Estimation of snowshoe hare population density from turd transects

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We counted the number of snowshoe hare (*Lepus americanus*) fecal pellets on 50 quadrats of 0.155 m^2 on each of six areas near Kluane Lake, Yukon Territory, once a year from 1977 to 1983. On four of these areas we livetrapped hares once a month and estimated population density from the Jolly–Seber model. Average hare density for the year was linearly related to fecal pellet counts ($r = 0.94$) over the range 0–10 hares/ha. Mean turd counts also are related to the variance of these counts by Taylor's power law with exponent 1.30, indicating a clumped pattern in turd deposition. Fecal pellet counts provide a quick and accurate method for snowshoe hare censuses on an extensive scale.

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Une fois par année, de 1977 à 1983, nous avons recensé les fèces des lièvres (*Lepus americanus*) dans des grilles de 50 carrés échantillons mesurant chacun 0,155 m^2 en six régions voisines de Kluane Lake, Yukon. En quatre de ces régions, nous avons capturé des lièvres vivants une fois par mois, ce qui a permis d'obtenir une estimation de la densité de la population d'après le modèle de Jolly–Seber. À une densité de 0–10 lièvres/ha, il y a une relation linéaire entre la densité annuelle moyenne des lièvres et le nombre de fèces (r = 0,94). Les nombres moyens de crottes sont également reliés à la variance de ces nombres selon la loi de Taylor (exposant 1,30), ce qui indique que les crottes ont une répartition contagieuse. Le dénombrement des fèces constitue une méthode rapide et précise d'évaluation de la densité des lièvres sur une grande échelle.

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Introduction

Snowshoe hares (*Lepus americanus*) are a dominant herbivore in much of the boreal forests of Canada. Estimating snowshoe hare density is labor intensive if conventional mark–recapture techniques are used (Keith *et al.* 1984; Krebs *et al.* 1986) and additional techniques are needed for large-scale surveys of changes in hare abundance. Since hares produce large numbers of fecal pellets and drop them as they move about, it should be possible to count fecal pellets to estimate absolute density of hares. We have used this approach as part of a long-term study of snowshoe hares at Kluane Lake, Yukon Territory, and in this paper we present evidence that counts of fecal pellets can provide an accurate and precise estimate of hare density.

Methods

Our basic approach was to establish 50 sampling quadrats on each of six areas near Kluane Lake (61° N, 138° W). We first had to decide on the size and shape of the quadrats. In August 1976 we counted the accumulated fecal pellets on 50 quadrats of five different shapes (square, rectangular) and sizes (0.25–0.08 m^2), and determined that the optimal quadrats for sampling hare turds in this area were 5.08 × 305 cm covering an area of 0.155 m^2. These long, thin quadrats produced estimates with the lowest variances and could be effectively sampled by one or two persons. We set out 50 quadrats on each area because our preliminary data suggested that this sample size would produce turd estimates accurate within ±20% of the mean (on average). We sampled six areas. Three of these were 10 × 10 checkerboard livetrapping areas with 30 m between the points. We picked 50 of the 100 available trap points at random and set out permanent markers at the centre and the ends of each quadrat. On the other three sites (Bullion Creek, spruce–moss, Beaver Pond), we set out 50 quadrats systematically along two parallel transect lines. At Beaver Pond these transects were along the edge of the livetrapping grid. We marked the quadrats with flagging so that field workers would avoid walking on them. We cleared hare turds from the area around each quadrat in August 1976 (when hares were very scarce) so that all turds present in the future had to be newly deposited.

We deliberately set quadrats out in six areas of variable habitat to test the robustness of the estimation procedure. The spruce–moss site was a mature closed stand of white spruce (*Picea glauca*) and bog birch (*Betula glandulosa*). Silver Creek and the East Slims sites were also closed spruce forest, but with more willow and a variable forest floor with *Arctostaphylos uva-ursi, A. rubra, Shepherdia canadensis*, and *Lupinus arcticus*. Beaver Pond was an open white-spruce forest dominated by bog birch and grayleaf willow, and Microwave site was even more open, dominated by shrubs (birch, willow) with abundant grasses. Bullion Creek was a pure stand of balsam poplar (*Populus balsamifera*) with a few scattered spruce trees.

We counted hare turds on each quadrat every June from 1977 to 1983. We cleared each quadrat as it was counted. Old turds accidentally kicked on to our quadrats were not counted; they could be recognized by their uniform dark grey colour and lack of light brown material in the centre of the turds when broken open.

We compared these turd counts with hare population density estimated by mark–recapture techniques with the Jolly–Seber model (see Krebs *et al.* 1986). Since turd counts were made once a year, we compared them with mean population densities from the previous year determined by averaging the Jolly–Seber estimates for the period June 1 to May 31 and dividing this by 25 ha, the approximate effective grid size (Krebs *et al.* 1986). This mean density for the year $t - 1$ to t was regressed against the turd counts obtained in year t.

Results

Figure 1 shows the relationship between turd counts and snowshoe hare population density. The relationship is very close ($r = 0.94$) and 89% of the variation in hare density from year to year can be explained statistically by the changing turd counts. There is no indication from our data that this regression is not linear over the range from 0 to 10 hares/ha. Note that the higher hare densities all come from a food-supplemented area (Microwave) in which added winter food tripled carrying capacity (Krebs *et al.* 1986). We used regression through the origin to estimate the predictive equation: mean hare density per hectare = 0.2903 (mean number of turds). Confidence limits for

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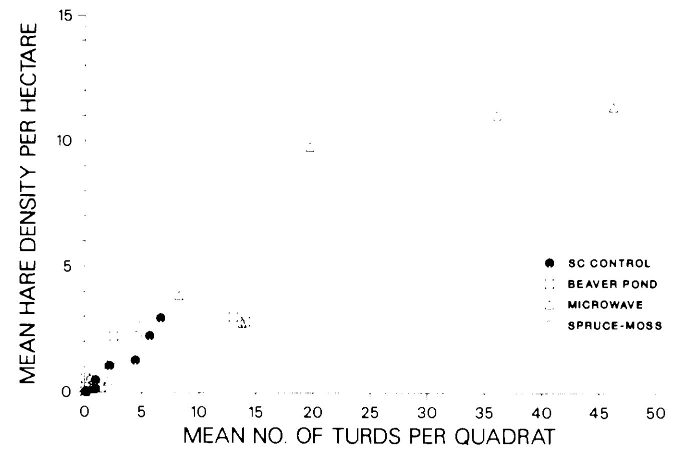

FIG. 1. Relationship between mean snowshoe hare density per hectare (in the previous year) to mean turd counts done once a year in June on 50 quadrats of 0.155 m^2. Kluane Lake, Yukon Territory, 1977–1983. $Y = 0.27X + 0.42$; $SE(b) = 0.019$; $r = 0.94$.

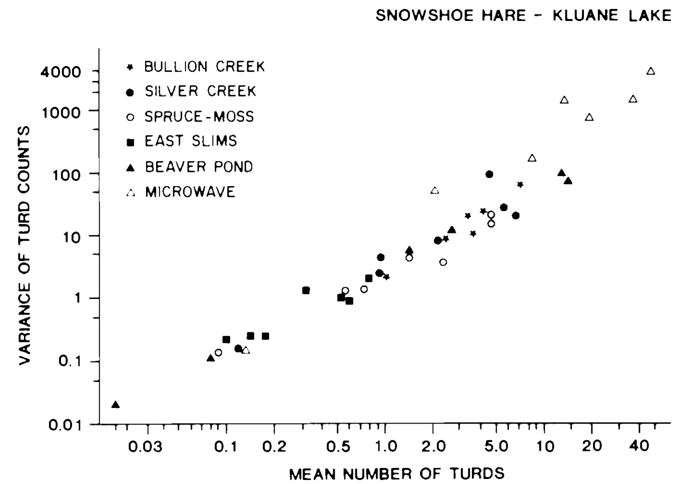

FIG. 2. Taylor plot of the variance of snowshoe hare turd counts on 0.155-m^2 quadrats against the mean counts for six areas. $n = 50$ for all points. Each point represents 1 year on one area. Kluane Lake, 1977–1983.

the slope parameter of this regression are 0.2557 to 0.3249, for the 95% level of confidence. Errors in the slope estimate are not serious for the range of hare densities from 0 to 4/ha. A more serious source of error is in the estimation of the mean number of turds per quadrat. Standard regression analysis assumes that the x variable is measured without error, but this is not the case here.

We also calculated a linear regression for these data without the constraint of passing through the origin and the results are nearly identical with those given above ($r = 0.94$: $y = 0.2726x + 0.4248$; confidence limits on slope 0.2330 to 0.3122). We also tried square root and logarithmic transforms on both variables in the regression and found that no transformation improved the fit of the line and all correlations ranged from 0.85 to 0.93. It is clear that the predictive regression is robust and we think that the simple linear regression is preferable (Fig. 1).

We tested with analysis of covariance the assumption that one equation with a common slope was an adequate description of these data. The null hypothesis of a common slope was accepted ($F = 1.86$; df 3, 20; $p = 0.17$), as was the null hypothesis of a common regression for all four areas ($F = 1.11$; df 3, 23; $p = 0.36$).

Turd counts show a clumped pattern within a study site and this pattern is simply described by Taylor's (1961) power law model (Fig. 2) in which the variances of the counts are linearly related to the mean counts on a log-log plot. This relationship is described by $\log s^2 = 0.47 + 1.30 (\log \bar{x})$, with data for Microwave omitted.

Data from all six of our sites seem to fit this line with the exception of the Microwave food grid, which shows higher variances for a given mean count and a significantly higher slope (1.66). The explanation for this exception is simple: Microwave was a very patchy habitat over the winter and this patchiness was aggravated by our artificial feeding stations which clumped hares near feeding stations (10–20 sites) where food was provided and cover was more dense.

If we combine the errors of estimating the mean number of turds with those of the slope of the regression in Fig. 1, we can estimate the confidence limits for each estimate of density. The resulting estimates are less precise than we had originally planned. For example, Beaver Pond in 1981 had a mean turd count of 13.0 with 95% confidence limits of 10.29 and 15.71. From these limits we obtain for estimates of average hare density over the previous year (June 1980 – May 1981): best estimate = 4.0 hares/ha; lower limit = 3.2; upper limit = 4.7. The observed hare density was 3.0 hares/ha.

If we use only the slope error, we would get upper and lower limits of 3.0 to 4.1 for this case. It is clear that the reliability of our estimates is only approximately ±30% of the mean, and that we could increase the precision by counting more turd transects than the 50 we decided to use. Because the standard error of small counts of turds is less than that of large counts for a fixed sample size (Fig. 2), the best sampling program would be to count larger numbers of quadrats at lower hare densities. A compromise sampling scheme for our situation that would provide relative accuracy of ±20% of the mean would involve counting about 500 turd transects when there are 0.5 hares/ha and 150 transects when there are 3.0 hares/ha. Alternatively, we could specify a sampling program with an absolute accuracy of ±0.4 hares/ha at all densities (with 95% confidence). This would provide an estimate of sample size as follows (Mace 1964): $n = 25\ s^2$, where the variance can be estimated from the regression in Fig. 2.

Discussion

Counts of fecal pellets have been used by several workers to estimate density. Angerbjörn (1983) estimated density of mountain hares (*Lepus timidus*) in Sweden from counts on square-shaped quadrats of 0.1 m^2 and obtained the log–log regression: log (turds) = 1.02 log (hare density) + 0.44, where hare density is per hectare. It is not clear why he preferred a log–log regression to a simple linear regression, since the slope of the log–log plot is very nearly 1.0. A log–log regression could also be fitted to our data (slope = 0.829; intercept = −0.3324; $r = 0.90$). Angerbjörn (1983) found a close relationship between turd counts and hare numbers ($r^2 = 0.91$).

Taylor and Williams (1956) developed a model to estimate the density of European rabbits (*Oryctolagus cuniculus*) from estimates of fecal pellets. We have avoided the complexity of this approach in favour of an empirical relationship between density and pellet counts (Fig. 1). Because we clear our plots each year, we do not need to have estimates of rates of fecal pellet breakdown for snowshoe hares. It is clear that hare pellets at Kluane Lake take at least 10 years to break down and may last two or three times this long in the field.

Counting fecal pellets (or pellet groups) has been a popular census technique with deer (Neff 1968; White and Eberhardt 1980). This technique is more complex for ungulates because of the need to recognize pellet groups (Batcheler 1975); in hares we count individual pellets which are less ambiguous. Davis (1982) suggests that counts of pellet groups in deer can be an accurate census technique.

In contrast, Wolff (1982) states for snowshoe hares that "pellet counts can be used to indicate habitat use or population trends, but not to estimate population numbers" (p. 141). We suggest that the data presented here show that fecal pellet counts can provide a rapid and precise estimate of snowshoe hare density. Monitoring of snowshoe hare density changes on an extensive spatial scale could be done with this simple technique.

We did not test the possibility that optimal quadrat size and shape changes with habitat and with hare population density. It is possible that an optimal sampling strategy would involve changes in quadrat size at different hare densities and in various habitats. This analysis has yet to be done for snowshoe hares.

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