Estimating low-density snowshoe hare populations using fecal pellet counts

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Abstract: Snowshoe hare (*Lepus americanus*) populations found at high densities can be estimated using fecal pellet densities on rectangular plots, but this method has yet to be evaluated for low-density populations. We further tested the use of fecal pellet plots for estimating hare populations by correlating pellet densities with estimated hare numbers on 12 intensive study areas in Idaho; pellet counts from extensive transects (n = 615) across northern Idaho enabled rectangular plots (0.155 m^2) to be compared with paired small (0.155 m^2) and large (1 m^2) circular plots (metre-circle plots). Metre-circle plots had higher pellet prevalence, lower sample variance, and lower estimates of pellet density than the other plot types. Transects comprising circular plots required less establishment time, and observer training reduced the pellet-count bias attributable to plot shape. The number of hares occupying intensive study sites was correlated with pellet density on all plot types, but rectangular plots provided a slightly closer linear fit to hare numbers than did metre-circle plots. The relationship between pellet density and hare number may have been curvilinear rather than linear, but linear and nonlinear models provided similar numerical estimates over much of the range of pellet densities. These results indicate that pellet counts are a robust estimator of hare numbers in low-density populations, and that metre-circle plots represent an improvement over standard rectangular plots in terms of unbiased pellet counts, sacrificing little predictive power. We recommend using pellet counts in metre-circle plots for estimating populations of snowshoe hares in their southern distribution.

Résumé : On peut évaluer les populations de lièvres d'Amérique (*Lepus americanus*) de forte densité à partir de la densité des défécations sur des aires d'échantillonnage rectangulaires, mais la méthode n'a pas encore été validée chez des populations de faible densité. Nous avons aussi éprouvé la méthode en établissant des corrélations entre la densité des défécations et le nombre estimé de lièvres dans 12 régions d'étude intensive en Idaho; des décomptes de défécations sur de nombreux (n = 615) transects dans le nord de l'Idaho ont permis de comparer les résultats obtenus sur des surfaces rectangulaires (0,155 m^2) et sur de petites (0,155 m^2) et grandes (1 m^2) aires circulaires. Les plus grandes aires circulaires ont une fréquence plus élevée de défécations, une variance d'échantillon plus faible et des estimations plus faibles de la densité des défécations que les autres aires. Les transects formés d'aires circulaires requièrent moins de temps d'installation et un entraînement des observateurs réduit les erreurs d'estimation de la densité des défécations reliées à la forme de l'aire d'échantillonnage. Le nombre de lièvres sur les sites d'étude intensive est en corrélation avec la densité des défécations sur tous les types d'aires d'échantillonnage, mais l'ajustement linéaire de la courbe est meilleur pour les aires rectangulaires que pour les aires circulaires de 1 m^2. La relation entre la densité des défécations et le nombre de lièvres est peut-être de type exponentiel plutôt que linéaire, mais les modèles linéaires et non linéaires génèrent des estimations numériques similaires sur presque toute l'étendue des densités de défécations. Les décomptes de défécations s'avèrent donc être des méthodes robustes d'estimation des densités de populations de lièvres de faible densité et les aires d'échantillonnage de 1 m^2 produisent moins d'erreurs d'estimation que les aires rectangulaires habituelles, sans pour autant diminuer de beaucoup le pouvoir de prédiction. Nous recommandons donc l'utilisation des décomptes de défécations sur des aires circulaires de 1 m^2 pour estimer les densités des populations de lièvres dans la partie sud de leur aire de répartition.

[Traduit par la Rédaction]

Introduction

The snowshoe hare (*Lepus americanus*) is an important herbivore in the boreal forests of North America. In the southern portion of its range (southern Canada and the northern U.S.A.), limited field data suggest that snowshoe hare populations do not undergo their characteristic 10-year cycles, but experience more stable dynamics at notably lower

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population densities (Keith 1990; Murray 2000). Yet the general demographic attributes and habitat requirements of southern snowshoe hare populations are poorly understood relative to those of their northern counterparts, and to address this deficiency, research efforts at lower latitudes should include long-term hare population monitoring over a broad geographic scale (Murray 2003).

Estimating population densities of free-ranging mammals typically involves mark–recapture procedures, which are both labor-intensive and costly, and thus tend not to be applied at the landscape level. For snowshoe hares, counts of fecal pellets have proved to be a viable alternative method with demonstrated accuracy and precision (Krebs et al. 1987, 2001). This technique relies upon annual pellet counts on pre-established transects, where the number of pellets accumulated during 1 year corresponds well to the number of hares residing in the study area. Although only validated for Yukon study sites where hare densities tend to be high and fluctuate dramatically, this method has been used to assess hare abundance elsewhere across the northern boreal forest (e.g., Poole 1995; Slough and Mowat 1996). In a recent re-evaluation of the pellet-plot method, Krebs et al. (2001) cautioned that the existing regression equation characterizing pellet density and hare numbers may not hold for other areas of the hare's distribution, particularly the southern boreal and montane forests of the western U.S.A. Indeed, across herbivore taxa, pellet loss or decomposition rates are known to vary with habitat, while defecation rates themselves can differ according to habitat, diet, and population age structure (Rogers et al. 1958; Cochran and Stains 1961; Smith 1964; Angerbjörn 1983). Because snowshoe hare diet and habitat use appear to differ fundamentally across the species' range (Hodges 2000; Murray 2003), the relationship between pellet count and hare abundance could vary regionally.

The optimal size and shape of pellet plots should be related to pellet density, pellet detectability, plot establishment and sampling ease, potential sampling bias, and sample variance. Krebs et al. (1987, 2001) used long (5.08 × 305 cm) rectangular plots to monitor pellet accumulation, reporting that these dimensions provide lower variance than plots of other shapes or sizes. This finding allegedly is due to the clumped distribution of pellets and the likelihood that a long thin plot is more likely to intercept a patch of pellets, but a smaller percentage of those pellets actually should fall within the plot (Krebs 1999). However, plots with these dimensions necessarily have a high perimeter:area ratio, which could lead to sampling bias when observers must decide whether or not to include pellets found along the edge of the plot. Such problems often produce a positive bias because eager researchers prefer to include rather than ignore data (Krebs 1999); this factor may be particularly important in areas of low hare (and pellet) density, where inappropriate inclusion of even a modest number of pellets through observer bias could have a substantial impact on pellet counts and thus on hare population estimates. In theory, use of a larger plot with a lower perimeter:area ratio should increase the likelihood of finding pellets while reducing potential observer bias; yet such a plot type might not be optimal if the clumped pattern of pellets results in high sample variance (see Krebs 1999) if pellet densities are biased low because of reduced detection rates (see Neff 1968; Smith 1968), or if plot establishment or counting times are substantially longer because of the larger sampling area (see Smith 1968).

The generally low density and patchy distribution of snowshoe hares and their pellets in the southern part of their range necessitates further testing of the pellet-plot method for estimating hare numbers. Accordingly, the objectives of the present study were to (*i*) evaluate the optimal size and shape of plots used for hare pellet counts among low-density hare populations along their southern range, and (*ii*) examine the relationship between pellet count and hare abundance for such low-density populations. We predicted that large (1 m^2) circular plots would provide more representative samples of actual hare pellet densities (i.e., higher pellet prevalence, lower variance, lower observer bias) than would standard rectangular (0.155 m^2) plots, owing to a larger area and a lower perimeter:area ratio. Pellet numbers from these larger plots also should correspond well to known hare numbers on sites where population size is known from mark–recapture efforts. Finally, we predicted that circular plots would be less time-consuming to establish and recheck than standard rectangular plots, a finding that could be relevant to studies of southern hare populations, given their low density and patchy distribution, and thus the need to sample hare habitat both intensively and extensively to obtain representative samples.

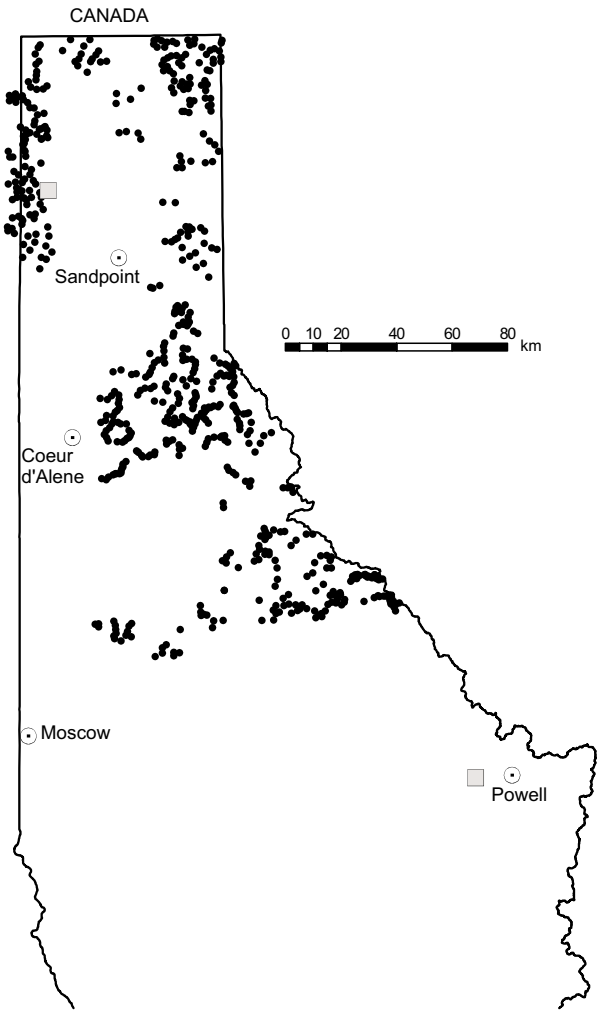
Materials and methods

Pellet transect establishment and plot counts

We established 615 pellet transects between June and October of 1999 across the Idaho Panhandle National Forest (IPNF; 49°N, 117° to 47°N, 115°W; Fig. 1). The eventual goal of this effort will be to evaluate hare habitat suitability extensively across forest types and stand-management practices, and this necessitated the present assessment of the linkage between pellet counts recorded on transects and hare numbers. Pellet counts have been used previously for hare habitat analysis (e.g., Orr and Dodds 1982; Wolfe et al. 1982; Koehler 1990; Murray et al. 1994), but in studies in which pellet counts were converted to hare densities, Krebs et al.'s (1987) algorithm was used without further testing of the relationship between pellet density and hare number.

Transects were placed throughout the IPNF (see Fig. 1), roughly perpendicular to existing roadways and spaced at least 1 km apart. Transect locations were chosen by U.S. Forest Service personnel using existing GIS databases to reflect the variety of stand types and management practices occurring in the forest, and therefore did not necessarily represent a random sample of available hare habitat. Transect-point selection involved identifying relevant stand characteristics (forest type, size class, thinning activity, and habitat-type classification) that provided a range of forest types potentially available to hares on the IPNF. Each transect contained 10 plot locations arranged in a single line with 30-m spacing. At each plot location, two plot types were established 10 m apart: one rectangular (5.08 × 305 cm) quadrat similar to those used previously by Krebs et al. (1987, 2001) and a circular plot of the same area (0.155 m^2) with a concentric 1-m^2 circular plot (hereinafter metre-circle plot) around it. This configuration effectively resulted in two parallel paired sets of plot types for each transect. Rectangular plots were marked using wooden stakes at each end and the plot periph-

Fig. 1. Locations of 615 fecal-pellet transects (●) for snowshoe hares (*Lepus americanus*) in the Idaho Panhandle National Forest. Each transect contained 10 rectangular and 10 circular plots. The shaded squares indicate locations of areas in which snowshoe hare populations were estimated (six study areas for each site).



ery was delineated during counts by placing a cord around both stakes; circular plots were marked with a metal reinforcing bar stake in the center of the circle and counts were conducted by rotating a string marked with the appropriate radius around the stake. Transects were cleared and pellets counted in May–October 1999 and pellets were counted again in May–September 2000 to determine yearly pellet accumulation. Transects were visited in roughly the same sequence each year, although 39 of the 615 transects were not revisited in 2000 because of road closures, flooding, inability to relocate the transect starting point, etc. From the time that a transect was cleared of pellets in 1999 and rechecked in 2000, 323 ± 37 (mean ± SD) days (n = 567 transects) elapsed.

Pellet decomposition rates

Rates of decomposition of snowshoe hare pellets are unknown, but rates can vary with habitat in kangaroos (Vernes 1999), ungulates (Harestad and Bunnell 1987; Lehmkuhl et al. 1994; Massei et al. 1998; Vernes 1999), and possibly mountain hares (*Lepus timidus*) (Angerbjörn 1983). Thus, pellet numbers on uncleared transects in 1999 may not reflect absolute or even relative hare abundance. Yet when comparing the effect of plot size and shape on pellet counts, pairing plot types spatially allowed us to use pellet densities to evaluate optimal plot shape/size. The rate of pellet decomposition was determined by collecting fresh pellets from traps containing recently captured hares (see below), freezing the pellets, and later scattering them in 18 circular plots (1 m^2) placed in recent clearcuts (n = 9) and mature forest (n = 9). Because the size and consistency of pellets produced by hares vary with seasonal changes in diet, we placed in each plot a mixture of 10 pellets produced in winter, 10 pellets produced by adult hares during summer, and 10 pellets produced by juvenile hares (i.e., <3 months old) during summer. We then counted the pellets that remained in each plot after 1 year to estimate natural pellet decomposition rates in habitat characteristic of northern Idaho. Each plot was separated by a minimum of 200 m, and the disparity in habitats chosen for such plots enabled us to evaluate the effect of sunlight and exposure on pellet degradation. Because degradation plots were placed in a region of the forest known for its low hare densities (i.e., <0.3/ha), we assumed that pellets found in plots after 1 year remained from our experiment and had not been deposited by free-ranging hares.

Transect establishment and rechecking time

During 1999, transect establishment time was determined for a sample of 10 transects containing only rectangular plots and 10 transects containing only circular plots. Establishment time included time required to measure and delineate plots as well as to count and remove pellets from plots. During 2000, we recorded time required by observers to count and remove pellets on a sample of 20 transects that had been established during the previous year. Reported times for circular plots included the time required to establish/recheck both the small and large circular plots, and therefore such counts overestimated to a degree the time required to establish/recheck metre-circle plots. To minimize individual bias we used a single pair of well-trained observers to measure transect establishment and rechecking times.

Hare population estimation

Snowshoe hare numbers were estimated on twelve 10-ha study areas during intensive studies of hare demography (Wirsing et al. 2002; E. Ellsworth, unpublished data). Six areas were established on the Clearwater National Forest (CNF; 46°N, 114°W), while the remaining six were on the IPNF (48°N, 116°W). Most of the study areas consisted of small patches of 15- to 25-year-old stands with grand fir (*Abies grandis*), Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), western red-cedar (*Thuja plicata*), and western larch (*Larix occidentalis*) as the predominant tree species (moderate to high hare numbers); a few areas were composed of more mature pine/fir forest with low understory cover (low hare numbers). Pellet transects were established in fall 1998 and fall 1999 on the CNF and IPNF sites, respectively. On each study area we placed 5 parallel transects comprising 10 sets of rectangular and small circle / metre-circle plots; plots were positioned on each transect according

to the above protocol, with each transect separated by 60–70 m. Pellet counts on intensive-study areas were made exclusively by three observers who had been trained extensively in the unbiased collection of fecal pellets according to plot shape. The sampling intensity characterizing our study areas (50 plots per study area; 5 plots/ha) exceeded that used to validate pellet counts on Yukon sites (Krebs et al. 1987, 2001). We counted all hare pellets on CNF study areas during fall 1999 and fall 2000 and on IPNF sites during fall 2000 and fall 2001, providing a total sample of 24 fecal pellet – hare density measures for statistical analysis.

We livetrapped (Tomahawk Live Trap Co., Tomahawk, Wis., U.S.A.) hares on each study area for 7–10 consecutive days during each season. Captured hares were handled in accordance with standard guidelines (Canadian Council on Animal Care 1984; University of Idaho Animal Care and Use Committee protocol No. 1999-22); each captured animal was identified by numbered fingerling tags attached to the interdigital web of hind feet (Keith et al. 1968). Between 80 and 90% of all captured animals weighing >700 g also received a mortality-sensitive radio collar (Telemetry Solutions Inc., Concord, Calif., U.S.A.), and survival was monitored daily with transmitters from dead hares redeployed on new individuals during subsequent trapping periods. Radio-collared hares were located via telemetry 1–3 days prior to each trapping period and classified as being either on, near (<200 m), or off (>200 m) the study area; animals found to be off the area were considered to be unavailable for recapture when making mark–recapture estimates (Murray 1999; also see below). The 200-m residency threshold, while somewhat arbitrary, corresponds closely to the average diameter estimated for snowshoe hare home ranges (see review by Keith 1990), with animals occurring within the boundary likely occupying the same home range that they occupied when previously captured on the study area. The assumption that individuals found beyond the 200-m threshold would not be available for recapture was corroborated by the low (approximately 5%) recapture success for animals found to be off a study area during the pretrapping period. We did not target specific radio-collared individuals during our trapping efforts, and because traps were moved frequently across the study area during a given trapping period, our sampling effort likely provided a representative sample of the resident hare population.

Analysis of data

Because the distance between consecutive plots within a transect (30 m) was less than the mean diameter of a snowshoe hare's home range, whereas the distance between our extensive sampling effort on the IPNF (transects >1 km) was larger than typical nondispersal movement distances for hares (see Hodges 2000; Murray 2003), we regarded transect pellet counts on the extensive study sites as the unit of measure and deemed plots to be subsamples. To standardize the variances we analyzed the $\log_e$-transformed mean pellet density, with +1/6 correction to allow transformation of zero values. Non-parametric paired comparisons (Wilcoxon's sign-ranks test) were used to compare plot types for pellet prevalence (proportion of plots in each transect that were not empty) and pellet density (number/m^2). We calculated observer bias due to plot shape by comparing pellet counts from paired rectangular and small circular plots, using only transects in which at least one of these counts was not zero, and compared observer bias in data collected by trained observers with bias in those collected by untrained observers (untrained observers were taught how to establish transects and count pellets but were not trained with respect to potential observer error and bias; trained observers received detailed instruction on unbiased pellet collection with respect to plot shape and perimeter). Variance in pellet counts within each transect was described by the coefficient of variation (CV) for each plot type; pellet-count variance increased with the mean number of pellets and this relationship was described using Taylor's Power Law (Krebs 1999). Differences in the mean/variance relationship between years and among plot types were tested with analysis of covariance (ANCOVA) (Sokal and Rohlf 1995).

The notably low hare numbers on some study areas limited the utility of standard mark–recapture procedures for population estimation, owing to the need for high capture/recapture rates when populations are small (see Eberhardt 1990; Pollock et al. 1990; Krebs 1999). Instead, we estimated hare populations by (*i*) minimum number alive (MNA), which included the number of animals captured on study areas during a given trapping period and likely corresponded well to our low densities (see Krebs et al. 1986), and (*ii*) enhanced minimum number alive (EMNA), which combined the estimated MNA with the number of radio-collared animals known to be on or near study areas but that evaded capture during the trapping effort (see Wirsing et al. 2002). We also utilized a modified Lincoln–Petersen estimator, which is a mark–recapture estimator designed to improve upon standard Lincoln–Petersen estimation by including only radio-collared animals known to be on or near study areas to estimate the size of the previously marked cohort (see Murray 1999). From the four seasonal population estimates obtained on each area, a mean annual population estimate was calculated that could be correlated with pellet counts. Intuitively, the EMNA should be the most relevant estimator for our purposes because it reduces the underestimation bias that is characteristic of MNA estimation (see Hilborn et al. 1976), but does not suffer from the requirement for high capture/ recapture rates for accurate mark–recapture estimation. In addition, EMNA estimation should closely reflect "true" population size, given the intensity and frequency of our radio-collaring effort and the strong likelihood that most of the population on each site was radio-monitored (on average, >70% of captures made during a trapping period consisted of previously collared individuals, implying that most resident animals that remained uncaptured during a trapping period were known from a telemetry standpoint). We found that estimates provided by all three estimators were highly correlated (all $r > 0.91$, $P < 0.001$, $n = 24$), with EMNA estimates averaging 48 and 13% more than those from MNA and modified Lincoln–Petersen estimation, respectively. Statistical analysis of fecal pellets and hare numbers provided qualitatively similar results irrespective of the particular estimator used, and henceforth we report results from EMNA estimation exclusively.

We added 1/6 to both pellet counts and hare numbers to remove zero values, and then log-transformed both variables to standardize their variances. We compared the fit of regressions

Table 1. Plot attributes and prevalence, counts, density, and variability of snowshoe hare (*Lepus americanus*) fecal pellets on each of three plot types sampled in northern Idaho.

	Rectangular plots	Small circular plots	Meter-circle plots
Area (m^2)	0.155	0.155	1.0
Perimeter/area ratio	40.0	9.0	3.5
1999 (*n* = 615)			
Prevalence of pellets on transects[a]	0.615 (0.591–0.646)	0.488 (0.457–0.519)	0.667 (0.644–0.696)
Mean number of pellets/plot	0.814 (0.638–0.990)	0.400 (0.313–0.488)	1.466 (1.178–1.755)
Mean pellet density (no./m^2)	5.25 (4.11–6.38)	2.58 (2.02–3.15)	1.47 (1.18–1.75)
CV[b]	2.26 (2.18–2.33)	2.47 (2.39–2.55)	2.22 (2.15–2.30)
2000 (*n* = 576)			
Prevalence of pellets on transects[a]	0.476 (0.442–0.507)	0.424 (0.391–0.453)	0.628 (0.605–0.659)
Mean number of pellets/plot	0.245 (0.203–0.288)	0.209 (0.157–0.262)	1.114 (0.856–1.372)
Mean pellet density (no./m^2)	1.58 (1.31–1.86)	1.35 (1.01–1.69)	1.11 (0.856–1.37)
CV[b]	2.47 (2.39–2.55)	2.53 (2.45–2.61)	2.25 (2.18–2.32)

Note: Values in parentheses show the 95% confidence intervals.
[a]Proportion of transects on which pellets were found.
[b]Standard deviation/mean number pellets per plot, averaged over the entire transect.

using Aikike's Information Criterion with small-sample correction (AIC_c), where ΔAIC_c values >2.0 were considered significant (Burnham and Anderson 1998; Anderson et al. 2000). Pellet densities and hare numbers were first correlated using linear regression equations, but following qualitative examination of the data we further examined the nature of the relationship by fitting nonlinear exponential curves to the data. Despite the fact that error was likely present in both the dependent (hare number) and independent (pellet density) variables, we opted for Model I rather than Model II regression (for definitions see Sokal and Rohlf 1995) because (*i*) all correlation coefficients were high, implying that the results from both model types should be similar (see Jensen 1986), and (*ii*) use of Model I regression facilitated a comparison of results from linear and nonlinear fits.

Estimating population density, as opposed to population size, is a tenuous process in the case of many wildlife species because of difficulties associated with estimating the size of the effective trapping area when converting numbers of animals to number per unit area. When estimating hare population density, an arbitrary boundary strip is usually included to adjust for animals that only partially occupy the study area (e.g., Krebs et al. 1986; Murray 1999), and Krebs et al. (2001) included a boundary strip of unspecified size in their hare density calculations derived from pellet counts. However, because home-range size and site occupancy in hares may differ according to a variety of factors (see Murray 2003), and the influence of such factors on hare movement patterns and site occupancy in the marginal habitat characterizing our areas is poorly known, we predicted hare numbers rather than hare densities in our regressions. Hare numbers were translated to hare densities in order to put our results into the same context as those from Krebs et al. (2001) by scaling by 10 ha for an estimate of the number of hares using the area (which is a liberal estimate of density because it includes no boundary strip) and by 19 ha (study area plus a boundary strip 60 m wide; see Krebs et al. 1986) for a more conservative estimate of hare densities on study areas. Based on observations of daily movements of radio-marked hares on our study areas (E. Ellsworth, unpublished data; A. Wirsing, unpublished data), we feel that the latter density estimate probably is a close approximation of the true densities on our areas.

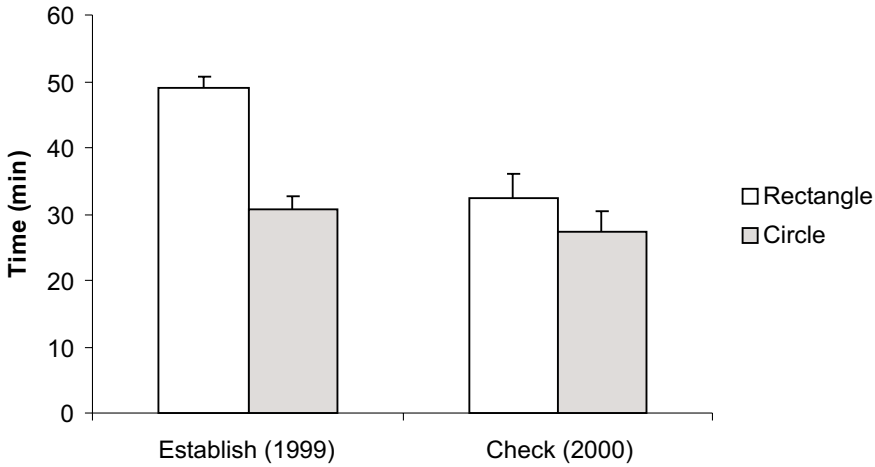
Results

Comparison of plot shapes and sizes

The large (1 m^2) circular plots were more likely to intercept hare pellets than were plots of either of the smaller types (Table 1). In both 1999 and 2000, fewer of the rectangular plots were devoid of fecal pellets than the small circular plots on the same area (Wilcoxon's signed-ranks test, 1999: $Z_c = 9.921$, $n = 615$, $P < 0.001$; 2000: $Z_c = 3.606$, $n = 576$, $P = 0.003$), while rectangular plots were empty more often than the metre-circle plots (1999: $Z_c = 5.260$, $n = 615$, $P < 0.001$; 2000: $Z_c = 12.093$, $n = 576$, $P < 0.001$). Thus, the metre-circle plots were more likely to intercept fecal pellets than either of the smaller type of plot (Table 1).

The mean density of pellets varied among the three plot types (Table 1). Pellet densities were higher on the standard rectangular plots than on small circular plots of the same area in both 1999 ($Z_c = 8.971$, $n = 615$, $P < 0.001$) and 2000 ($Z_c = 3.084$, $n = 576$, $P = 0.002$). Pellet densities also were higher on rectangular plots than on the metre-circle plots in both years (1999: $Z_c = 11.266$, $n = 576$, $P < 0.001$; 2000: $Z_c = 2.935$, $n = 576$, $P = 0.003$). To test for the effect of training on observer bias, we compared results from transects established in 1999 by 4 trained observers with those from transects established by 37 untrained observers. The extent of observer bias (proportion of pellets found on the rectangular plots) was less for the well-trained observers (0.60 ± 0.03 (mean ± SE), $n = 88$) than for those who received less training (0.67 ± 0.02, $n = 341$) (Mann–Whitney U test, $U = 12\,462$, $P = 0.014$). This difference was apparently reflected in the disparity in relative numbers of pellets per plot during both years of the study: during 1999, when trained personnel counted pellets on only 18.7% of transects, the rectangular plots had a 2.0-fold higher pellet density than the small circles, compared with a 1.2-fold difference observed during 2000, when trained personnel counted pellets on 87.1% of

Fig. 2. Time (mean ± SE) required to establish and recheck snowshoe hare fecal pellet transects (n = 10 transects per estimate, with 10 plots per transect). Transects comprised of circular plots include concentric plots of the same area as rectangular plots (0.155 m^2) as well as 1-m^2 circular (metre-circle) plots.



transects (Table 1). This discrepancy was magnified if densities of rectangular plots were compared with those of metre-circle plots (3.6- and 1.4-fold higher on rectangular plots in 1999 and 2000, respectively).

When predicting hare abundance, numerical precision is more important than accuracy, as any constant bias will be accounted for in the regression equations. The CV of pellet counts varied among the three plot types (Table 1). For the 1999 data, the CVs of pellet counts from rectangular plots were lower than those from the small circular plots (Z_c = 6.321, n = 249 transects where the CV was defined for both plot types, P < 0.001), but the CVs for rectangular plots were marginally higher than those for the metre-circle plots (Z_c = 1.658, n = 325, P = 0.097; Table 1). In 2000, the CVs for the rectangular plots again were smaller than the CVs for the small circular plots (Z_c = 2.433, n = 271, P = 0.015), while the metre-circle plots had lower CVs than the rectangular plots (Z_c = 6.623, n = 224, P < 0.001). Thus, although pellet counts from the rectangular plots were less variable than those from the small circular plots, the even lower CVs of the metre-circle plots imply that the aggregated distribution of pellets was less important for circular plots at the 1-m^2 scale.

The variance in pellet counts increased with the mean number of pellets per plot for all plot types. Following Krebs et al. (2001), we described this relationship using Taylor's Power Law (Krebs 1999). The regression equations were Y = 1.046 + 1.648X for the rectangular plots, Y = 1.044 + 1.633X for the small circular plots, and Y = 1.183 + 1.744X for the large circular plots. The relationship between mean and variance did not differ between years (ANCOVA, $F_{[1,3566]}$ = 2.97, P < 0.085) but did differ among the three plot types ($F_{[2,3566]}$ = 6.94, P < 0.001).

Pellet degradation

In the circular plots where we placed fecal pellets in order to estimate the rate of pellet degradation, 75% (22.4 ± 1.3 pellets per plot (mean ± SE), n = 18 plots) of the 30 original pellets were recovered after 1 year. Because these pellets were fresh when placed on plots, these results imply that not all pellets "survive" an entire year when exposed to natural conditions. Our small sample of degradation plots failed to reveal a differential rate of pellet degradation between clearcuts and mature forest sites ($F_{[1,16]}$ = 0.677, P = 0.43).

Plot establishment time

The circular plots took 63% of the time required to establish the rectangular plots ($F_{[1,18]}$ = 43.061, P < 0.001; Fig. 2). This difference represents a conservative estimate of establishment time because circular plots contained two concentric circles that needed to be established and checked. However, we found that time required to check precleared circular plots was similar (about 85%) to that required to check rectangular plots ($F_{[1,18]}$ = 1.032, P = 0.32) (Fig. 2).

Hare population estimation

We estimated that there were 7.32 ± 1.15 (mean ± SE) hares per study area (range 0.00–21.25). We estimated that there were 1.25 ± 0.26 pellets per plot (range 0.00–5.14) on the rectangular plots, 0.42 ± 0.11 (range 0.00–2.12) on the small circular plots, and 2.05 ± 0.39 (range 0.02–6.96) on the 1-m^2 circular plots. Estimated numbers of hares on study areas were correlated with numbers of pellets collected on the rectangular (t_{22} = 67.453, P < 0.001), small circular (t_{22} = 25.810, P < 0.001), and metre-circle (t_{22} = 57.626, P < 0.001) plots.

The fit of the linear regression equation using both the rectangular (ΔAIC_c = 15.037) and the metre-circle (ΔAIC_c = 12.246) plots was better than that using the small circular plots (Table 2, Fig. 3). The linear fit of the rectangular plots was better than that of the metre-circle plots (ΔAIC_c = 2.790), but the difference in correlation coefficients and root mean square errors indicated that this disparity was modest (see Table 2, Fig. 3). The nonlinear fit was better than the linear fit for the rectangular (ΔAIC_c = 11.774), small circular (ΔAIC_c = 8.864), and metre-circle (ΔAIC_c = 5.678) plots (Table 2, Fig. 3). The nonlinear fit of the rectangular plots was better correlated with hare numbers than was the nonlinear fit of either the small (ΔAIC_c = 17.946) or 1-m^2 (ΔAIC_c = 8.886) circular plots. From a purely statistical perspective, therefore, the pellet density – hare number relationship was best described by an exponential relationship using rectangular

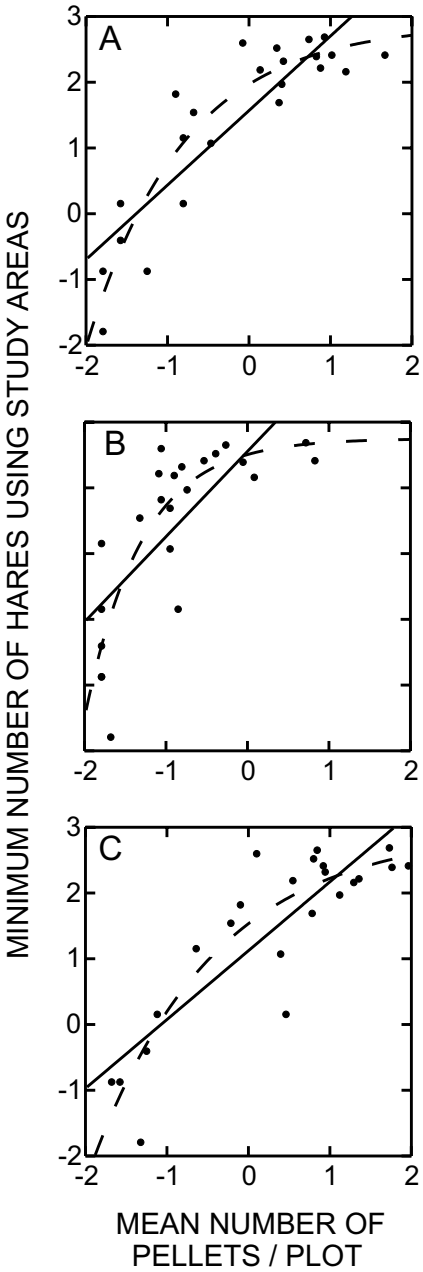
Table 2. Relationship between the mean number of snowshoe hare fecal pellets and mean hare numbers on three plot types.

Plot type	Relationship	Equation	95% CI Intercept	95% CI Slope 1	95% CI Slope 2	r	RMSE[a]	AIC_c
Rectangle	Linear	$Y = 1.569 + 1.133X$	1.294, 1.844	0.863, 1.403	—	0.87	0.685	−13.048
Small circle	Linear	$Y = 2.554 + 1.297X$	2.002, 3.106	0.797, 1.797	—	0.74	0.937	1.988
Metre circle	Linear	$Y = 1.112 + 1.047X$	0.807, 1.417	0.777, 1.317	—	0.85	0.726	−10.258
Rectangle	Exponential	$Y = 0.917 \times (3.146 - e^{-0.839X})$	0.702, 1.132	2.935, 3.357	−1.050, −0.627	0.93	0.536	−24.822
Small circle	Exponential	$Y = 0.244 \times (11.270 - e^{-1.429X})$	−0.215, 0.703	10.854, 11.686	−1.884, −1.013	0.83	0.779	−6.876
Metre circle	Exponential	$Y = 1.423 \times (2.077 - e^{-0.662X})$	1.152, 1.694	1.836, 2.317	−0.902, −0.422	0.89	0.645	−15.937

Note: Fifty plots of each type were surveyed on twelve 10-ha study areas, with study areas surveyed in 2 consecutive years (n = 24). Pellet counts and hare numbers were transformed by adding 1/6 and converting to $\log_e$.

[a]Root mean square error.

Fig. 3. Mean number of fecal pellets per plot versus hare numbers on 12 snowshoe hare study areas in Idaho. Plots corresponded to the 5.08 × 305 cm rectangle (0.155 m^2) (identical with that used previously by Krebs et al. 1987, 2001) (A), a circle of the same area (0.155 m^2) as the rectangular plot (B), and a 1-m^2 circle (C). Pellet densities and hare numbers were transformed to the natural log (value + 1/6) to standardize the variances and enable transformation of zero values. Regression equations are provided in Table 2 and descriptions of predicted numerical estimates in Table 3.



plots. Yet all equations for the rectangular and metre-circle plots had high (r > 0.84) correlation coefficients, and the disparity in linear fit for the two plot types was limited in terms of predictive power.

Hare population estimates were not biased by differential capture success among study areas; overall capture success

Table 3. Predicted numbers of snowshoe hares relative to the number of fecal pellets per plot on each plot type using linear and exponential equations reported in Table 2.

		Y-intercept		Counts proportional to area				Mean pellet count on study area			
Plot type	CF	No. of pellets	No. of hares	No. of pellets	No. of hares	No. of pellets	No. of hares	No. of pellets[a]	No. of hares[a]	No. of pellets[b]	No. of hares[b]
Linear											
Rectangle	1.41	0	0.65	0.155	1.64	0.31	2.69	1.25	9.81	0.25	2.27
Small circle	1.60	0	1.74	0.155	4.45	0.31	7.59	0.42	10.02	0.21	5.52
Metre circle	1.44	0	0.43	1.0	4.91	2.0	9.60	2.05	9.84	1.11	5.41
Exponential											
Rectangle	1.31	0	0.16	0.155	1.96	0.31	4.03	1.25	11.61	0.25	3.25
Small circle	1.48	0	0.74	0.155	6.94	0.31	11.21	0.42	13.48	0.21	8.40
Metre circle	1.38	0	0.02	1.0	7.11	2.0	11.07	2.05	11.21	1.11	7.67

Note: Hare numbers were back-transformed and then multiplied by a correction factor (CF = $e^{(RMSE/2)}$, where RMSE is root mean square error) to adjust for biased predictions produced by log–log regressions (Sprugel 1983). Sample calculations are made assuming pellet counts of zero (*Y*-intercept), assuming that pellet numbers are proportional to plot area (no observer bias due to plot shape or size) and using actual pellet counts from intensive- and extensive-study areas (incorporating potential observer bias). Hare density estimates may be obtained by dividing hare numbers by 10 ha for a liberal density estimate or 19 ha for a conservative density estimate (see the text). Estimated hare numbers on extensive transects were selected according to forest type and thus do not represent average hare numbers across northern Idaho.

[a]Mean number of fecal pellets per plot on intensive-study areas.

[b]Mean number of fecal pellets per plot on extensive-study area in 2000.

for residents averaged 64.9% and was not correlated with estimated hare numbers (P = 0.99). Also, on average, 16% of radio-monitored hares were found to be off a study area during pretrapping monitoring and this percentage was not related to hare numbers on study areas (P = 0.23), implying that differential rates of study-area residency likely did not influence population estimates.

The six equations under consideration (Table 2) provided qualitatively different estimates of hare numbers over a range of pellet densities. We used these equations to predict hare density under three pellet-density scenarios (empty plots, pellet numbers proportional to plot area, and actual mean pellet counts from our intensive and extensive study areas), and compared the numbers of hares estimated by the six equations (Table 3). Equations derived from the small circular plots generally yielded a higher *Y*-intercept and wider confidence intervals than those derived from the remaining plot types (Tables 2, 3), therefore this plot type is clearly less desirable than the other two. For plots devoid of pellets, curvilinear fits using both rectangular and metre-circle plots predicted considerably lower hare numbers than linear regressions (Table 3). Predicted hare numbers on plots lacking pellets represent densities <0.04 and <0.07 hares/ha (assuming an effective trapping area of 19 and 10 ha, respectively) for the linear relationship and <0.01 and <0.02 hares/ha for the exponential relationship (assuming a trapping area of 19 and 10 ha, respectively). By comparison, Krebs et al.'s (2001) equation predicts a mean hare density of <0.01/ha from a density of 0.01 pellets per rectangular plot.

If pellet counts are proportional to the size of a plot (i.e., plot shape has no effect and pellet densities are equivalent across plot types), the metre-circle plots consistently predict higher hare numbers than do rectangular plots (Table 2). This difference implies that the pellet counts used to generate our equations were strongly biased according to plot shape/size. Using similar pellet densities, the estimated number of hares derived from linear equations was consistently lower than that obtained for their nonlinear counterparts.

Using mean pellet densities recorded on our intensive study areas, hare abundance predicted by the rectangular plots was very similar to that predicted by the metre-circle plots, and the nonlinear equations predicted hare numbers that were about 16% higher than did their linear counterparts. Mean pellet densities from our extensive sampling effort predicted hare numbers that were about twice as high using metre-circle versus rectangular plots. To put our results in perspective, Krebs et al.'s (2001) equation predicts a mean density of 0.57 hares/ha on our intensive study areas (using our mean of 1.25 pellets per plot from our rectangular plots; see Table 3) and 0.14 hares/ha (mean = 0.25 pellets per plot; see Table 3) on our extensive study sites. These numbers correspond reasonably well to estimates generated from our linear equation derived from rectangular plots: we predicted mean densities of 0.51–0.98 hares/ha for the intensive study areas and 0.12–0.23 hares/ha for the extensive study areas, assuming an effective trapping area of 19 or 10 ha, respectively.

Discussion

Krebs et al. (2001) argued that further testing of the pellet-plot method for estimating snowshoe hare populations is warranted. They recognized that the 5.08 × 305 cm plots which were deemed optimal for sampling pellets on Yukon sites (see also Krebs et al. 1987) might not best predict hare numbers in other areas across the geographic range. In addition, they felt that the predictive power of their equation relating pellet densities to hare numbers could differ regionally, and thus require testing against other models in different areas. Indeed, the generally lower density and greater spatial heterogeneity of hare populations along the southern boundary of their range (see Hodges 2000; Murray 2000) might cause differential patterns of pellet distribution and abundance that could fundamentally affect the hare number – pellet density relationship. Accordingly, the development of tools for accurately and precisely estimating hare densities in areas where numbers are low should be a priority.

Krebs et al. (2001) provided a recipe for further tests of the pellet-plot technique: (*i*) determine the optimal size and shape of plots for a given area, (*ii*) evaluate the relationship

between sample mean and variance to determine sampling intensity, (*iii*) estimate hare densities via mark–recapture methods on intensive-study areas, and (*iv*) calculate the regression equation between hare numbers and pellet densities for the new area. Given the low density of hare populations in Idaho and our desire to apply the pellet-plot method broadly to evaluate hare habitat-selection patterns across the northern tier of the state, we considered that the optimal size/shape of pellet plots would show (*i*) a high probability of detecting pellets placed in hare habitat, as well as low sample variation, (*ii*) low sampling bias due to either sampling outside the plot or overlooking pellets within the plot, and (*iii*) a short establishment and rechecking time. Our results demonstrate that the metre-circle plots intercepted as many or more pellets as did the rectangular plots, implying that the larger plot surface area reduced the likelihood of a Type II statistical error (i.e., acceptance of a false null hypothesis of no pellets). Also, variability in pellet counts was lower in the metre-circle plots. The apparent bias in estimated pellet density related to the edge effect caused by differences in the perimeter:area ratio would not necessarily be a cause for concern if it were constant over time or among observers. However, this bias appeared to be lower in data collected by trained personnel (but not on our intensive-study areas) and decreased in our second year of study, when transects were largely surveyed by such observers. Krebs et al. (2001) noted that the greater variability in their data than in an earlier analysis (Krebs et al. 1987) could have been due at least in part to the larger number of observers counting pellets for the later dataset. In 2000 we placed greater emphasis on personnel training and protocol standardization, which certainly helped with data quality control.

The time required to establish circular plots was less than that required for rectangular plots, an important factor in deciding on an optimal plot size and shape (Krebs 1999). Thus, the metre-circle plots appear to be the most efficient from both a statistical and a logistical perspective. Although we considered only two plot sizes, circular plots that are even larger could produce more reliable counts, although at some point increasing the plot size becomes less efficient as time requirements increase and confidence in thorough pellet detection decreases (see Neff 1968).

Pellet degradation

The issue of pellet degradation is important in light of recent efforts to use counts from uncleared plots to estimate hare density (e.g., see Kloor 1999; Bartmann and Byrne 2001). Although temptingly straightforward, such an approach may be misleading either if pellets degrade at a slow rate and thus pellets counted in a given year reflect hare numbers from several previous years, or if degradation rates differ according to diet, habitat, or weather conditions. Although our small sample of degradation plots failed to indicate a disparity in pellet breakdown between clearcut and mature forest habitat, problems with the use of uncleared plots for population estimation or habitat evaluation have been suggested for leporids (Taylor and Williams 1956; Cochran and Stains 1961), macropods (Vernes 1999), and ungulates (Wigley and Johnson 1981; Harestad and Bunnell 1987; Lehmkuhl et al. 1994; Massei et al. 1998). Our results indicated that, on average, 75% of the pellets used in degradation trials remained after 1 year, implying that (*i*) not all pellets deposited annually on plots remained available for hare abundance estimation, and (*ii*) pellets may withstand complete degradation for several years. We have observed that most hare pellets counted on plots are characteristic of those produced during winter (i.e., contain coarse woody material), suggesting that summer pellets (with softer plant material) may not withstand harsh winter conditions or are preferentially consumed by detritivores (see Neff 1968). Doubtless this loss could add substantive error to hare habitat assessment via pellet-plot surveys, and thus should be given further attention.

Although it may be appropriate in some cases to use the presence of pellets from uncleared plots as an index of herbivore habitat suitability or space use in an area (e.g., Eberhardt and Van Etten 1956; Loft and Kie 1988), the reciprocal use of pellet absence to indicate hare absence will always be subject to potential Type II statistical error. In any future effort that relies upon pellet counts from uncleared plots to either estimate hare densities or evaluate hare habitat use, pellet degradation rates *must* be determined first across a broad range of habitat types and environmental conditions, or the potential effect of differential degradation confirmed to be so small that it can be ignored. In light of the significant effort that would be required to demonstrate such relationships, and the added uncertainty of using pellets of unknown age to describe current numbers, it seems logical that annual pellet counts on precleared plots will remain the superior method of hare population estimation (see also Neff 1968).

Population estimation

Logically, two considerations in choosing the most appropriate predictive equation for hare population estimation are that the *Y*-intercept approaches zero and that the regression slope is low enough to capture small changes in hare numbers through larger changes in pellet density. The *Y*-intercepts of our rectangular- and metre-circle-plot equations approach zero, as does the intercept of Krebs et al.'s (2001) equation. Our slopes also are comparable, although that for the metre-circle plots is slightly more gradual than that for our rectangular plots, an advantage likely conferred by the larger area and higher pellet numbers encountered in the former plot type. The poorer correlation coefficients, wide confidence intervals, and relatively large *Y*-intercept associated with equations for the small circular plots cause us to reject that particular plot type altogether for estimating hare numbers. Notably, the correlation coefficient for Krebs et al.'s (2001) equation (0.76) was lower than that obtained for our regressions using rectangular and metre-circle plots, despite our 72% smaller sample size. Thus, all of our equations derived from rectangular and metre-circle plots have reasonable predictive power.

The better fit of the exponential curve relating hare numbers to pellet densities was unexpected, given the strong linear fit observed previously on Yukon sites (Krebs et al. 2001; but for an apparently curvilinear pattern see Fig. 1 of Krebs et al. 1987). Intuitively this relationship should be linear, so the poorer fit could be due to the fact that our samples were smaller than those of Krebs et al. (2001) or to bias in the measurement of either hare or pellet numbers. For example, if pellet numbers at low hare densities were underestimated, perhaps because of low detectability by observers when few

pellets were present, this could account for the observed curvilinearity. Yet we allowed only well-trained observers to check transects on our intensive-study sites, which implies that observer bias should have been lessened for those data. Alternatively, if hare numbers were underestimated at high densities because of differential catchability of hares or inconsistent bias in the EMNA estimator, this also could have elicited a curvilinear relationship. The latter scenario also seems unlikely, given the lack of correlation between capture success or off-area residency and estimated hare numbers on a site.

Differential defecation rates among study areas also could account for the observed curvilinearity in our data. Lagomorphs are known to experience differential pellet deposition rates when subjected to different foods, defecation rates being higher in individuals feeding on abundant high-quality food (Cochran and Stains 1961). Increased pellet production by individual hares in areas with high-quality forage (and likely high hare densities) would alter the slope relating density of pellets to number of hares in our regression equation, and theoretically could lead to a curvilinear relationship similar to that which we found. It follows that dietary differences between hares on our good versus marginal sites might account for a disparity in pellet deposition rates that weakens the linear correlation between pellet density and hare numbers. However, at this juncture we are unable to rigorously evaluate this possibility.

The most appropriate equation for predicting hare numbers via pellet plots should not only have high predictive power but also possess biological relevance and generality and ease of application. Despite the statistical differences between the curvilinear and linear regressions, the disparity in estimated numbers of hares was biologically modest over much of the range of pellet counts encompassed by our study. Within the range of about 0.06–4.3 pellets/plot (which corresponds to post-transformation values of approximately –1.5 to 1.5 pellets per plot; see Fig. 3), differences between estimated hare numbers were modest, while at pellet densities above or below these thresholds, estimates differed more dramatically. Thus, for most low-density hare populations the linear fit apparently provides a simpler, more intuitive approximation that yields reasonable predictive power. A final advantage of linear over curvilinear depiction of the pellet density – hare number relationship involves the likely poor fit of any of our curves to hare populations above the densities reported for our intensive-study sites.

The linear versions of the rectangular and large circular plots provide somewhat similar estimates of hare numbers. Yet at substantially low pellet densities (such as those found on our extensive study areas), the circular-plot method can more likely be used with reasonable confidence to predict hare numbers, owing to its larger plot surface area and lower perimeter:area ratio. The potential shortcomings of rectangular plots are further illustrated by the fact that on our intensive-study areas such plots had 61% of pellets found on metre-circle plots, despite a 16% plot area and rigorous observer training in the unbiased collection of pellets relative to plot shape. This renders suspect regression equations derived from such plots. Thus, the metre-circle plot may be most desirable because of (*i*) the lower likelihood of the meter-circle plot either being devoid of pellets or providing biased pellet counts, (*ii*) the ease and rapidity of establishing meter-circle plots, and (*iii*) the small *Y*-intercept and shallow slope of the regression equation derived from the metre-circle plots versus that derived from the rectangular plots. This is an important finding because the low density and spatial heterogeneity of southern hare populations require that areas be sampled both at a high intensity and extensively across the landscape, and our results indicate that such efforts may be most fruitful if an alternative method to that commonly used in northern areas is employed. This conclusion resonates particularly loudly as attempts are made to preserve or restore carnivore populations in marginal hare habitat, and the establishment of hare-pellet transects across entire national forests or geographical regions is considered (see Murray 2003); such initial steps already have been undertaken in Colorado, Montana, and Idaho (see Kloor 1999; Malloy 2000; Bartmann and Byrne 2001; this study). However, while metre-circle pellet plots and linear regression appear to be most effective for estimating hare populations in our study area, alternative sampling protocols should be further tested across the southern part of the hares' range so that, ultimately, procedures may be standardized to the greatest extent possible.

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