 2002; Mills et al., 2005; Homyack et al., 2006; McCann et al., 2008). Because different plot sizes and shapes produce different estimates of the mean and variance of pellet density (McKelvey et al., 2002; Murray et al., 2002), researchers using pellet counts to infer snowshoe hare abundance should use equations relating to the particular plot type

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0378-1127/$ – see front matter
doi:10.1016/j.foreco.2008.07.015

they used. These different estimates with plot type may arise from inclusion bias (falsely counting pellets on plot edges) or undercount bias (missing pellets inside plots). Some researchers have therefore explored the proportion of plots with pellets as an index of abundance, rather than relying on mean pellet density (Roppe and Hein, 1978; Fuller and Heisey, 1986; Murray et al., 2002).

Several studies have focused on decomposition rates in different habitats as a possible source of bias, and on whether to use annually or semi-annually cleared plots or uncleared plots that integrate over an unknown time period (Prugh and Krebs, 2004; Murray et al., 2005). Uncleared plots typically yield higher counts than annually cleared plots (Prugh and Krebs, 2004; Murray et al., 2005). Prugh and Krebs (2004) additionally demonstrated that observers have difficulty aging pellets accurately, making it difficult to correct uncleared plots to a 1-year interval, and Murray et al. (2005) suggested differential decomposition rates in different habitats might cause problems with uncleared plots. However, using cleared plots doubles the labor, requires permanent markers, and adds a delay, as crews need to clear and mark plots in the first year and then count the cleared plots in the subsequent year.

We are not aware of any studies that have explicitly addressed how many pellet plots of several common plot types should be counted per stand to balance the conflicting goals of high accuracy and precision of mean pellet density versus minimizing the time taken per stand survey. Previous studies have used sample sizes of 10–130 or more plots per stand, but seldom with any justification for the chosen sampling intensity. Given the variability in mean and variance related to plot type, the optimal sampling effort per plot type is likely to vary too.

Our objective in this paper is therefore to provide recommendations for choosing the number of plots to sample per stand for pellet plot surveys for snowshoe hares. We focus on four common plot types (varying in size and shape) to illustrate patterns general to all plot types and also to recommend which ones are best suited to efficient sampling. Our focus is on assessing accuracy and precision per stand because in many cases good knowledge about a particular stand is required; we recognize but do not address the additional trade-offs in designing a multi-stand survey, i.e. improving accuracy and precision per stand by using more plots versus sampling additional stands but with fewer plots and poorer estimates per stand.

Specifically, we (a) evaluate the effect of sample size and plot type on bias, (b) determine the sample size of each plot type needed to obtain desirable precision for different densities of pellets, and (c) rank the plot types by their efficiency in sampling a stand. We also explore sampling designs for cleared versus uncleared plots.

2. Study area

In summer 2001, we established 13 study sites in western Montana (Tally Lake Ranger District, Flathead National Forest). The study area was a ~300-km^2 drainage basin in subalpine forest with elevations of 1300–2000 m. The area was a mosaic of stand types resulting from fire and extensive forestry activities. The dominant tree species were subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), Western larch (*Larix occidentalis*), and Engelmann spruce (*Picea engelmannii*). We established 20-ha study sites on four never-harvested mature multi-storied stands, four stands that were clear-cut 15–25 years previously and have since regenerated to dense young stands with tree densities of 4900–7400 stems >61 cm (2 ft) tall per hectare, and five stands that were clear-cut 15–25 years previously and precommercially thinned 4–10 years previously to stand densities of 850–1250 stems per hectare.

3. Methods

On each of the 13 study sites, we established 80 pellet plot arrays with 50 m between each array. Each array was situated at a uniform distance and bearing away from permanent markers at each point in our study grid. We counted 4 uncleared plot types per array in 2001, recounted these as cleared plots in 2002, and also counted 4 new uncleared plots per array in 2002. The four plot types were a 5.08 cm × 305 cm small rectangle (2 in. × 10 ft; Krebs et al., 1987, 2001), a 10 cm × 10 m large rectangle, a 22.2 cm-radius small circle, and a 56.4 cm-radius large circle (see also McKelvey et al., 2002; Murray et al., 2002). The two small plot types had identical areas (0.155 m^2), as did the two large plot types (1 m^2). The small plots were nested inside the large plots of the same shape. Pellets had to be intact and more than half inside a plot boundary to be counted. We cleared all pellets from the plots while counting.

The total time necessary to sample a stand involves travel between plots and pellet counting. For 150 plots of each type, eight experienced observers recorded how long it took to establish and count each plot. Values for the small rectangles and circles nested inside the larger plots were counted first, then added to the time taken to search the remaining area of the large rectangles and circles, respectively. This design slightly inflates the estimate of time needed for large plots because of the need to scan the edges of the small plots. We estimated travel time by calculating the time it took to walk an entire study site, then scaling to the 50 m between plots. The estimated travel time for the 50 m walk between the pellet plots was measured as approximately 45–90 s, with speed differences due to amount and type of vegetation, downed wood, and slope.

If observers consistently age pellets in the same way (as younger or older than 1 year), it would be possible to remove old pellets from counts of uncleared plots to make these counts comparable to cleared plots (Prugh and Krebs, 2004; Murray et al., 2005). We tested five experienced observers to see if people aged pellets in the same way. Each person was presented with 50 samples of 10 pellets each and asked to identify the number of pellets younger or older than 1 year. True pellet ages were unknown, so this test simply asked whether people were consistent with each other in how they aged pellets.

4. Data analysis

We compared among plot types in three ways. First, we used our field data to examine precision and the proportion of plots with no pellets in them. Second, we used analytic techniques based on Taylor regressions for count data (Taylor, 1961) to estimate the sample sizes needed for given levels of precision and to develop stopping rules for sequential counts (Green, 1970). Third, we used the parameters from the Taylor regressions to develop large simulated data sets, then explored the bias and precision resulting from using different sample sizes. The analytic approaches are especially useful for predicting the sample size required for a specified precision, whereas the simulations highlight the variability in bias and precision that still occur for any one realization at an analytically chosen sample size. Randomizations were conducted with PopTools (Hood, 2005) in Excel (MicroSoft, 2003) and statistical analyses were conducted in Statistica (StatSoft, 1995).

5. Analytic approaches

The analytic approaches were based on analyzing the distribution of pellets, using Taylor's Power Law (Taylor, 1961) for negative binomially distributed data:

$$\ln(\text{variance}) = \ln(a) + b \times \ln(\bar{x}) \tag{1}$$

where $\bar{x}$ is the mean pellet count. The variables a and b were then used to evaluate sampling designs. First, we calculated 'stopping lines' (Green, 1970) that indicate for a given number of plots counted how many pellets must have been counted for a specified precision:

$$\ln P_n = \frac{\ln(D^2/a)}{b-2} + \frac{b-1}{b-2} \cdot \ln n \tag{2}$$

where P_n is the cumulative number of pellets counted, n is the number of plots counted, a and b are the constants fitted from the Taylor regression, and D is the desired precision measured as coefficient of variation (CV) (S.E./$\bar{x}$). Second, we estimated how many plots are needed for a given mean density of pellets to obtain a specified level of precision (Chandler and Allsopp, 1995). We calculated these values as:

$$n = \frac{a\bar{x}^{(b-2)}}{D^2} \tag{3}$$

where n, a, b, D, and $\bar{x}$ are as above. Finally, to assess how precision and sampling time interact, we calculated the relative net precision (RNP) following Cho et al. (1995):

$$\text{RNP} = \frac{100}{D \cdot T_s} \tag{4}$$

where D is the CV and T_s is the time required for sampling. Higher values of RNP indicate more efficient sampling.

6. Simulations

We used simulated data sets to address the effects of pellet density, plot type, and sample size on bias, precision, and estimation of the percentage of plots with no pellets in them. We used the Taylor regression equations from our field data to populate six negative binomial data sets with 10,000 values each. To address the effect of pellet density on bias and precision, three data sets were based on the small rectangles, with true mean pellet densities of 0.5, 1.5, and 5 pellets/plot, with variances calculated from the field-based regressions. To address the effect of plot type, the remaining three data sets were at a density of 0.5 pellets per small plot (= 3.2 per large plot), with one data set for each plot type. We performed 1000 simulations for each data set and each sample size (number of plots), with sample sizes ranging from 10 to 200 at 10-plot intervals.

We performed one more set of simulations to examine a management scenario that might occur for identifying snowshoe hare (and possible lynx) habitat. Mills et al. (2005) found that pellet densities of 0.6 and 1.6 per small rectangular plot in western Montana were useful thresholds, as pellet densities <0.6 signified hare densities <0.3 hares/ha, while pellet densities of >1.6 indicated hare densities >0.7 hares/ha; in between, the relationship between hare density and pellet density was too variable for reliable inference about hare density.

In a lynx management context, 0.5 hares/ha has been mentioned as a possible threshold for supporting lynx (Ruggiero et al., 2000), so accurately identifying stands above the 1.6 pellet threshold is a good indication the stand may be important to lynx. We therefore created one final set of simulations to test how sample size affected the performance of the small rectangular plots used in the development of these thresholds. We populated negative binomial data sets with true pellet densities of 0.1, 0.3, . . ., 2.5 per small rectangular plot, then ran 1000 simulations for each sample size (n = 10, 20, . . ., 500) and counted the number of trials in which the observed pellet density was correctly categorized.

7. Results

7.1. Field data

Our sites had a range of pellet densities. On the 1-m^2 circles, mean densities ranged from 0.35 to 44.9 across sites; for the small rectangles, the range was 0.01–10.7 pellets per 0.155 m^2. Across the 80 plots of each type per site sampled across the 13 study sites, circular plots yielded means that were on average 81% of means from rectangular plots of the same area. Large circular plots had means 6-fold higher than the small plots, but were 6.45 times the area, thus yielding means ~93% as large as expected relative to the small circles. In contrast, large rectangular plots had 105% as many pellets as expected from the mean counts on small rectangular plots. Despite these differences, the pellet counts from the four plot types were highly correlated with each other (Table 1).

On average, small rectangles had 62% plots empty, small circles 71%, large rectangles 29%, and large circles 41%. For all plot types, pellet density was highly predictive of the proportion of plots with no pellets (Table 1). Small plots were more likely to have no pellets in them than were large plots, and circles were more likely to have no pellets than were rectangles.

Small plots had higher CVs than large ones and circles had higher CVs than rectangles. On average, CVs of small circles were 142% larger than those of the large circles; CVs of small rectangles were 153% larger than those of the large rectangles. Shape had less effect than size, as small circles had CVs 123% bigger than small rectangles, and large circles had CVs 130% bigger than large rectangles.

Uncleared plots yielded higher counts than did cleared plots, but for all plot types the relationship between cleared and uncleared plots was linear and all r^2 values were above 0.91 (Table 1). For rectangular plots, counts of uncleared plots were on average 1.1-fold higher than cleared plots, whereas for circles uncleared plots were 1.7-fold higher. Both cleared and uncleared plots were highly correlated with snowshoe hare density estimates from mark-recapture data (Mills et al., 2005; Hodges and Mills, unpublished data).

Table 1
Regression summary of the results from our field data of snowshoe hare pellets counted on different plot types in northwestern Montana

Comparison[a]	Regression equation	r^2
Plot size and shape		
Small rectangle vs. small circle	$y = 0.23 + 0.66x$	0.93
Large rectangle vs. large circle	$y = 0.55 + 0.73x$	0.97
Small rectangle vs. large rectangle	$y = 0.78 + 5.63x$	0.98
Small circle vs. large circle	$y = -0.08 + 6.09x$	0.98
Pellet mean vs. % plots empty[b]		
Small rectangle	$y = 0.09 + \exp(-0.15 - 0.41x)$	0.91
Small circle	$y = 0.24 + \exp(-0.38 - 0.35x)$	0.86
Large rectangle	$y = 0.06 + \exp(-0.31 - 0.21x)$	0.84
Large circle	$y = 0.16 + \exp(-0.34 - 0.25x)$	0.82
Cleared vs. uncleared plots		
Small rectangle	$y = -0.24 + 1.33x$	0.94
Small circle	$y = -0.13 + 1.60x$	0.91
Large rectangle	$y = -0.96 + 1.29x$	0.96
Large circle	$y = -0.85 + 1.52x$	0.96

[a] All P were <0.01. The sample size for size vs. shape comparisons and mean vs. % empty was 39 per comparison, and for cleared vs. uncleared plots, 13 per comparison.

[b] In all cases, the negative exponential equation fit significantly better than a linear equation.

People were not consistent at aging pellets of unknown age as >1-year-old or <1-year-old. In 50 trials of 10 pellets each, in no case did all five people age pellets the same. Instead, for 9% of tests, all five people disagreed on how many young versus old pellets were present; in 85% of cases, only two or three people agreed. In only 3% of cases was the disagreement by one pellet, whereas in 40% of cases people diverged by 4–6 pellets out of the 10 pellets in each trial.

7.2. Analytic results

The analytic 'stop lines' (Fig. 1) that result from using the fitted Taylor constants (Table 2) show how many pellets must have been counted cumulatively for a given number of pellet plots to achieve the specified CV. For example, in Fig. 1A, for 50 small rectangular plots achieving 75% precision requires that at least 3 pellets have been counted, whereas 25% precision requires at least 95 pellets. Circles are less precise than rectangles of the same size, and small plots are less precise than large ones. An alternative approach is to ask how many pellet plots are needed to obtain a specified precision at a specified pellet density (Fig. 2). This approach also confirms that far fewer plots are required for higher pellet densities, rectangles outperform circles, and large plots slightly outperform small plots.

7.3. Simulations

Not surprisingly, small sample sizes performed far worse than large ones at consistently coming close to the true mean, having low CVs, and accurately estimating the proportion of plots with no pellets (Fig. 3). In particular, the wide quartile ranges (Fig. 3A) with smaller sample sizes suggest that surveys using lower sample sizes are unlikely to obtain good estimates of pellet density. Similarly, lower sample sizes have lower power because their CVs are much higher (Fig. 3B). Smaller sample sizes also performed more poorly at correctly identifying the proportion of plots that had no pellets (Fig. 3C).

Table 2
Taylor's power law[a] results for snowshoe hare pellet count data from different plot types

Kind of plot	$a \pm$ S.E.	$b \pm$ S.E.	t	P	r^2
Small rectangle (5.08 cm × 305 cm)	4.62 ± 0.25	1.39 ± 0.04	34.2	<0.01	0.97
Small circle (22.2 cm radius)	6.00 ± 0.53	1.51 ± 0.06	23.4	<0.01	0.94
Large rectangle (10 cm × 10 m)	5.92 ± 0.95	1.47 ± 0.07	19.5	<0.01	0.91
Large circle (56.4 cm radius)	6.47 ± 1.05	1.62 ± 0.07	21.3	<0.01	0.94

[a] Taylor's expression is ln(variance) = ln $(a) + b \times$ ln(mean count). T-test values are given for the slope. Small plots are 0.155 m^2 and large plots are 1 m^2.

In the simulations, circles performed worse than rectangles (Table 3). Circles had wider ranges around the true mean and larger CVs than rectangles. Large plots performed slightly better than small ones, mainly because pellet counts were higher because more area was searched. As in Fig. 3, increasing sample size improved all sample statistics (the full simulation results from $n = 10$ to 200 are not shown). The plot types performed comparably at estimating the proportion of plots without any pellets.

In our simulation trials for small rectangular plots of the sample sizes at which pellet densities were accurately placed relative to the thresholds of 0.6 pellets/plot and 1.6 pellets/plot (Mills et al., 2005), we found that the biggest gains in correct categorization occurred in adding samples at the lower sample sizes—the gain in correct inference from 20 to 50 plots, and from 50 to 80 plots, was substantially higher than the gain from counting 200 rather than 100 plots. We also found the unsurprising result that performance at all sample sizes improved when true pellet density was far from the thresholds (Fig. 4). At the very lowest pellet densities (means of 0.1 and 0.3 pellets/plot in our simulations), even sample sizes as low as 20 plots correctly categorized pellet density into the lowest category over 90% of the time. As pellet density increased, sample size had much more impact on correct placement into categories, although no sample sizes performed well when the true pellet density was close to the threshold values of 0.6 or 1.6 pellets/plot.

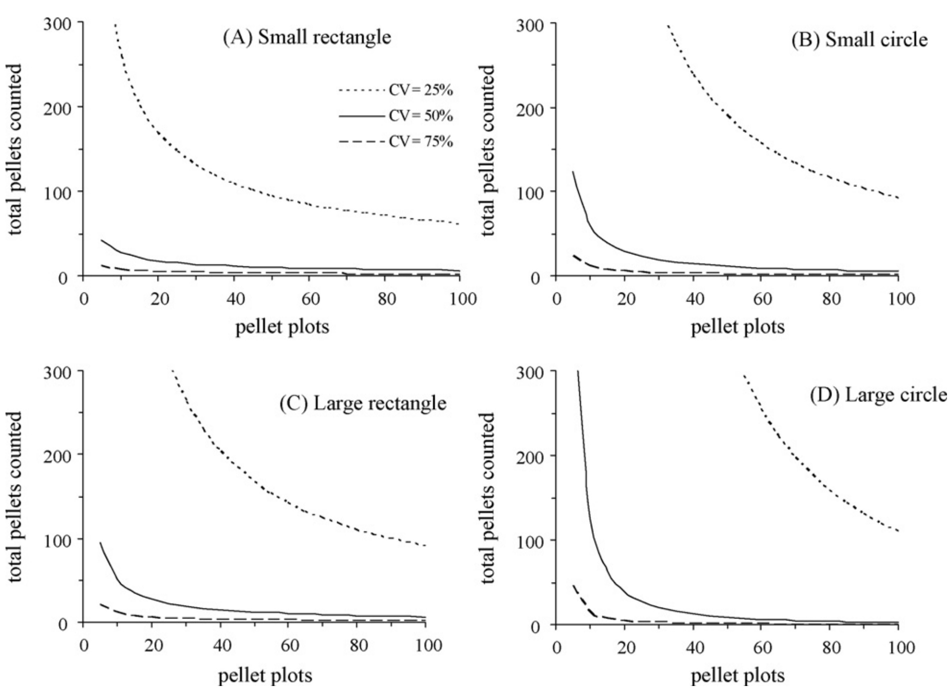

Fig. 1. Stopping lines derived from the Taylor power law relationships. For a given number of plots counted, the lines indicate how many snowshoe hare fecal pellets must have been counted cumulatively to obtain the specified precision (S.E./$\bar{x}$). From top to bottom the lines give precision of 25% (dotted line), 50% (solid line), and 75% (dashed line). The y-axis was truncated at 300; for all plot types with 0.25 precision, cumulative counts >300 are required when fewer plots are counted.

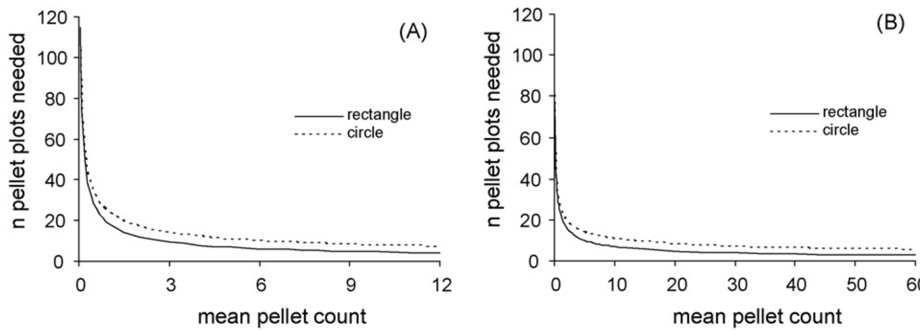

Fig. 2. The number of fecal pellet plots required for the average coefficient of variation (S.E./$\bar{x}$) to be $\leq$50%. The values are derived from our field data for snowshoe hares in Montana, using Eq. (3) and the Taylor coefficients. (A) Small plots and (B) large plots.

7.4. Sampling efficiency

Rectangular plots took more time to count than circular plots (Table 4). Combining CVs and sampling time to yield relative net precision (RNP; Eq. (4)) showed that on a per plot basis the small plots were more efficient than the big plots: the speed with which small plots were counted offset their higher average CV. Similarly, circles had somewhat higher RNP than rectangles, but this difference was small relative to the plot size comparison. The magnitude of difference in RNP was reduced as travel time became a larger proportion of total sampling time. At 45 s of travel between plots, the small rectangles became nearly as efficient as the small circles; at 90 s of travel, the differences in RNP were essentially eliminated among all types.

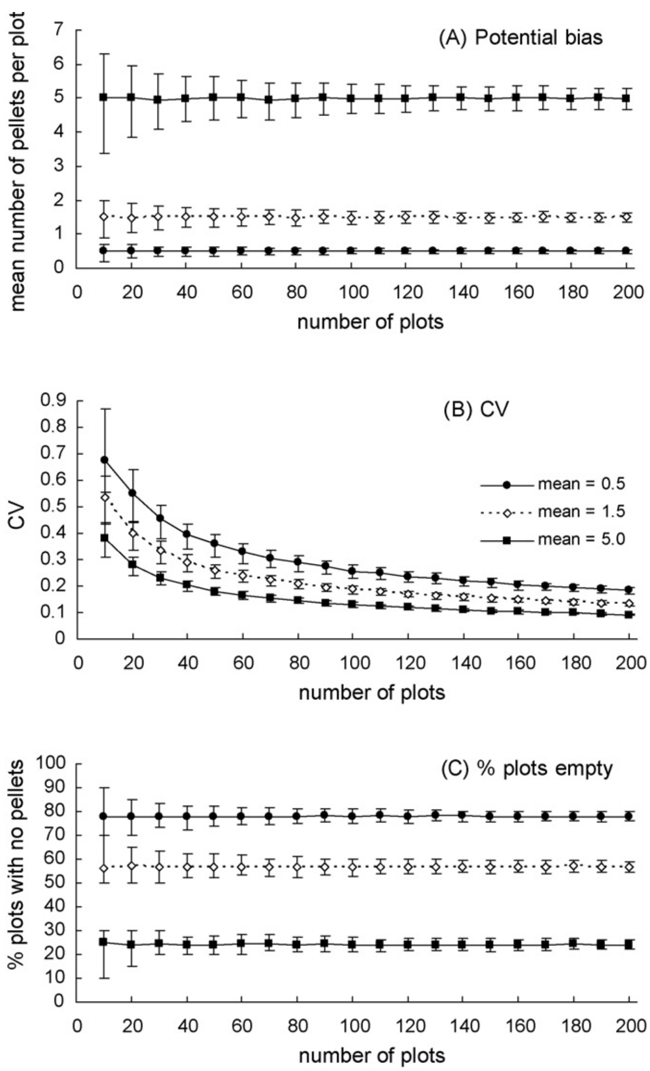

Fig. 3. Simulation results showing the effects of sample size and fecal pellet density on sample statistics. These simulations are for small rectangular plots, with three pellet densities, 0.5, 1.5, and 5.0. Each simulation was run 1000 times. Values are means (points) and quartiles (lines) of the 1000 simulations per sample size. (A) Estimated pellet density. (B) CV. (C) The percentage of plots without any pellets in them.

In Table 5, we address how each plot type would perform while sampling a stand. If one sampled based on the number of plots needed to achieve a 50% CV (i.e. from Eq. (3), as shown in Fig. 1), then different numbers of plots of each type need to be counted. No plot type was consistently the fastest in this exploration: at a low pellet density (0.5 pellets/small plot), surveys with large plots are fastest, but at a high pellet density (5 pellets/small plot), the small plot types are the fastest. If one counted a fixed number of plots instead, the small plot surveys are considerably faster than the large plot surveys. As travel time increases, the proportional difference among types decreases, but small plots retain their speed advantage.

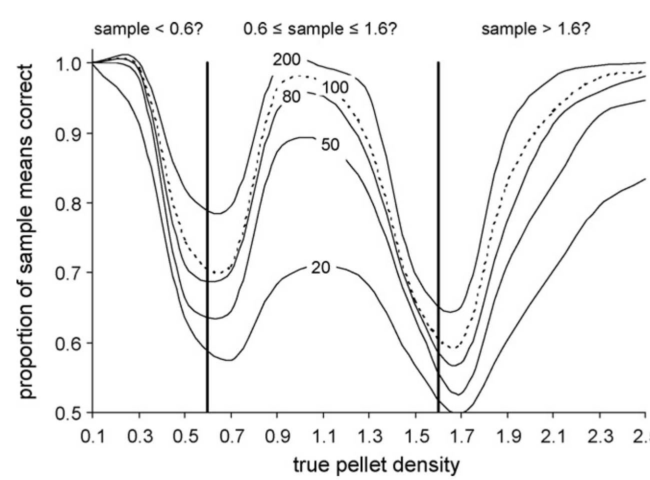

Fig. 4. The ability of different sample sizes of small rectangular plots to provide a sample mean that correctly falls within one of three categories of pellet densities. Mills et al. (2005) found that with this plot type, pellet densities <0.6 signified snowshoe hare densities <0.3 hares/ha, while pellet densities of >1.6 indicated hare densities >0.7 hares/ha; in between, the relationship between hare density and pellet density was too variable for clearly identifying hare density. We simulated data sets with true means of 0.1, 0.3, . . ., 2.5 pellets/plot, then asked what proportion of 1000 samples at each sample size provided sample means that were in the correct category. The text at the top of the figure shows what the sample means were compared to and the vertical lines show the thresholds of 0.6 and 1.6 pellets/plot. The number in each line indicates the sample size of plots.

Table 3
Simulation results for the effect of pellet plot types[a] on sample statistics

	Small rectangle (0.155 m^2)	Small circle (0.155 m^2)	Large rectangle (1 m^2)	Large circle (1 m^2)
20 Plots				
Quartiles of mean	0.30–0.70	0.25–0.70	2.25–3.95	2.15–4.10
Mean CV	0.552	0.577	0.366	0.409
Quartiles of CV	0.441–0.639	0.467–0.677	0.308–0.407	0.344–0.457
Quartiles of % plots with 0 pellets[b]	70.0–85.0	75.0–85.0	40.0–50.0	43.8–60.0
50 Plots				
Quartiles of mean	0.36–0.62	0.34–0.62	2.64–3.80	2.60–3.82
Mean CV	0.359	0.384	0.244	0.272
Quartiles of CV	0.309–0.397	0.327–0.424	0.215–0.264	0.239–0.293
Quartiles of % plots with 0 pellets[b]	74.0–82.0	76.0–84.0	40.0–48.0	46.0–54.0
100 Plots				
Quartiles of mean	0.41–0.59	0.39–0.59	2.88–3.60	2.75–3.62
Mean CV	0.257	0.279	0.175	0.197
Quartiles of CV	0.229–0.279	0.246–0.303	0.159–0.188	0.177–0.212
Quartiles of % plots with 0 pellets[b]	75.0–81.0	77.0–83.0	41.0–48.0	47.0–54.0

[a] In all cases, the true mean density was 0.50 pellets per small plot (= 3.2 pellets per large plot).
[b] The true percentages of plots without any pellets were: small rectangle, 77.9; small circle, 80.0; large rectangle, 44.6; large circle, 50.5.

Table 4
Time needed to count different snowshoe hare pellet plot types and relative net precision

Plot type	Time to count one plot (mean s ± S.E.)	Average CV[a] (S.E./$\bar{x}$)	RNP[b] count only	RNP[b], 45 s travel	RNP[b], 90 s travel
Small rectangle (5.08 × 305 cm)	23.5 ± 1.2	0.359	0.24	0.081	0.049
Small circle (22.2 cm radius)	13.7 ± 0.7	0.384	0.38	0.089	0.050
Large rectangle (10 cm × 10 m)	81.2 ± 3.8	0.244	0.10	0.065	0.048
Large circle (56.4 cm radius)	49.4 ± 2.7	0.272	0.15	0.078	0.053

[a] The average coefficient of variation (CV) was calculated from the simulations for 50 plots.
[b] High values of relative net precision (RNP; Eq. (4)) indicate more efficient sampling. We calculated RNP assuming 50 plots were sampled. We show values for counting time only, or assuming travel times of 45 or 90 s between plots.

8. Discussion

The accuracy and precision of surveys of snowshoe hare pellets on a forest stand depend critically on plot type, pellet density, and sample size. Given the important consequences of pellet surveys for management decisions, especially for conservation related to Canada lynx (e.g. Kloor, 1999), our results suggest that researchers should explicitly address the power of their sampling design for estimating pellet densities correctly. Equations to relate pellet density estimates to hare density are developed in several other papers (Krebs et al., 1987, 2001; Murray et al., 2002; Mills et al., 2005; Homyack et al., 2006; McCann et al., 2008); our work adds to this literature by highlighting ways to improve pellet surveys themselves to ensure the per stand pellet values used to link to hare density are as accurate as possible.

Table 5
Number of samples and sampling time required to achieve a CV (S.E./$\bar{x}$) of 50% for surveys of snowshoe hare pellets at different pellet densities with different plot types

	n plots needed	Area searched (m^2)	Time needed[a] (min)	
			45 s travel	90 s travel
Mean count = 0.5[b]				
Small rectangle	28	4.8	32	53
Small circle	34	4.5	33	59
Large rectangle	13	12	27	37
Large circle	17	17	27	40
Mean count = 1.0[b]				
Small rectangle	19	2.6	22	36
Small circle	24	3.3	23	41
Large rectangle	9	8	19	26
Large circle	13	19	20	30
Mean count = 5.0[b]				
Small rectangle	7	1.1	8	13
Small circle	11	1.9	11	19
Large rectangle	4	5	8	11
Large circle	7	7	11	16
Fixed sampling of 50 plots				
Small rectangle	50	7.8	57	95
Small circle	50	7.8	49	86
Large rectangle	50	50	105	143
Large circle	50	50	79	116

[a] The time needed is calculated from seconds needed per plot type (Table 3) and assuming either 45 or 90 s of travel time between plots.
[b] The 'mean count' is per small plot; we multiplied by 6.45 to get the comparable mean count per large plot.

Plot type affects the estimates of pellet density. Our field data confirmed several previous studies that also found that different plot types yield different estimates of pellet density on the same study sites (McKelvey et al., 2002; Murray et al., 2002). It is unknown which plot type yields the estimate closest to true pellet density. The plot types may differ in their pellet density estimates because of inclusion bias (falsely counting pellets on the edges of plots) or undercounting bias (missing pellets in a plot) (McKelvey et al., 2002; Murray et al., 2002). We suspect these mechanisms are inadequate to fully explain the differences. On some of our study areas, inclusion bias would require falsely including dozens to several hundred pellets, while undercounting large circles would require missing hundreds of pellets in the 80-plot surveys we did (on one site, >1200 pellets would have to be missed).

We suspect that 'habitat bias' also occurs, i.e. that different plot types sample genuinely different areas of the forest floor. The 1-m^2 circle has a 113 cm diameter, so it may not be able to sample under elevated downed wood, along the edge of large trees, or in thickets, whereas thin rectangles may have a greater ability to sample in these areas. Because pellets are not randomly distributed, as snowshoe hares prefer some microhabitats over others while foraging (hares typically defecate while foraging, not while resting, Hodges, 1999), plot types may vary in their ability to sample the complete distribution of hare pellets. It is not clear from the literature if researchers have made the same decisions with respect to whether to count plots regardless of debris or tree stems or to move plots to nearby areas of forest floor. Nor is it clear if western coniferous forests and eastern mixed deciduous-coniferous forests exhibit similar habitat bias. Further work could examine the effect of such decision rules on estimates of pellet density by the different plot types.

The simulations showed that circles generally performed worse than rectangles of the same size, with circular plots both more likely to be far from the true mean and having worse precision. Large plots slightly outperformed small plots. These patterns occurred primarily because large plots and rectangular plots had higher means than small plots and circular plots. Because precision is weighted by the mean, plots that provide higher counts had lower CVs. The relative net precision analysis showed that travel time between plots had a large impact on how different the plot types were when sampling a stand; this result suggests that in stands with very high travel times using larger but fewer plots might be more cost-effective.

Unsurprisingly, small sample sizes performed worse than large sample sizes. Small sample sizes were more likely to be biased (i.e. larger quartiles of sample means), had larger CVs, were worse at estimating the true proportion of plots with no pellets, and were more likely to miscategorize a sample into one of three pellet density categories relevant to lynx management in the west ($\bar{x} < 0.6$, $0.6 \le \bar{x} \le 1.6$, $\bar{x} > 1.6$ per small rectangular plot). The biggest gains in performance occurred in increasing sample sizes from 20 to 50 s and again up to about 100; gains from increasing sampling above 100 plots were modest.

The stop line and specified precision techniques offer ways for researchers who know the mean–variance relationships for pellet plots in their study area to assess different strategies for sampling. However, our simulations highlighted the inherent variability of sampling, such that any one sample was unlikely to achieve the target precision. Additionally, although the analytic approaches to sample size determination suggest that good precision can occur at fairly small sample sizes, we strongly recommend avoiding small sample sizes because the danger of obtaining a poor estimate of the true pellet density is highest for low sample sizes. In this regard, small pellet plots are also advantageous over large ones, because for the same sampling effort more small plots can be counted.

The problem of whether to clear plots or count uncleared plots is an interesting one. From a statistical standpoint, uncleared plots have the nice property of having slightly higher counts, thus needing smaller sample sizes for good estimation of the true density of pellets. They also offer a substantial gain in field efficiency, because no permanent markers are needed and the first year of data can be used. Their major drawback is in the problem of interpreting what timeframe is sampled by uncleared plots, especially in regions with strong differential decomposition of pellets. Our test of how often observers agreed on aging pellets of unknown pellets agreed with earlier work (on pellets of known age, Prugh and Krebs, 2004): pellets cannot be reliably separated into age classifications. Despite these concerns, counts from cleared and uncleared plots are typically highly correlated, suggesting that either can be used with the choice dependent on the exact research question and the caveat that separate regression equations relating pellet densities to hare densities should be developed for cleared and uncleared plots (Mills et al., 2005).

8.1. Recommendations for pellet sampling

The most critical step is to decide whether the research questions are amenable to the use of pellet plots, or whether it would be better to employ more rigorous methodologies (i.e. mark-recapture techniques). If pellet counts are employed, some researchers may address questions in which greater replication across stands is preferred over high per-stand accuracy and precision. The analytic approaches we have outlined can inform the design of a pellet-based study by projecting accuracy and precision per stand for a given sample size and plot type. Below, we also outline our specific rule-of-thumb recommendations for studies using pellet plots, based on the assumption that high accuracy and good precision are desired on a per-stand basis.

(A) The small rectangles and 1-m^2 circles are both acceptable and outperformed the other plot types in our analysis; for new studies, we recommend the small rectangles because they appear to perform better in predicting snowshoe hare densities (Murray et al., 2002; Mills et al., 2005), as well as enabling higher precision and perhaps less bias for the same sampling effort. If, however, an established study is based on the 1-m^2 circles, we do not recommend switching plot types.

(B) Sample sizes of small rectangles or 1-m^2 circles should be in the range of 50–100 per stand. Smaller sample sizes run into serious problems with poor estimates of pellet density and poor precision. Sample sizes above about 100 yield decreasing returns in increased precision and accuracy. Researchers can improve the value of their pellet surveys by providing estimates of power for their pellet surveys to address the particular questions of interest; our simulations show several ways for doing so.

(C) We do not recommend using the percentage of plots with pellets as an index rather than mean pellet count. The proportion with pellets did not perform substantially better than the mean, nor is its relationship to hare density estimates well established.

(D) Uncleared plots cannot be converted to cleared plots by removing ‘old’ pellets, because people cannot consistently estimate the age of pellets. Despite this inability to age pellets, uncleared plots can be useful indicators of relative abundance of snowshoe hares, but estimates are usually higher than cleared plots. In cases where areas are simply being screened for relative hare abundance, uncleared plots may be sufficient. In cases where pellet plots are being used for time series, cleared plots are preferable (Prugh and Krebs, 2004).

These recommendations are likely applicable broadly across the range of snowshoe hares for five main reasons. First, our simulated results tested values of the parameter *b* (the slope of the Taylor regression of variance on mean) from 1.39 to 1.62. In all cases, low sample sizes (20s to 50s) performed fairly badly at our tests of accuracy, precision, and discrimination relative to the threshold values relating to hare density estimates. If the variance–mean slope is higher, then even higher sample sizes will be needed for adequate estimation. This relationship is clearly affected by plot type, but we sampled across a wide range of pellet densities and stand types. We do not expect that other researchers would find substantially more variance than we did, especially since the majority of other plot sizes in the literature are larger, which would tend towards lower variance–mean relationships.

Second, we sampled a wide range of pellet densities (~0.35–45 pellets/1 m^2 circle). Our highest sites had higher densities of pellets than have been recently observed in British Columbia (Sullivan et al., 2006), Idaho (Murray et al., 2002; McKelvey et al., 2002), elsewhere in Montana (Malloy, 2000; McKelvey et al., 2002; Ausband and Baty, 2005), Minnesota (McCann et al., 2008), Quebec (de Bellefeuille et al., 2001; Potvin et al., 2005), Labrador (Newbury and Simon, 2005) and Maine (Homyack et al., 2006). In contrast, higher pellet densities have been observed in Alaska (Prugh and Krebs, 2004) and the Yukon (Krebs et al., 2001), so our results should be interpreted with caution in these far northern areas with higher hare and pellet densities.

Third, it is a well-known property of binomially distributed data that variance will be reduced by plots that have higher edge to area ratios; that will hold true across the range of hares. Fourth, we expect that the distribution of snowshoe hare pellets across a forest floor is guided by consistent behavioural patterns in different regions, leading to similar distributions (but not absolute abundance) of pellets among regions. Habitat and foraging studies on snowshoe hares have shown broad agreement across a wide range of forest types in terms of the structural elements hares use (reviewed in Hodges, 2000a,b). We therefore expect that the range of Taylor law results we found will be similar to those derived from other regions. Fifth, studies in other regions that used these plot types observed similar patterns in relation to mean densities and variances among plot types (McKelvey et al., 2002; Murray et al., 2002).

Our results differ slightly from previous recommendations about plot types. Both McKelvey et al. (2002) and Murray et al. (2002) recommended using 1-m^2 circles over the 0.155-m^2 rectangles, based largely on ease for field crews and concerns about inclusion bias. In contrast to their recommendations, we found that the small increase in precision that large circles afford over small rectangles is offset by their increased survey time and area, as well as concerns about habitat bias. Furthermore, the relationship between pellet counts and snowshoe hare density estimated from live-trapping is better established for the small rectangular plots than for the circles (Krebs et al., 1987, 2001; Murray et al., 2002; Mills et al., 2005).

9. Conclusions

Although this paper focuses on choosing an appropriate sample size for a given plot type when designing a pellet plot survey for snowshoe hares, the deeper issue is the relationship between pellet counts and snowshoe hare densities. Although the relationship between pellets and hare densities is reasonably consistent through time and across space (Krebs et al., 1987, 2001; Murray et al., 2002; Homyack et al., 2006; McCann et al., 2008), questions that require rigorous evaluation of hare densities across time or space should rely on mark-recapture studies (Mills et al., 2005). Pellet counts appear to be useful as a coarse-filter approach distinguishing low from high hare densities, but should not be relied upon for studies requiring detailed information.

Our results and approach are also broadly applicable to pellet counts for other species, and even to other count-based index methods. Specifically, plot sizes and shapes may yield different estimates of the mean density of pellets, and inferential power per sampled area will be related to sample size of plots, the density of pellets, and the type of plot used. For snowshoe hares, each pellet is counted; additional complexities will arise for species where pellet groups are counted (e.g. for ungulates). Given the variability in bias and precision we observed, we recommend that researchers explicitly address the power of their surveys to detect relevant differences in pellet density among stand types, years, or regions.

Acknowledgments

Primary funding was obtained from the USFS Rocky Mountain Research Station. L.S.M. also acknowledges support from NSF DEB-9870654. This work benefited from conversations with L. Ruggiero and P. Griffin. E. Sutherland, A. Jacobs, N. Rhodes, and E. Lieser provided support in Tally Lake Ranger District. Numerous field assistants cheerfully counted the 12,480 plots and 60,036 pellets that form the data set. The manuscript benefited from comments by C.J. Krebs, K. McKelvey, L. Prugh, and two anonymous reviewers.

References

Anderson, D.R., 2001. The need to get the basics right in wildlife field studies. Wildl. Soc. Bull. 29, 1294–1297.
Anderson, D.R., 2003. Response to Engeman: index values rarely constitute reliable information. Wildl. Soc. Bull. 31, 288–291.
Ausband, D.E., Baty, G.R., 2005. Effects of precommercial thinning on snowshoe hare habitat use during winter in low-elevation montane forests. Can. J. For. Res. 35, 206–210.
Bailey, L.L., Simons, T.R., Pollock, K.H., 2004. Estimating site occupancy and species detection probability parameters for terrestrial salamanders. Ecol. Appl. 14, 692–702.
Campbell, D., Swanson, G.M., Sales, J., 2004. Comparing the precision and cost-effectiveness of faecal pellet group count methods. J. Appl. Ecol. 41, 1185–1196.
Chandler, K.J., Allsopp, P.G., 1995. Sampling adults of *Eoscarta carnifex* (Hemiptera: Cercopidae) and their associated symptoms on sugarcane. J. Econ. Entomol. 88, 1301–1306.
Cho, K., Eckel, C.S., Walgenbach, J.F., Kennedy, G.G., 1995. Spatial distribution and sampling procedures for *Frankliniella* spp. (Thysanoptera: Thripidae) in staked tomato. J. Econ. Entomol. 88, 1658–1665.
Darveau, M., Huot, J., Belanger, L., 1998. Riparian forest strips as habitat for snowshoe hare in a boreal balsam fir forest. Can. J. For. Res. 28, 1494–1500.
de Bellefeuille, S., Belanger, L., Huot, J., Cimon, A., 2001. Clear-cutting and regeneration practices in Quebec boreal balsam fir forest: effects on snowshoe hare. Can. J. For. Res. 31, 41–51.
Forys, E.A., Humphrey, S.R., 1997. Comparison of 2 methods to estimate density of an endangered lagomorph. J. Wildl. Manage 61, 86–92.
Fuller, A.K., Harrison, D.J., Vashon, J.H., 2007. Winter habitat selection by Canada Lynx in Maine: prey abundance or accessibility? J. Wildl. Manage. 71, 1980–1986.
Fuller, T.K., Heisey, D.M., 1986. Density-related changes in winter distribution of snowshoe hares in north-central Minnesota. J. Wildl. Manage. 50, 261–264.
Green, R.H., 1970. On fixed precision level sequential sampling. Res. Popul. Ecol. 12, 249–251.
Griffin, P.C., Mills, L.S., 2007. Precommercial thinning reduces snowshoe hare abundance in the short term. J. Wildl. Manage. 71, 559–564.
Hodges, K.E., 1999. Proximate factors affecting snowshoe hare movements during a cyclic population low phase. Ecoscience 6, 487–496.
Hodges, K.E., 2000a. The ecology of snowshoe hares in Northern Boreal Forests. In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Koehler, G.M., Krebs, C.J., McKelvey, K.S., Squires, J.R. (Eds.), Ecology and Conservation of Lynx in the United States. University Press of Colorado, Colorado, pp. 117–162.
Hodges, K.E., 2000b. Ecology of snowshoe hares in Southern Boreal and Montane Forests. In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Koehler, G.M., Krebs, C.J., McKelvey, K.S., Squires, J.R. (Eds.), Ecology and Conservation of Lynx in the United States. University Press of Colorado, Colorado, pp. 163–206.
Homyack, J.A., Harrison, D.J., Krohn, W.B., 2007. Effects of precommercial thinning on snowshoe hares in Maine. J. Wildl. Manage. 71, 4–13.
Homyack, J.A., Harrison, D.J., Litvaitis, J.A., Krohn, W.B., 2006. Quantifying densities of snowshoe hares in Maine using pellet plots. Wildl. Soc. Bull. 34, 74–80.
Hood, G. M., 2005. PopTools version 2.7.1. Available at http://www.cse.csiro.au/poptools.
Kloor, K., 1999. Conservation biology—Lynx and biologists try to recover after disastrous start. Science 285, 320–321.
Krebs, C.J., Gilbert, B.S., Boutin, S., Boonstra, R., 1987. Estimation of snowshoe hare population density from turd transects. Can. J. Zool. 65, 565–567.
Krebs, C.J., Boonstra, R., Nams, V., O'Donoghue, M., Hodges, K.E., Boutin, S., 2001. Estimation of snowshoe hare population density from pellet plots—a further evaluation. Can. J. Zool. 79, 1–4.
Langbein, J., Hutchings, M.R., Harris, S., Stoate, C., Tapper, S.C., Wray, S., 1999. Techniques for assessing the abundance of brown hares, *Lepus europaeus*. Mamm. Rev. 29, 93–116.
Malloy, J.C., 2000. Snowshoe hare, *Lepus americanus*, fecal pellet fluctuations in western Montana. Can. Field Nat. 114, 409–412.
Massei, G., Bacon, P., Genov, P.V., 1998. Fallow deer and wild boar pellet group disappearance in a Mediterranean area. J. Wildl. Manage. 62, 1086–1094.
McCann, N.P., Moen, R.A., Niemi, G.J., 2008. Using pellet counts to estimate snowshoe hare numbers in Minnesota. J. Wildl. Manage. 72, 955–958.
McKelvey, K.S., McDaniel, G.W., Mills, L.S., Griffin, P.C., 2002. Effects of plot size and shape on pellet density estimates for snowshoe hares. Wildl. Soc. Bull. 30, 751–755.
McKelvey, K.S., Pearson, D.E., 2001. Population estimation with sparse data: the role of estimators versus indices revisited. Can. J. Zool. 79, 1754–1765.
MicroSoft Inc., 2003. Microsoft Office Professional Edition.
Mills, L.S., Griffin, P.G., Hodges, K.E., McKelvey, K., Ruggiero, L., Henderson, C., Ulizio, T., 2005. Pellet count indices compared to mark-recapture estimates for evaluating snowshoe hare density. J. Wildl. Manage. 69, 1053–1062.
Murray, D.L., Ellsworth, E., Zack, A., 2005. Assessment of potential bias with snowshoe hare fecal pellet-plot counts. J. Wildl. Manage. 69, 385–395.

Murray, D.L., Roth, J.D., Ellsworth, E., Wirsing, A.J., Steury, T.D., 2002. Estimating low-density snowshoe hare populations using fecal pellet counts. Can. J. Zool. 80, 771–781.
Newbury, T.L., Simon, N.P.P., 2005. The effects of clearcutting on snowshoe hare (*Lepus americanus*) relative abundance in central Labrador. For. Ecol. Manage. 210, 131–142.
Potvin, F., Breton, L., Courtois, R., 2005. Response of beaver, moose, and snowshoe hare to clear-cutting in a Quebec boreal forest: a reassessment 10 years after cut. Can. J. For. Res. 35, 151–160.
Prugh, L.R., Krebs, C.J., 2004. Snowshoe hare pellet-decay rates and aging in different habitats. Wildl. Soc. Bull. 32, 386–393.
Roppe, J.A., Hein, D., 1978. Effects of fire on wildlife in a lodgepole pine forest. Southwest. Nat. 23, 279–288.
Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Koehler, G.M., Krebs, C.J., McKelvey, K.S., Squires, J.R., 2000. The scientific basis for lynx conservation: qualified insights. In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Koehler, G.M., Krebs, C.J., McKelvey, K.S., Squires, J.R. (Eds.), Ecology and Conservation of Lynx in the United States. University Press of Colorado, Colorado, pp. 443–454.
StatSoft Inc., 1995. Statistica for Windows, Version 5. Tulsa, Oklahoma, USA.
Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., Boateng, J.O., 2002. Influence of conventional and chemical thinning on stand structure and diversity of plant and mammal communities in young lodgepole pine forest. For. Ecol. Manage. 170, 173–187.
Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., Ransome, D.B., 2006. Influence of repeated fertilization on forest ecosystems: relative habitat use by snowshoe hares (*Lepus americanus*). Can. J. For. Res. 36, 2080–2089.
Taylor, L.R., 1961. Aggregation, variance and the mean. Nature 189, 732–735.
USFWS (U.S. Fish and Wildlife Service), 2000. Determination of threatened status for the contiguous U.S. distinct population segment of the Canada Lynx and related rule. Federal Register 65, pp. 16052–16086.
Vernes, K., 1999. Pellet counts to estimate density of a rainforest kangaroo. Wildl. Soc. Bull. 27, 991–996.
Walsh, P.D., White, L.J.T., Mbina, C., Idiata, D., Mihindou, Y., Maisels, F., Thibault, M., 2001. Estimates of forest elephant abundance: projecting the relationship between precision and effort. J. Appl. Ecol. 38, 217–228.