

Snowshoe hare pellet-decay rates and aging in different habitats

Laura R. Prugh and Charles J. Krebs

Abstract Snowshoe hare (*Lepus americanus*) pellet surveys are an efficient tool for monitoring population trends, but there is no standard methodology used to conduct surveys. To assist researchers in developing protocols, we evaluated pellet-decay rates and aging in 3 snowshoe hare habitat types in Alaska during the peak and decline of the hare population from 1999–2002. We found significant differences in decay rates among habitat types and recommend measuring decay rates if pellet counts are to be compared among habitats or regions. Our experiments with known-age pellets indicated that pellets could not be aged reliably, but results from side-by-side comparisons of survey methods provided contrary evidence. Counts from uncleared plots, in which observers subjectively decided whether pellets were “new” (<1 year old), were not statistically different from counts on annually cleared plots. We evaluated 4 methods for conducting pellet surveys: 1) cleared plots with counts of “new” pellets; 2) cleared plots with counts of all pellets; 3) uncleared plots with counts of “new” pellets; 4) uncleared plots with counts of all pellets. Annual trends in pellet counts were similar using the first 3 methods, but counts from method 4 were inflated in 2002 due to a high prevalence of “old” pellets. We conclude that cleared plots are preferable to uncleared plots, and we suggest that using subjective criteria to age pellets may be useful if tallies are kept of both “new” and “old” pellets for each plot.

Key words Alaska, decomposition, density estimate, fecal pellet counts, *Lepus americanus*, population index

Indices of population size are commonly used in ecological studies because obtaining actual abundance estimates can be costly and time-consuming. For a population index to be useful, it must be a precise and accurate indicator of change in actual population density. Fecal pellet counts often are used as a population index for snowshoe hares (*Lepus americanus*), as the relationship between pellet counts and hare density has been shown to be precise and accurate over a wide range of densities (Krebs et al. 1987, Krebs et al. 2001).

With the listing of the Canada lynx (*Lynx canadensis*) as threatened in the United States and recent lynx reintroductions to Colorado, wildlife managers are under pressure to estimate snowshoe hare densities over large areas because hares are the primary food source for lynx (Kloor 1999,

Ruggiero and McKelvey 2000). Pellet plots are being used extensively, but the relationship between pellets per plot and hares per hectare may not be consistent across large geographical areas. Krebs et al. (2001) caution researchers against using their regression equation to predict hare densities from pellet counts without further testing of the relationship. Differences in pellet-decay rates, defecation rates, or survey methods could affect the number of pellets detected in surveys across North America (e.g., Smith 1964, Harestad and Bunnell 1987, Lehmkuhl et al. 1994, Massei et al. 1998). Most studies that have used pellet counts to infer habitat-specific hare abundance have not measured decay rates, though differential decay rates could lead to faulty conclusions about relative hare density in different habitat types (e.g., Wolfe et al. 1982,

Authors' address: Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, BC, V6T 1Z4, Canada; e-mail for Prugh: prugh@zoology.ubc.ca.

Pietz and Tester 1983, Koehler 1990, Malloy 2000).

In addition to considerations of geographic scale and habitat-specific differences, managers must consider methodology when designing a hare pellet survey. Most surveys use permanent plots that are cleared periodically, with researchers either counting all pellets together or subjectively deciding whether pellets are new or old. Alternatively, uncleared plots may be used (Eaton 1993, Langbein et al. 1999), and researchers may or may not attempt to age pellets.

The ability to age pellets accurately would be useful for 2 main reasons. First, losses in data collection would be reduced because researchers would be able to use the first year of data, when plots are established and not yet cleared. Researchers may also wish to add new plots to existing grids to increase sample size (Krebs et al. 2001). Second, the confounding effects of old pellets would be reduced. Old pellets may be kicked into the plot by humans and wildlife or roll into the plot if the grid is on a hillside. Counting all pellets in uncleared plots regardless of age may produce results that are difficult to interpret, because old pellets persisting for years could mask annual population trends or cause the survey data to lag behind actual trends. In particular, old pellets could obscure detection of a population decline, which is a population trend of particular interest for lynx conservation. Though some researchers have used subjective criteria to age pellets (Eberhardt and Etten 1956, Krebs et al. 1987, Loft and Kie 1988, Krebs et al. 2001), none have tested their criteria against observations of pellets of known age.

In this paper we present data on snowshoe hare pellet-decay rates and aging in 3 habitat types in central Alaska. We monitored pellets of known age using pellet cages, and we compared pellet survey methods to examine the effect of pellet age and decay rates on pellet-count data. Our objectives were to measure habitat-specific pellet-decay rates, evaluate whether pellets can be aged accurately, and compare counts between cleared and uncleared plots.

Study area

This study was conducted from May 1999–July 2002 in the central Alaska Range (63°57'N, 147° 18' W). The area encompassed 1,000 km² of mountains and foothills on the northern edge of the range, approximately 80 km south of Fairbanks. Average



Snowshoe hare browse and winter fecal pellets during peak hare abundance, January 1999 in the Alaska Range.

June temperatures during this study were 14°C, and average January temperatures were -10°C. Average annual precipitation was 350 mm, and snow cover usually persisted from October through April. Snowshoe hare habitat consisted of willow (*Salix* spp.) and alder (*Alnus* spp.) thickets and closed-canopy white spruce (*Picea glauca*) forests, and these cover types made up approximately 43% of the study area (unpublished data).

Methods

Pellet cages

We collected fresh hare pellets from the top of the snow layer in January 2000 and stored them frozen until May 2000. We constructed 30 pellet cages (25 × 25 × 15 cm high) out of 6.3-mm mesh hardware cloth. This mesh ensured that pellets could not enter or leave the cage. The bottom of the cage was open, but the top was covered in hardware cloth to prevent new pellets from entering during winter, when snow cover would allow hares to freely walk and defecate above them. We placed 10 cages in each of 3 permanently estab-

lished pellet-count grids, in 3 different snowshoe hare habitat types: spruce (thick, mossy ground cover), willow (riparian gravel bar), and alder (deciduous litter and mossy ground cover).

We placed 30 fresh pellets under each cage after removing pre-existing pellets. We established cages 17 May 2000 and checked them monthly through-out summers 2000 and 2001. The final check was in June 2002. At each check we counted pellets and recorded outer color, texture, and moisture. We categorized overall pellet moisture in each cage as wet, damp, or dry during each session ($n=206$). In addition, we removed and broke 2 pellets to examine inner color. We recorded whether pellets appeared “new” or “old” (i.e., less than or more than 1 year old) based on our subjective aging criteria, which we had adopted from the methods of the Kluane Boreal Forest Ecosystem Project (Krebs et al. 2001). Based on these criteria, we considered a pellet “new” if it had a greenish hue on the inside, and “old” if it was brownish inside. To a lesser extent, we considered outer color; most pellets that were light orange outside were considered new, and most pellets that were dark brown or black outside were considered old.

We analyzed differences in pellet-decay rates using repeated-measures ANOVA. We considered pellets decayed if they were missing or more than half decomposed. We compared the proportion of pellets surviving in each cage among habitat types at 4 intervals: 4 months, 12 months, 16 months, and 24 months. Arcsine square-root transformation of data did not affect statistical results, so untransformed data are presented. A Kaplan-Meier survival analysis of pellets gave the same results but is not reported.

Pellet plots

The data set for this study was 64,838 pellets counted on 2,654 plots over 4 years. We established 8 grids during the summer of 1999 throughout the study area in 3 habitat types (spruce, willow, and alder) and established 5 more grids in the following years (2000–2002). We established at least 50 permanent plots spaced 15 m apart on each grid; on grids with higher variability, we added more plots (4 of the 13 grids had >50 plots; max = 126 plots). We used circular plots of 25-cm radius (0.20 m²) on grids with high pellet density and used plots of 50-cm radius (0.79 m²) on grids with low pellet density. We counted and cleared plots once per year.

Each year of this study, a project leader (L. Prugh) and 1–3 field assistants conducted pellet surveys. In total, 8 different observers counted pellets during the 4-year study, and each assistant received the same training from the project leader. We used the same pellet survey protocol for cleared and uncleared plots. To delineate the plots, we rotated a string of the appropriate radius around a metal stake situated at the plot center. To reduce observer subjectivity, we included in the count every pellet that had any overlap with the plot boundary. We removed all pellets and leaf litter from plots during the counts.

We recorded separate tallies of new and old pellets for each plot using the aging criteria described above. Pellets <4 mm were excluded from counts because they disappeared into moss and were found only on willow gravel bar grids. We made no distinction between summer and winter pellets, except that summer pellets tended to have a darker outer color and therefore the aging criteria was based almost exclusively on inner color for summer pellets (summer pellets were irregularly shaped and dense



Pellet cages used to study decay rates and aging of snowshoe hare feces in the Alaska Range, 2000–2002.

due to succulent forage, whereas winter pellets were uniform in shape and tended to be larger).

We examined pellet plot data to determine whether the proportion of pellets considered "new" varied by habitat type, observer, or year (i.e., phase in the hare cycle). Data were arcsine square-root transformed prior to analysis, and we conducted a 2-factor analysis of variance using year as one factor and observer or habitat type as a second factor.

We conducted an experiment in June 2000 to determine whether grid estimates differed using cleared versus uncleared plots. We made 2 side-by-side comparisons of cleared and uncleared plots using 1 willow and 1 alder grid. In both grids, cleared plots had a 25-cm radius and had been cleared the previous summer. We conducted uncleared-plot counts 3 m from each cleared plot. We used the Wilcoxon paired-sample test to test for differences in counts of new pellets from cleared and uncleared plots to examine the validity of aging criteria. We conducted all statistical analyses using JMPIN 4.0 (SAS Institute 2000).

Results

Habitat-specific decay rates

Pellet-decay rates were significantly higher in alder and spruce habitats compared with willow ($F_{2,26}=5.11, P=0.01$), but alder and spruce sites had similar decay rates (Figure 1). Only 1% of pellets in the willow habitat disappeared after 1 year, whereas 14% of pellets disappeared after 1 year in alder and spruce sites. Median persistence time of pellets in the environment was approximately 6 years.

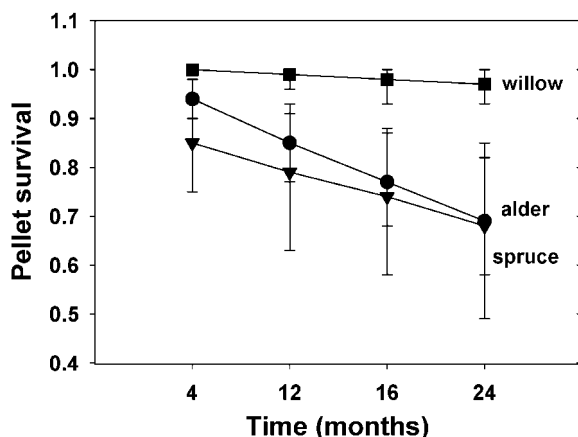


Figure 1. Decay rates of snowshoe hare pellets in 3 habitat types in Alaska. Pellets of known age were placed in cages and monitored from May 2000–June 2002 ($n = 30$ pellets per cage, 10 cages per habitat type). Error bars show 95% confidence limits from bootstrapped means.

The difference in decay rates among habitat types may be related to differences in moisture. Pellets in the alder grid tended to be wet or damp more often than pellets in the spruce grid (Likelihood Ratio $\chi^2_1=3.75, P=0.053$), and pellets in the spruce grid tended to be wet or damp more often than pellets in the willow grid ($\chi^2_1=3.64, P=0.056$; overall $\chi^2_2=14.4, P<0.001$).

Reliability of aging criteria

After 1 summer of monitoring caged pellets of known age, our subjective aging criteria correctly classified 88% of pellets as new ($n=60$). After 1 year, however, 48% of pellets were still classified as new ($n=60$). After 2 years, 30% of pellets were classified as new ($n=30$). Thus, even after 2 years, 30% of pellets still appeared new based on our aging criteria. These results indicated that our subjective aging criteria were highly inaccurate. We did not notice a diagnostic trait in pellet appearance that would indicate whether a pellet was greater or less than 1 year old.

Based on these data, we predicted that counts of new pellets on uncleared plots would be higher than counts of pellets on cleared grids, since the cage experiment indicated that pellets tended to be incorrectly classified as new more often than vice versa. To test this prediction, we conducted 2 side-by-side comparisons of cleared and uncleared plots in June 2000. In both cases, counts of new pellets did not differ between plot types (alder: $Z_{1,43}=-1.24, P=0.21$; willow: $Z_{1,47}=1.36, P=0.17$; Figure 2).

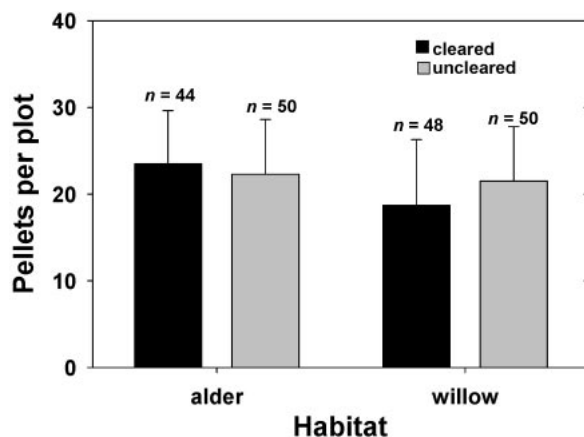


Figure 2. Side-by-side comparisons of snowshoe hare pellet counts in cleared and uncleared plots in 2 habitat types in Alaska, June 2000. Data presented were from counts of "new" pellets only (pellets judged to be <1 year old). Sample sizes indicate the number of plots for each treatment, and error bars show 95% confidence limits from bootstrapped means.

Our next analyses investigated whether the ability to age pellets accurately varied by habitat type. After 4 months there were no habitat-specific differences in the appearance of caged pellets (Fisher's Exact Test, $P=0.48$). After 1 year, however, most caged pellets still appeared new in the willow habitat, whereas most pellets were aged correctly in spruce and alder habitats (Likelihood Ratio $\chi^2_2=10.6$, $P=0.005$, Table 1). After 2 years, there were no significant differences in pellet appearance among habitat types (Fisher's Exact Test, $P=0.88$).

The proportion of pellets considered new versus old differed significantly among habitat types and years during the pellet plot surveys from 1999–2002. Five percent more pellets were considered new in spruce than in willow plots, and 6% more pellets were considered new in willow than in alder plots ($F_{2,2598}=36.8$, $P<0.001$). This pattern was inconsistent with data from the pellet cage experiments, in which pellets looked newer in willow than in spruce and alder sites.

The proportion of pellets considered new in plot counts was not significantly different between 1999 and 2000, but declined significantly from 2000–2002 (range = 0.37–0.75; $F_{3,2598}=223.7$, $P<0.001$). This trend most likely occurred due to a decline in snowshoe hare numbers during these years: pellet counts were not significantly different between 1999 or 2000 but declined from 2000–2002 ($F_{3,2650}=173.9$, $P<0.001$), and winter track counts of hares declined from 2000–2002 (unpublished data). Thus, proportionally fewer new pellets were encountered during years when hare densities were declining.

Since most pellets appear borderline with respect to age, the potential for observer bias in aging pellets is high. To test for observer bias in aging pellets, the proportion of pellets in each plot

considered new was compared among observers. We lumped together assistants in years with more than one field assistant because the project leader conducted approximately 50% of plots each year. Despite consistent training among the 8 observers, there was observer bias in the proportion of pellets considered new in 3 out of 4 years for uncleared plots ($F_{1,1175}=33.3$, $P<0.001$) and in 2 out of 3 years for cleared plots ($F_{1,1421}=12.6$, $P<0.001$). On average, the project leader considered 10% more pellets per plot to be new than assistants did.

Pellet counts from cleared and uncleared plots

Our results indicated that aging pellets was inconsistent and arbitrary. In our direct side-by-side comparisons in which we counted new pellets on cleared and uncleared plots, however, we did not find any difference in the counts. In this section we go further and ask what the count data look like from our full surveys with and without aging pellets. Specifically, we addressed 4 types of counts:

1. On cleared plots, we kept separate tallies for new and old pellets and used the “new” tally as the plot count
2. On cleared plots, we summed these tallies and used the total count
3. On uncleared plots, we kept separate tallies and used the “new” tally
4. On uncleared plots, we summed tallies and used the total count

For cleared plots, counts of all pellets showed similar trends over time as counts of new pellets only (Figure 3, Table 2). For uncleared plots, however, pellet aging had a strong impact on trends. Counts of new pellets from uncleared plots matched trends of cleared plots, particularly in 2001 and 2002, but counts of all pellets in uncleared plots deviated sharply in 2002 and were higher than other methods in all years (Figure 3). Winter track counts provide an independent measure of relative hare density and show a steady decline from 2000–2002 consistent with pellet data from cleared plots and from uncleared plots using new pellets only (unpublished data).

Discussion

We found significant differences in pellet-decay rates in different snowshoe hare habitat types and

Table 1. Appearance of known-age snowshoe hare pellets after 1 year in 3 habitat types in Alaska, May 2000–May 2001. Pellets were considered “new” or “old” based on a priori aging criteria.*

Habitat	Pellet appearance		Totals
	New	Old	
Alder	5	15	20
Willow	15	5	20
Spruce	9	11	20
Totals	29	31	60

* 100% accuracy would have resulted in all pellets recorded as old.

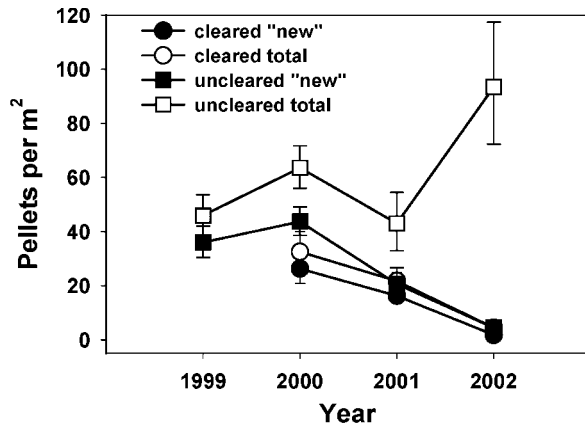


Figure 3. Annual estimates of snowshoe hare pellet density from plots that were previously cleared (circles), 2000–2002 and from uncleared plots (squares), 1999–2002. Open symbols represent total counts of pellets, and filled symbols represent counts of "new" pellets only (pellets judged to be <1 year old). Error bars represent 95% confidence limits, calculated using bootstrapping methods.

recommend that researchers measure decay rates if fecal counts are to be compared among habitats. We also recommend that researchers use cleared plots to conduct surveys. We found pellet aging to be of questionable usefulness, as our results were mixed. Although we recommend that researchers use aging criteria in certain circumstances, more evaluation of aging criteria is needed. We explain the reasoning behind these recommendations below.

Pellet-decay rates. When using pellet counts to compare relative hare abundance in different habi-

Table 2. Grid and plot sample sizes* for snowshoe hare pellet surveys in Alaska, 1999–2002.

	Year			
	1999	2000	2001	2002
Cleared plots				
<i>n</i> plots		453	590	552
<i>n</i> grids		8	10	9
Uncleared plots				
<i>n</i> plots	485	373	142	59
<i>n</i> grids	8	8	3	1

* A total of 13 different grids were established over the course of the study, and plots were "uncleared" the first year of establishment and "cleared" in subsequent years of sampling. For example, in 1999 all plots were uncleared because it was the first year of our study, and these were the cleared plots in 2000 (the slight drop in sample size was due to plot markers disappearing between years). Therefore, cleared and uncleared plots were counted on different grids, except when pre-established grids were expanded to include more plots (4 grids were expanded in 2000 and 3 were expanded in 2001).

tats, habitat-specific decay rates are an important consideration. This study has shown that habitat type can affect pellet-decay rates, which was likely due to differences in microsite moisture levels and substrate type. Other pellet-decay studies have found moisture to be the most important factor influencing decay rates (e.g., Wigley and Johnston 1981, Harestad and Bunnell 1987, Lehmkuhl et al. 1994, Massei et al. 1998). On average, pellets in our study area had relatively low decay rates, similar to the long persistence time of pellets thought to occur at Kluane, Yukon (C. Krebs, personal observation).

The presence of leaf litter, like moisture, can accelerate the degradation of hare pellets (Eaton 1993). Leaf litter was excluded in this study, as the cages were close-topped to prevent new pellets from entering over winter. Thus, actual decay rates may be higher than those reported in this paper, particularly in sites with a deciduous overstory.

Conducting a pellet-decay study requires minimal effort and is recommended for all researchers using pellet plots, particularly when actual hare density estimates are lacking. Pellet cages ensure that pellets are of known age, but they protect pellets from natural processes such as trampling from animals and litter accumulation. Covering pellets with loose mesh fabric, in which leaf litter would be in direct contact with pellets, would allow researchers to ensure that pellets are of known age while maximizing exposure of pellets to natural processes. Measuring decay rates of summer pellets as well as winter pellets would also be advantageous, as rates could differ between pellet types and affect plot counts.

Knowing the magnitude of decay rates may also help researchers determine whether plot clearing will affect data quality, because areas with low decay rates will have a higher prevalence of old pellets than areas with high decay rates. If pellets decay at a rapid rate (i.e., within 6 months), researchers may need to conduct surveys more than once a year to obtain data that are comparable to other studies.

Pellet aging and plot clearing. We found that aging pellets was inaccurate, affected by habitat type, and prone to observer bias. The pellet cage experiment indicated that old pellets often appeared new, whereas new pellets rarely appeared old. However, we found no difference in mean counts of "new" pellets on cleared and uncleared plots during our side-by-side comparisons. These

results indicated that the subjective criteria used to age pellets may be more accurate than the cage experiments suggest. This discrepancy may be due to the exclusion of leaf litter from the pellet cages because leaf litter probably darkens pellets and causes them to appear older. The influence of leaf litter may also explain the habitat-specific differences in pellet appearance found in our surveys. The amount of leaf litter decreases from alder to willow to spruce habitats, and the proportion of pellets considered "old" in the surveys decreased in that order as well.

Observer bias previously has been reported for pellet-count data (Eberhardt and Etten 1956, Murray et al. 2002), so it is not surprising that we found observer bias in the subjective aging of pellets. We attempted to minimize bias by frequently consulting each other regarding questionable pellets, but this was phased out once the observers were consistently agreeing with each others' decisions. It was likely the observers later deviated from one another, with the project leader being more inclined to call borderline pellets "new" than assistants were. A systematic approach to observer training and rechecking, employed for the duration of the project, is recommended to minimize observer bias.

Despite these biases and the questionable ability of observers to accurately age pellets, annual trends from uncleared plots in which only new pellets were included had mean counts similar to those of cleared plots using either new pellets only or all pellets. This pattern indicated that using consistent aging criteria may allow researchers to obtain data from uncleared plots that are comparable to data from cleared plots. Though our evidence on the validity of pellet aging was mixed, we believe there is enough promise in our results to warrant further investigation.

Of the 4 survey methods evaluated in this paper (counting new pellets in cleared plots, all pellets in cleared plots, new pellets in uncleared plots, and all pellets in uncleared plots), the only method that appeared inaccurate was counting all pellets in uncleared plots. The inaccuracy was primarily due to the 2002 survey, in which counts from this method were greatly inflated compared with the other methods and winter track counts. Counts from uncleared plots in 2002 were from one grid that was added in the alder, the preferred hare habitat type. The abundance of old pellets in this area may therefore be unusually high, but it highlights

the potential problem of using total counts from uncleared plots to track hare density in areas with large population fluctuations and multi-annual pellet persistence.

Poor performance of total counts from uncleared plots makes sense from a theoretical standpoint as well. In our study area, pellets disappeared at an average rate of 10% per year. If all the hares were suddenly removed from this area, a survey using total counts from uncleared plots would show only a 10% population decline each year, whereas cleared plots would show the absence of hares in the first survey. In fact, uncleared plots should be less accurate than cleared plots any time hare populations decline more rapidly than pellet-decay rates.

Based on our results, we recommend that researchers use cleared plots and keep separate tallies of new and old pellets. Tallies can always be summed to avoid problems and biases associated with pellet aging. Although the confounding effects of old pellets were negligible on our cleared plots, aging pellets is still worthwhile because it allows researchers to expand grids of cleared plots or add grids without losing a year's worth of data. Studies that have examined the effect of pellet density on the precision of counts recommend increasing sample size when pellet densities are low (Krebs et al. 2001). The ability to use a mixture of cleared and uncleared plots would increase the feasibility of a variable sample size design. More testing with pellets of known age, subjected to natural conditions (including leaf litter), are needed before pellet aging can be employed with confidence.

If resources do not permit the added time necessary for observer training and testing of aging criteria, we recommend that researchers use total counts from cleared plots. Cleared plots are preferable to uncleared plots from the perspective of data quality, as the researcher has much greater certainty in the time frame being sampled. If researchers choose to use uncleared plots, our results indicate that attempting to age pellets will be worth the added time, as data from total counts on uncleared plots may be invalid.

It should be noted that these recommendations are based on data from an area with relatively low pellet-decay rates. In areas with higher decay rates, old pellets would make up a more negligible component of the pellet population and might not confound results. If the majority of pellets decay within one year, for example, plot clearing would not be

necessary to obtain a good annual index of hare abundance.

In summary, we recommend using cleared plots to conduct pellet surveys, and we highlight the importance of measuring pellet-decay rates in different habitat types. We strongly caution against the use of total counts on uncleared plots, particularly in areas with large fluctuations in hare numbers, unless most (>90%) pellets decay within one year. We suggest that aging pellets may be a useful tool, but more experiments with pellets of known age subjected to natural conditions are needed to test the validity of pellet aging.

Acknowledgments. Funding for this project was provided by the Alaska Department of Fish and Game (ADF&G) and the Natural Sciences and Engineering Council of Canada. L. Prugh was supported by a National Science Foundation Graduate Fellowship during fieldwork, and by a Welder Wildlife Foundation Fellowship during manuscript preparation (Contribution # 604). ADF&G provided logistical assistance, and housing in private cabins was generously provided by the Newman Creek shareholders, the Rockstads, and the Burnells. Field assistance was provided by A. Hayward, M. Tung, J. Hughes, L. Butler, S. Szepanski, P. Del Vecchio, and S. Arthur. Earlier versions were improved by comments from K. Hodges, T. Karels, D. Murray, K. McKelvey, and 3 anonymous reviewers.

Literature cited

- EATON, B. R. 1993. Estimates of snowshoe hare abundance from pellet plot counts: a critical evaluation. Thesis, Acadia University, Wolfville, Nova Scotia, Canada.
- EBERHARDT, L., AND R. C. V. EITEN. 1956. Evaluation of the pellet group count as a deer census method. *Journal of Wildlife Management* 20:70-74.
- HARESTAD, A. S., AND F. L. BUNNELL. 1987. Persistence of black-tailed deer fecal pellets in coastal habitats. *Journal of Wildlife Management* 51:33-37.
- KLOOR, K. 1999. Conservation biology—Lynx and biologists try to recover after disastrous start. *Science* 285:320-321.
- KOEHLER, G. M. 1990. Snowshoe hare, *Lepus americanus*, use of forest successional stages and population changes during 1985-1989 in north-central Washington. *Canadian Field-Naturalist* 105:291-293.
- KREBS, C. J., R. BOONSTRA, V. NAMS, M. O'DONOGHUE, K. E. HODGES, AND S. BOUTIN. 2001. Estimating snowshoe hare population density from pellet plots: a further evaluation. *Canadian Journal of Zoology* 79:1-4.
- KREBS, C. J., B. S. GILBERT, S. BOUTIN, AND R. BOONSTRA. 1987. Estimation of snowshoe hare population density from turd transects. *Canadian Journal of Zoology* 65:565-567.
- LANGBEIN, J., M. R. HUTCHINGS, S. HARRIS, C. STOATE, S. C. TAPPER, AND S. WRAY. 1999. Techniques for assessing the abundance of Brown Hares, *Lepus europaeus*. *Mammal Review* 29:93-116.
- LEHMKUHL, J. E., C. A. HANSEN, AND K. SLOAN. 1994. Elk pellet-group decomposition and detectability in coastal forests of Washington. *Journal of Wildlife Management* 58:664-669.
- LOFT, E. R., AND J. G. KIE. 1988. Comparison of pellet-group and radio triangulation methods for assessing deer habitat use. *Journal of Wildlife Management* 52:524-527.
- MALLOY, J. C. 2000. Snowshoe hare, *Lepus americanus*, fecal pellet fluctuations in western Montana. *Canadian Field-Naturalist* 114:409-412.
- MASSEI, G., P. BACON, AND P. V. GENOV. 1998. Fallow deer and wild boar pellet group disappearance in a Mediterranean area. *Journal of Wildlife Management* 62:1086-1094.
- MURRAY, D. L., J. D. ROTH, E. ELLSWORTH, A. J. WIRSING, AND T. D. STEURY. 2002. Estimating low-density snowshoe hare populations using fecal pellet counts. *Canadian Journal of Zoology* 80:771-781.
- PIETZ, P. J., AND J. R. TESTER. 1983. Habitat selection by snowshoe hares in north central Minnesota. *Journal of Wildlife Management* 47:686-696.
- RUGGIERO, L. E., AND K. S. MCKELVEY. 2000. Toward a defensible lynx conservation strategy: a framework for planning in the face of uncertainty. Pages 5-20 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. *Ecology and conservation of lynx in the United States*. University Press of Colorado, Denver, USA.
- SAS INSTITUTE INC. 2000. JMP-IN 4.0. Cary, North Carolina, USA.
- SMITH, A. D. 1964. Defecation rates of mule deer. *Journal of Wildlife Management* 28:435-444.
- WIGLEY, T. B., AND M. J. JOHNSTON. 1981. Disappearance rates for deer pellets in the southeast. *Journal of Wildlife Management* 45:251-253.
- WOLFE, M. L., N. V. DEBYLE, C. S. WINCHELL, AND T. R. MCCABE. 1982. Snowshoe hare cover relationships in northern Utah. *Journal of Wildlife Management* 46:662-670.



Laura Prugh (photo) is a Ph.D. candidate at the University of British Columbia. She received her B.A. in Biology from Earlham College, Indiana, in 1996. Her thesis research examines the response of coyotes to changes in snowshoe hare density and how this affects alternative prey populations. She is also using fecal genotyping to study coyote population dynamics and individual diets. **Charles J. Krebs** is a professor emeritus at the University of British Columbia. He has studied snowshoe hares in the Yukon since 1973 and continues to study small mammals in Australia and the Yukon.

Associate editor: Murray

