PELLET COUNT INDICES COMPARED TO MARK–RECAPTURE ESTIMATES FOR EVALUATING SNOWSHOE HARE DENSITY

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Abstract: Snowshoe hares (*Lepus americanus*) undergo remarkable cycles and are the primary prey base of Canada lynx (*Lynx canadensis*), a carnivore recently listed as threatened in the contiguous United States. Efforts to evaluate hare densities using pellets have traditionally been based on regression equations developed in the Yukon, Canada. In western Montana, we evaluated whether or not local regression equations performed better than the most recent Yukon equation and assessed whether there was concordance between pellet-based predictions and mark–recapture density estimates of hares. We developed local Montana regression equations based on 224 data points consisting of mark-recapture estimates and pellet counts, derived from 38 sites in 2 different areas sampled for 1 to 5 years using 2 different pellet plot shapes. We evaluated concordance between estimated density and predicted density based on pellet counts coupled with regression equations at 436 site-area-season combinations different from those used to develop the regression equations. At densities below 0.3 hares/ha, predicted density based on pellets tended to be greater than for mark–recapture; the difference was usually <1 hare per ha on an absolute scale, but at low densities this translated to proportional differences of 1,000% or greater. At densities above 0.7 hares/ha, pellet regressions tended to predict lower density than mark–recapture. Because local regression equations did not outperform the Yukon equation, we see little merit in further development of local regression equations unless a study is to be conducted in a formal double-sampling framework. We recommend that widespread pellet sampling be used to identify areas with very low hare densities; subsequent surveys using mark–recapture methodology can then focus on higher density areas where density inferences are more reliable.

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Snowshoe hare population dynamics are of intense interest because of their remarkable 10-year cycles (Keith 1990, Royama 1992) and because hares are the primary prey of several forest carnivores, especially Canada lynx. Lynx are considered sensitive species in all U.S. Forest Service (USFS) regions that support them (Koehler and Aubry 1994) and are listed as a threatened species in the contiguous United States (U.S. Fish and Wildlife Service 2000); management of lynx depends on evaluation of hare distribution and density.

Estimating abundance or density for most species is difficult, especially when, as for snowshoe hares, the scope of interest spans the continental United States and represents a time frme of many decades. On the one hand, mark–recapture (MR) techniques can provide statistically sound estimates of density, but the logistics (e.g., cost, time, expertise required) can make them difficult to implement. On the other hand, indirect indices are easier and less expensive to implement at large scales, but they confound density changes of animals with an unknown and potentially variable relationship between density and the index (Anderson 2001, Pollock et al. 2002, Tallmon and Mills 2005).

The need to measure snowshoe hare density at large spatial and temporal scales has led to the proposed use of indices ranging from questionnaires (Smith 1983) to harvest records (Keith 1963) to track and runway counts (Conroy et al. 1979, Koehler et al. 1979, Buehler and Keith 1982). Pellet counts have been the most widely used index, typically measuring relative abundance over time or across different habitat or vegetation types (Wolff 1980, Orr and Dodds 1982, Wolfe et al. 1982, Litvaitis et al. 1985).

In some cases, however, pellet-count indices have been used to infer hare absolute abundance or density, following the lead of Krebs et al. (1987:565) of hares who concluded from work in the Yukon, “we present evidence that counts of fecal pellets

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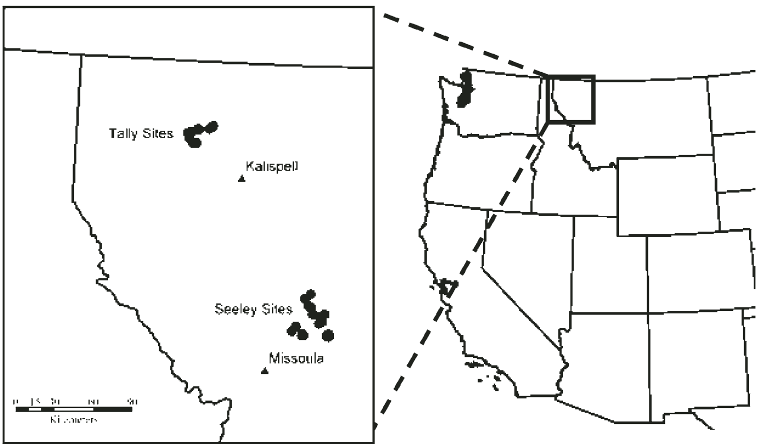

Fig. 1. Snowshoe hare study area in western Montana from 1998–2002, with locations of the 13 Tally area sites and 25 Seeley sites.

can provide an accurate and precise estimate of hare density." Subsequently, the Krebs et al. (1987) regression equation, or an updated Yukon equation (Krebs et al. 2001) formed the basis for deriving snowshoe hare densities in other areas based on average pellet counts (e.g., Poole 1994, Slough and Mowat 1996, Poole 1997). It is not clear, however, whether these equations reliably predict hare densities when densities are low or in regions and habitats different from the Yukon.

We used data from northwest Montana to evaluate the utility of pellet counts to infer snowshoe hare density over time and space. Specifically, we evaluated whether locally developed, Montana equations performed better than the most recent Yukon equation and whether there was concordance between pellet-based predictions and mark–recapture density estimates of hares. Together, our objectives evaluated how well characterization of hare population trends or habitat use using pellet counts (which are increasingly being conducted or considered in the context of lynx management) reflects hare densities estimated from live-trapping.

STUDY AREAS

We sampled 38 sites for up to 5 years in 2 different areas in western Montana. The 2 study areas (Seeley and Tally) were separated by approximately 160 km (Fig. 1). Seeley consisted of approximately 500 km^2 near Seeley Lake and contained mostly USFS and privately owned coniferous forest land that was largely unpopulated and had a wide array of uncut and harvested stands. Dominant tree species were lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), and subalpine fir (*Abies lasiocarpa*). The Seeley area included between 8 and 25 sites that we assessed for 5 summers (1998–2002) and 2 winters (2000, 2001). All sites were 1,300–2,000 meters in elevation.

The Tally area was a highly managed forest landscape of ~300 km^2 in the Salish mountains of the Flathead National Forest. Dominant tree species and elevation of sites were similar to those in Seeley. In Tally, we trapped 13 sites during the summers of 2001 and 2002, and performed 1-year pellet counts in 2002 and 2003.

METHODS

Ideally, an evaluation of a pellet index would compare pellet-based predictions to known true densities. In the case of free-ranging hares, the best surrogates for known densities are estimates based on mark–recapture sampling. We use $\hat{D}_{MR}$ to refer to the estimated mark–recapture density and $\tilde{D}$ to refer to the predicted density using pellet counts and a regression equation. Subscripts associated with $\tilde{D}$ refer to the source of the regression equation; for example $\tilde{D}_{Yukon}$ means that the predicted numbers of hares was based on pellet counts coupled with the Yukon equation.

Snowshoe Hare Sampling and $\hat{D}_{MR}$

All trapping grids consisted of live traps baited with alfalfa and apples and spaced at 50-m intervals. In the first 2 years (1998, 1999), we used 50 traps in a 10 × 5 trap array (covering 9 ha). After encountering low hare numbers, we increased the grid size to the largest size possible without overlapping multiple stand types. Thus, 13 of the sites sampled in 2000–2001 at Seeley were trapped with 84 traps in a 7 × 12 trap array covering 16.5 ha. At the Tally area, the grid consisted of 80 traps typically in an 8 × 10 trap array (15.75 ha), but 4 of the 13 arrays had 2 rows of 10 traps and 5 rows of 12 traps to fit within stands that were not wide enough for 8 rows.

The length of trapping sessions balanced the need for increased sample size against the negative effects of trapping on animals; thus, each session consisted of 3–5 nights. We trapped for ≥1 month during the summer and, in some cases, the winter (Table 1).

Table 1. Snowshoe hare mark-recapture and pellet sampling seasons, years, and sites in Montana, USA, 1998–2002.

Year and season[a]	No. of sites	No. trap sessions per season[b]	Pellet plot type(s)[c]	No. of plots per site[d]
Seeley Lake				
1998 summer	8	3 or 4	Large rectangle scaled to small rectangle	20
1999 summer	8	3	Large rectangle scaled to small rectangle	20
2000 summer	24	1 or 2	Small rectangle and circle	25
2001 summer	12	1	Small rectangle and circle	25
2002 summer	12	1	Circle	25
2000 winter	24	1	Small rectangle and circle	25
2001 winter	12	1	Small rectangle and circle	25
Tally Lake				
2001 summer	13	1	Small rectangle and circle	80
2002 summer	13	1	Small rectangle and circle	80

[a] The year and season refers to when the mark-recapture trapping was conducted. Winter trapping sessions extended into the next calendar year. The associated pellet counts were obtained in the summer following the given year (e.g., 1998 summer trapping was compared to summer 1999 pellet counts).

[b] Each trapping session lasted 3–5 nights.

[c] Large rectangles were 10 cm × 10 m for an area of 1 m^2. Small rectangle plots were 5.08 cm × 305 cm for an area of 0.155 m^2 (the same as used in the Yukon equations [Krebs et al. 1987, 2001]). Circles had a radius of 56.4 cm for an area of 1 m^2.

[d] This number applies to each type of plot.

Despite our efforts to maximize both trapping grid size and length of trapping session, numbers of captures remained small (<25 hares in >90% of sampling sessions), presenting challenges for the estimation of abundance. We initially explored the use of Program CAPTURE and its associated closed-population models (Otis et al. 1978, Pollock et al. 1990). There were no consistencies in the model selected by CAPTURE, as might be expected given the low power of the model selection procedure with small sample sizes (White et al. 1982, Menkens and Anderson 1988). We chose to estimate abundance with the 2-sample Lincoln-Petersen estimator (LP) adjusted for sample size (Chapman 1951, Seber 1982) for 3 reasons: (1) There was no compelling justification (either biologically or based on CAPTURE's model selection procedure) to assume the existence of a particular form of unequal trappability such as individual heterogeneity across all sites and times; if an estimator assuming a particular form of unequal trappability was used arbitrarily or inappropriately, the abundance estimates could be worse than those based on LP, especially at small sample sizes (Menkens and Anderson 1988, Manning et al. 1995). (2) LP can outperform other estimators in correctly determining relative abundance at small sample sizes (Davis et al. 2003). (3) The 2-sample LP estimator benefits from the pooling of ≥3 samples of trapping each session into 2 samples because number of captures in each sample is increased. Following Menkens and Anderson (1988), we divided the total number of trap nights approximately in half (if there was an odd number of nights, we included the extra day in the first session). We did not use minimum number known alive or total number captured as alternatives to abundance estimators because number of traps and trap nights differed among sites and years (McKelvey and Pearson 2001).

The conversion of estimated abundance to density requires estimation of effective area trapped (Bondrup-Nielsen 1983). We used the mean maximum distance moved method (Wilson and Anderson 1985, Karanth and Nichols 1998) whereby a grid-specific boundary width is 0.5 times the average maximum distance between traps for animals captured multiple times. Density estimates were based on the estimated abundance divided by the estimated effective area trapped (grid plus boundary), with accompanying variance incorporating the sampling variance of abundance and effective area. If there were multiple trapping sessions in a given site and season, we averaged them to derive $\hat{D}_{MR}$ for that season.

Pellet Sampling

Our pellet counts were based on 1-year accumulations, and they predicted hare density in the previous year (Table 1). Pellet plots in 1998 and 1999 were of the same rectangular shape recommended by Krebs et al. (1987, 2001), but they measured 1,000 cm × 10 cm = 1 m^2 instead of the original 305 × 5.08 cm = 0.155 m^2. To facilitate the use of the Yukon equations, which are based on the 0.155-m^2 plots, we multiplied the number of pellets counted on our 1-m^2 rectangle plots in 1998 and 1999 by 0.155. Because our ongoing work and that of others indicated that plot shape may influence the relationship between pellet counts and hare density, with 0.155-m^2 rectangles and 1-m^2 circles both recommended (McKelvey et al. 2002, Murray et al. 2002), we began using both of these plot shapes in 2000. Number of pellet plots per site ranged from 20 to 80 (Table 1).

Regression Analysis and Predicted Hare Density

The Seeley and Tally areas sampled over different sites, seasons, and years resulted in 224 data points with estimated hare densities and pellet counts (114 sampled using rectangle plots and 110 using circle plots). If we used each plot type (rectangle, circle) and each area-season-year combination (Table 1) to develop local pellet equations, there would be 11 Seeley equations (6 based on rectangle plots and 5 on circle plots) and 4 Tally equations (2 based on rectangle plots and 2 on circles). To explore the stability of the pellet-density relationship at this fine scale, we developed simple linear regression equations for these 15 local equations. The line was not constrained through the origin because at low hare densities, and given the temporal difference between when hares were captured and when pellets were deposited, it is biologically reasonable that either pellet counts or trapping estimates may be zero while the other is not.

The Yukon equation was based on sampling 10 sites for up to 9 years (Krebs et al. 2001). Therefore, we also created local Grand equations for Seeley and Tally that combined all sites sampled in all years (up to 5) in the summer for each area and for each pellet plot type ($N = 52$ for Seeley Grand rectangle, $N = 48$ for Seeley Grand circle, $N = 26$ each for Tally Grand rectangle and circle; we did not include the 72 Seeley winter plots). To make these equations comparable to the Yukon equation, we developed the Grand equations with ln-ln transformed functional regression (Krebs et al. 2001).

To simplify analysis and interpretation of the local (Montana) regression equations, we evaluated the relative effects of plot type (rectangle or circle), study area (Seeley or Tally), season (summer or winter), and year (1998–2001) on the relationship between pellets and hares. Using linear regression, we modeled all possible combinations of these variables, determining how they affected the pellet-density relationship.

Once we developed appropriate local regression equations, we asked how well each of the local Montana equations, or the Yukon equation, predicted hare densities in areas of Montana other than where the equation was developed. The predicted densities from pellets ($\tilde{D}$) came from a regression equation (Montana or Yukon) that used the mean number of pellets per plot at a particular site. The Yukon equation (Krebs et al. 2001) is:

$$\tilde{D}_{\text{Yukon}} = 1.567 * \exp(-1.203 + 0.889*\ln[\text{pellets}]).$$

We compared $\hat{D}_{\text{MR}}$ to $\tilde{D}$ using the percent deviation between the mark–recapture estimate and pellet-density prediction for a given grid during a given period:

Percent deviation = $([\tilde{D} - \hat{D}_{\text{MR}}] / \hat{D}_{\text{MR}}) \times 100$, omitting cases where $\hat{D}_{\text{MR}} = 0$.

We also calculated absolute deviation: $[\tilde{D} - \hat{D}_{\text{MR}}]$. This metric can be interpreted as how many more (or less) hares per hectare would be expected if one used pellet predictions instead of mark–recapture.

RESULTS

Capture probabilities averaged 0.5 for the Lincoln-Petersen estimator. However, hare abundances were low: 17 of 126 trapping sessions no hares were captured and >90% of sessions <25 hares were captured.

The linear regression that modeled all possible combinations of plot type, study area, season, and year on the relationship between pellets and hares indicated a strong relationship between hare densities and pellets ($P < 0.001$, $R^2 > 0.4$ in all cases; Table 2). Plot type

Table 2. *P*-values and R^2 for variables associated with the ability of pellet counts to predict snowshoe hare density in western Montana during 1998–2002. We used 224 data points, each of which had estimates of hare density and pellet counts. Data points come from 1 of 2 plot types (0.155-m^2 rectangle or 1-m^2 circle), 1 of 2 areas (Seeley or Tally), 1 of 2 seasons (summer or winter), and 1 of 5 years (1998–2002).

Model	Pellets	Plot type	Area	Season	Year	R^2
Pellets	<0.001					0.41
Pellets, plot type	<0.001	<0.001				0.46
Pellets, area	<0.001		<0.001			0.48
Pellets, season	<0.001			0.240		0.41
Pellets, year	<0.001				0.621	0.41
Pellets, plot type, area	<0.001	<0.001	<0.001			0.51
Pellets, plot type, season	<0.001	<0.001		0.340		0.46
Pellets, plot type, year	<0.001	<0.001			0.770	0.46
Pellets, plot type, area, season	<0.001	<0.001	<0.001	0.436		0.51
Pellets, plot type, area, year	<0.001	<0.001	<0.001		0.004	0.53
Pellets, plot type, area, season, year	<0.001	<0.001	<0.001	0.350	0.004	0.53

Table 3. The 4 natural logarithm (ln) transformed functional regression equations relating snowshoe hare pellets to estimated density in western Montana, USA, 1998–2002, and the Yukon equation (Krebs et al. 2001) for reference. The correlation coefficient *r* is presented to be comparable to Krebs et al. (2001). The *P* values for a *t*-test of the slope coefficient were all <0.005. The rectangular pellet plots were 0.155 m^2 and the circular plots 1 m^2.

Study area and plot type	*N*	Slope	95% CI	Intercept	*r*
Yukon rectangles	85	0.89	0.75–1.02	–1.20	0.76
Seeley Grand rectangles	52	1.16	0.85–1.47	–0.43	0.52
Tally Grand rectangles	26	0.73	0.52–0.94	–0.52	0.77
Seeley Grand circles	48	0.77	0.55–0.99	–1.67	0.51
Tally Grand circles	26	0.63	0.43– 0.83	–1.14	0.68

and study area were also significant, and together they explained an additional 10% of the variance between pellets and density. Season was not statistically significant in any models, and year was not significant in any models that did not also include plot type and area. Based on these results, we present detailed results for regression equations based on study area and plot type (i.e., the Seeley Grand and Tally Grand for rectangular and circular plots) but not for individual years. (The results at the level of individual years and seasons [e.g., Seeley Winter 2000, or Tally Summer 2001] show the same trends and may be found at http://www.forestry.umt.edu/JWM_hare_Mills.pdf).

The Seeley and Tally Grand equations developed with rectangular pellet plots showed similar intercepts but different slopes, with 95% confidence intervals barely overlapping each other (Table 3). Because these were ln-transformed functional regression equations using the same pellet plot type as Krebs et al. (2001) used, they can be directly compared to the Yukon equation; the Yukon equation slope of 0.89 falls between the Grand Seeley and Grand Tally slopes and within both of their confidence intervals. The Seeley and Tally Grand equations developed with circular plots differed from those developed with rectangular plots but were similar for the 2 areas (Table 3).

Concordance Between Densities Based on Pellet Predictions and MR Estimates

How well do either the Montana or Yukon equations, coupled with pellet counts, predict snowshoe hare density in Montana? Application of the 4 Montana equations and the Yukon equation to predict at different sites, seasons, and areas than those for which they were developed led to a surprising result (overall $N = 436$; Table 4); the Yukon equation, developed in a different area with different hare densities in a different decade, did not perform noticeably worse than the Montana equations. The median percent deviation when applying the Yukon equation to pellet data on rectangle plots was <50% in all but 1 case, with a mean of medians of –28.6% across all locations. By comparison, the mean of medians for the Seeley Grand and Tally Grand equations using rectangular pellet plots were 50% and 3%, respectively; for circular plots, the mean of medians was (–0.1%) for Seeley Grand and 76% for Tally Grand. Although not shown, the same trend held when we compared the predictions based on the Yukon equation against the 15 local regression equations developed using area-season-year-specific information (e.g., Seeley summer 1998 applied to all other sites-year-seasons; http://www.forestry.umt.edu/JWM_hare_Mills.pdf). Thus, the overall concordance between MR density estimates and pellet predictions using the Yukon equation and rectangle plots was not worse than most Montana regression equations developed with and applied to either rectangular or circular pellet plots.

Table 4. Median percent deviation ($100*(\tilde{D} - \hat{D}_{MR}) / \hat{D}_{MR}$) when a Yukon (Krebs et al. 2001) or Montana (Seeley or Tally grand) pellet-density regression equation was applied to pellet counts (using the same plot type) to predict hare density, 1998–2002. Positive deviations indicate that $\tilde{D}$ is > $\hat{D}_{MR}$; negative deviations indicate pellet counts ($\tilde{D}$) underpredict density relative to the mark-recapture estimates. We did not assess deviations in the same area where an equation was developed or when the pellet plot shape was not identical. Summaries are based on medians to minimize the effect of a few very large deviations. *N* indicates the number of deviations assessed in each application of 1 equation to other area-seasons.

	Seeley summer[a]					Seeley winter[a]		Tally summer[a]			Mean of
Area and plot type	1998	1999	2000	2001	2002	2000	2001	2001	2002	*N*	medians
Yukon rectangles	–51.9	–35.4	–25.8	–3.0		–44.1	–48.0	–22.4	2.1	114	–28.6
Seeley rectangles						–0.9	–11.3	70.8	140.7	62	49.8
Tally rectangles	–11.3	–13.9	9.2	57.7		–14.0	–8.6			88	3.2
Seeley circles						–3.5	9.8	0.8	–7.5	62	–0.1
Tally circles			73.5	220.7	51.9	20.4	13.9			110	76.1

[a] Each element is the median percent deviation for an area-season-year combination, comparing $\hat{D}_{MR}$ to the predicted $\tilde{D}$ from the equation indicated at the left of the row.

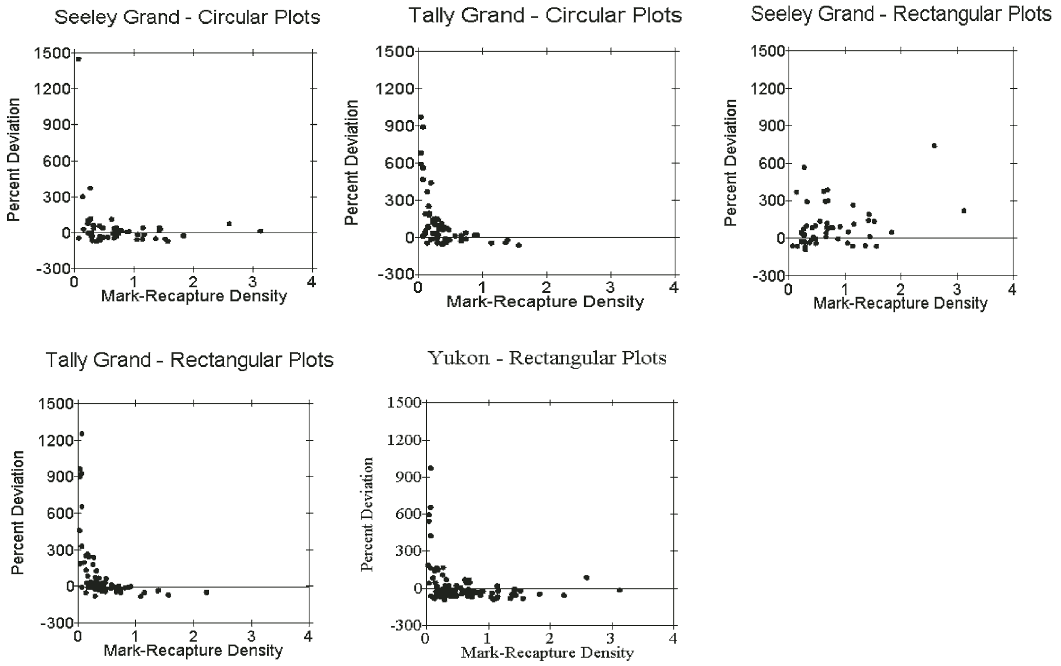

Fig. 2. The pattern of percent deviations {($\tilde{D}$ – $\hat{D}_{MR}$] / $\hat{D}_{MR}$) $\hat{D}_{MR}$ × 100} between snowshoe hare pellet plot predictions ($\tilde{D}$) and mark–recapture density estimates ($\hat{D}_{MR}$) in western Montana, USA, 1998–2002. Percent deviation is plotted for all applications of a particular pellet-density regression equation to predict hare density at area-year-season locations other than where the regression equation was developed. The place and plot names with each figure correspond to the data set used to estimate the regression. The solid line indicates zero percent deviation.

When we examined the concordance data (Table 4) more closely for each equation, percent deviation data tended to show slight negative percent deviations at higher hare densities and strongly positive percent deviations at very low hare densities (Fig. 2). Thus, at hare densities above about 0.7/ha, $\tilde{D}$ predictions tended to be lower than $\hat{D}_{MR}$, (i.e., negative percent deviations) with <100% deviations between the 2 measures. At hare densities below about 0.3/ha, however, pellets tended to predict hare densities greater than those estimated with mark–recapture. In some of these sites with the lowest hare densities, the percent deviation between the 2 measures was ≥1,000%.

A portrayal of the same data in terms of absolute deviations [$\tilde{D}$ – $\hat{D}_{MR}$] indicates that across all hare densities there was usually <1 hare/ha difference between predicted and estimated densities (Fig. 3); thus, the large percent deviations at low hare densities were mostly due to small hare densities in the denominator of the percent deviation equation. Like the percent deviation graphs, the absolute deviation graphs also showed the trend that pellet predictions ($\tilde{D}$) tended to be larger than $\hat{D}_{MR}$ at low hare densities (positive absolute deviations) but lower than $\hat{D}_{MR}$ at higher hare densities (negative absolute deviations).

DISCUSSION

An index can be a valid assay for trends in abundance of wildlife populations only if the relationship between the count index (pellets in this case) and true density does not systematically change (Pollock et al. 2002, Bart et al. 2005, Lancia et al. 2005). It is difficult to evaluate whether this is the case for snowshoe hare pellets because true density is unknown, and hares are sparse enough that both bias and low precision are likely inherent in not only pellet counts but also MR density estimators. Nevertheless, biologists and managers are using pellets to infer hare densities for the purposes of lynx management throughout the hare's geographic range, and that prompted us to explore the relationship between pellet-based density predictions and MR density estimates over time and space, and to ask whether hare studies would benefit from the use of locally developed pellet-density regression equations.

It is not surprising that regression equations developed in Montana with rectangular pellet plots differed from those based on circular plots. Although

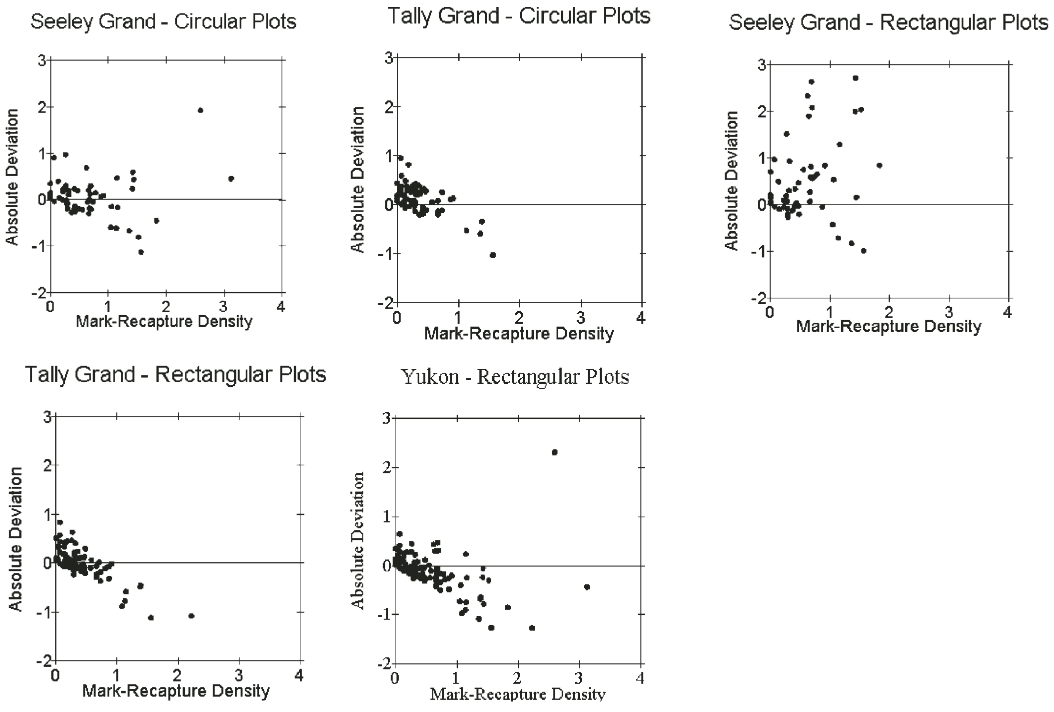

Fig. 3. The pattern of absolute deviations $\tilde{D} - \hat{D}_{MR}$] between snowshoe hare pellet plot predictions ($\tilde{D}$) and mark–recapture (MR) density estimates ($\hat{D}_{MR}$) in western Montana, USA, 1998–2002. Absolute deviation is plotted for all applications of a particular pellet-density regression equation to predict hare density at area-year-season locations other than where the regression equation was developed. The solid line indicates 0 deviation.

the most appropriate pellet sampling unit is still under discussion (e.g., McKelvey et al. 2002, Murray et al. 2002), density predictions from pellets should be based on the same pellet sampling frame as was used to develop the regression equation.

Pellet equations developed in different parts of Montana also varied, as did the strength of the correlation coefficients (0.51 to 0.77). Yet, regression equations showed the same general patterns between pellet-based predictions of density and mark–recapture (MR) estimates of density. At higher hare densities (>about 0.7 hares per ha), pellet predictions were usually within 100% of those of MR predictions and tended to be conservative predictors of density, indicating lower densities than mark–recapture based on the Lincoln-Petersen (LP) method. However, at low hare densities (below about 0.3 hares/ha), estimates of densities based on pellets ($\tilde{D}$) tended to be higher than those based on LP ($\hat{D}_{MR}$), by as much as 1,000%.

What mechanisms drive the consistent deviations between pellet- and MR-based density estimates? Mark–recapture sessions sample just 1 or a few periods, while pellets integrate densities and hare activity across the whole year. Thus, any hare that enters the grid at any time and defecates will leave pellets that could be sampled, which may explain why pellet-based densities are higher than mark–recapture at very low hare densities. Individual snowshoe hares produce >500 pellets per day (Hodges 1999), so just a few hares passing through an area could produce enough pellets for the observed pellet counts. At low hare densities, it is easy to imagine that one could observe pellets but not capture hares at a particular trap session.

In addition to the inherent differences in the time scale at which density is measured by pellets vs. trapping, the changing $\tilde{D}$ vs. $\hat{D}_{MR}$ relationship between high and low hare density could arise from bias in either pellet counts or $\hat{D}_{MR}$. Unfortunately, this issue is impossible to address from field data because we do not know true numbers of hares. However, the LP estimator of abundance is known to be negatively biased for small samples (Chapman 1951, Robson and Regier 1964, Seber 1982). We suspected that a mechanism driving our consistent pattern for percent deviations and absolute deviations was that, as hare density decreased, the $\hat{D}_{MR}$ became increasingly more negatively biased. We investigated this possibility through simulation and concluded that the negative bias of $\hat{D}_{MR}$ was insufficient to explain the disparity between $\tilde{D}$ and $\hat{D}_{MR}$ (K. McKelvey and L. S. Mills, unpublished simulations). Furthermore, the characteristic deviation patterns were manifest in the Yukon equation developed using different MR estimators and spanning much higher densities over 10 years.

We were surprised that the Yukon equation performed about as well as the Montana-derived regression equations in predicting Montana hare densities from pellets because the equation was developed at higher hare densities, in different forest types, and using different methods for estimating D_{MR} than in Montana. The Yukon equation did not lead to proportionate or absolute deviations substantially greater than most of the locally derived equations. In fact, the Yukon equation was similar to the locally derived equations, with a slope value between our 2 Grand local equations based on 0.155-m^2 rectangular plots and within both of their confidence intervals. The Yukon equation also worked reasonably well (compared to locally derived equations) at predicting hare densities in Idaho (Murray et al. 2002).

Ultimately, individual researchers must decide whether our results are an indictment against or an endorsement in favor of the use of pellets to sample snowshoe hare density. At low hare densities, hare pellet counts are likely to indicate densities that are much higher proportionally than are mark–recapture estimates. We do not know true numbers, so we cannot say whether pellet predictions or mark–recapture estimates (or both) are wrong. Both mark–recapture estimates and count-derived pellet estimates have potential for bias and low precision at low hare numbers (Pollock et al. 1990; Williams et al. 2002; K. E. Hodges and L. S. Mills, University of Montana, unpublished data). The small-sample problem cannot be resolved with larger grid sizes due to habitat heterogeneity, nor with increased trapping sessions due to stress on the animals. Thus, we conclude that when hare densities are <0.3 hares/ha we lack the tools to say much other than that densities are very low.

However, the positive correlation between pellets and $\hat{D}_{MR}$ implies that, in general, few pellets means few hares. Further, even though the proportional difference between $\tilde{D}$ and $\hat{D}_{MR}$ at low density is high, the absolute difference is modest. Therefore, it appears that pellets have an appropriate role in screening for areas of very low hare density (below 0.3 hares/ha), where abundance is hard to estimate and where the biological importance of hares as prey for sustaining lynx populations is probably limited. Specifically, if mean pellet counts on rectangular plots were <0.6 pellets (converting to 0.3 hares/ha with the Yukon equation) one could safely conclude that these areas were in the low hare density range, as MR estimates on these sites would likely indicate even fewer hares. In such areas it may be less useful to ask questions about hare density and more meaningful to turn to other metrics such as proportion of area occupied (Bailey et al. 2004).

Above 0.7 hares/ha, pellet counts typically underestimate the mark–recapture density by a relatively small amount. When $\hat{D}_{MR}$ exceeded 0.7 hares/ha, most (52%) of the pellet predictions based on $\tilde{D}_{Yukon}$ exceeded 0.7 hares/ha (62% exceeded 0.6 hares/ha). Thus, densities in excess of 0.7 hares/ha can be surmised from either $\hat{D}_{MR}$ > 0.7 hares/ha or from mean pellet counts exceeding 1.6 in rectangular plots ($\tilde{D}_{Yukon}$ > 0.7 hares/ha). Whether the underestimate of $\tilde{D}$ compared to $\hat{D}_{MR}$ at higher hare density is a barrier to reliable inference, and therefore whether mark–recapture should be employed, depends on perspective. For example, using the Yukon equation, 1 site sampled in 1998 had a predicted hare density of 0.95 and an estimated $\hat{D}_{MR}$ of 2.2 hares/ha, leading to a percent deviation of –57% and an absolute deviation of –1.3 hares/ha; most of our observations had smaller deviations. Whether such a difference is problematic depends on the research or management question being asked, but this is a zone where mark–recapture estimates will perform well.

If pellet counts per rectangular plot fall between 0.6 and 1.6 ($\tilde{D}_{Yukon}$ between 0.3 and 0.7 hares/ha) and fine density discrimination is required, it is essential to obtain more information using mark–recapture. In 83% of our cases where pellet counts fell between 0.6 and 1.6, the 2 measures of hare density were within 100% and within 0.5 hares/ha of each other. However, at these densities, a concordance within 0.5 hares/ha is not necessarily helpful. If a high resolution regarding density is required in this zone, as is the case when a particular number is proposed as a threshold for lynx persistence (0.5 hares/ha: Mowat et al. 2000, Ruggiero et al. 2000; or 1.1 hares/ha: Steury and Murray 2004), pellets alone are insufficient. In these instances, a well-planned mark–recapture study is necessary. If there is a pressing interest in using the pellets to infer densities, then a double sampling approach (whereby pellet count data are collected at many sites and density is estimated using mark–recapture at a subset of sites) could be valuable (Eberhardt and Simmons 1987, Williams et al. 2002). This approach requires reliable density estimates and a strong relationship between the pellet counts and the mark–recapture estimates; both of these are compromised at very low hare abundances, reinforcing our recommendation to screen out low density sites by using extensive pellet surveys prior to trapping.

MANAGEMENT IMPLICATIONS

We support the strong recommendations of others to use a rigorous mark–recapture framework to estimate abundance whenever possible (e.g., Nichols and Pollock 1983, Pollock et al. 2002, Lancia et al. 2005). However, in the western continental United States where hare population dynamics in fragmented habitats are of intense concern because of their importance to threatened lynx, hare densities will often be too low to produce precise and unbiased estimates.

To the extent that our 5-year, large-scale study of hare densities using pellets and mark–recapture in Montana reflects the pellet-hare relationship in other regions, we recommend the following procedure for snowshoe hare studies across large spatial scales. As a first step toward evaluating hare densities at new sites, we suggest pellet counts on 0.155-m^2 rectangular plots (5 cm × 3.1 m) at a sampling intensity of >50 plots/site (K. E. Hodges and L. S. Mills, unpublished data). Although our results indicate that circular plots performed comparably to rectangular plots, we recommend small rectangles because researchers can use the reasonably reliable Yukon equation (Krebs et al. 2001) with the 0.155-m^2 plots but not with 1-m^2 circular plots (McKelvey et al. 2002). Next, the pellet counts can be converted to density predictions using the Yukon equation (Krebs et al. 2001) and categorized into zones of relatively low, medium, and high apparent snowshoe hare density.

If mean pellet counts on 0.155-m^2 rectangular plots are <0.6 pellets (converting to <0.3 hares/ha with the Yukon equation) it would be prudent to conclude that the area had low hare density, without needing to use mark–recapture sampling. If pellet counts fall between 0.6 and 1.6 ($\tilde{D}_{\text{Yukon}}$ between 0.3 and 0.7 hares/ha), and if absolute density is of interest, then pellet sampling should be followed by mark–recapture sampling, with every attempt to maximize grid size. If pellet counts exceed 1.6 ($\tilde{D}_{\text{Yukon}} > 0.7$ hares/ha), the area could be considered to have relatively high hare densities, and mark–recapture studies would likely provide sound estimates of absolute densities over time and space. Finally, we stress that characterizing hare density with any method requires extensive sampling over time and space, and lynx management for an area ultimately depends on more than an estimate of hare density.

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