

Are lemming winter nest counts a good index of population density?

CHARLES J. KREBS,* FRÉDÉRIC BILODEAU, DONALD REID, GILLES GAUTHIER, ALICE J. KENNEY, SCOTT GILBERT, DAVID DUCHESNE, AND DEBORAH J. WILSON

Department of Zoology, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada (CJK, AJK)
Département de Biologie and Centre d'Etudes Nordiques, 1045 Ave de la Médecine, Université Laval, Québec City, Québec G1V 0A6, Canada (FB, GG, DD)

Wildlife Conservation Society Canada, 39 Harbottle Road, Whitehorse, Yukon Y1A 5T2, Canada (DR)

Renewable Resources Management Program, Yukon College, Whitehorse, Yukon Y1A 5K4, Canada (SG)

Landcare Research, Private Bag 1930, Dunedin, New Zealand 9054 (DJW)

* Correspondent: krebs@zoology.ubc.ca

Lemmings construct nests of grass and moss under the snow during winter, and counting these nests in spring is 1 method of obtaining an index of winter density and habitat use. We counted winter nests after snow melt on fixed grids on 5 areas scattered across the Canadian Arctic and compared these nest counts to population density estimated by mark–recapture on the same areas in spring and during the previous autumn. Collared lemmings were a common species in most areas, some sites had an abundance of brown lemmings, and only 2 sites had tundra voles. Winter nest counts were correlated with lemming densities estimated in the following spring ($r_s = 0.80$, $P < 0.001$), but less well correlated with densities the previous autumn ($r_s = 0.55$, $P < 0.001$). Winter nest counts can be used to predict spring lemming densities with a log-log regression that explains 64% of the observed variation. Winter nest counts are best treated as an approximate index and should not be used when precise, quantitative lemming density estimates are required. Nest counts also can be used to provide general information about habitat-use in winter, predation rates by weasels, and the extent of winter breeding.

Key words: brown lemming, collared lemming, *Dicrostonyx groenlandicus*, *Lemmus trimucronatus*, *Microtus oeconomus*, population index, tundra vole

© 2012 American Society of Mammalogists

DOI: 10.1644/11-MAMM-A-137.1

Small mammals in tundra ecosystems are difficult to study in winter, a relatively unstudied season during which much of the interesting population dynamics occurs (Angerbjörn et al. 2001; Gilg et al. 2003; Gruyer et al. 2008, 2010; Krebs et al. 2011). Winter breeding is an essential part of lemming ecology and typically much population growth occurs under the snow. It is tempting to utilize the remains of nests built by small mammals during the winter as an entrée into winter ecology, and in particular to assume that winter nest counts can give us a good estimate of lemming density at the end of winter.

The purpose of this paper is to investigate the accuracy of winter nest counts as an index of population density for tundra rodents. We achieved this by systematically counting nests on fixed grids in spring and relating these counts to mark–recapture estimates of collared lemming (*Dicrostonyx groenlandicus*), brown lemming (*Lemmus trimucronatus*), and tundra vole (*Microtus oeconomus*) numbers based on live-trapping in spring just when the nest counts are made and

estimates of lemming and vole density in the previous autumn before the winter snows begin. We attempt to answer 3 questions: Can winter nest counts be used as a predictor of tundra rodent population densities from the previous autumn or the following spring? Are relationships of nest counts to density specific for different habitats or geographic areas? Is there any evidence that the nest count–density relationship varies with different rodent species?

MATERIALS AND METHODS

We sampled winter nests and lemming and vole abundance at 5 tundra sites spread across Canada (Fig. 1). From west to east the study areas were at Komakuk Beach (69°35.1'N, 140°11.2'W) on the north Yukon coast; at Herschel Island



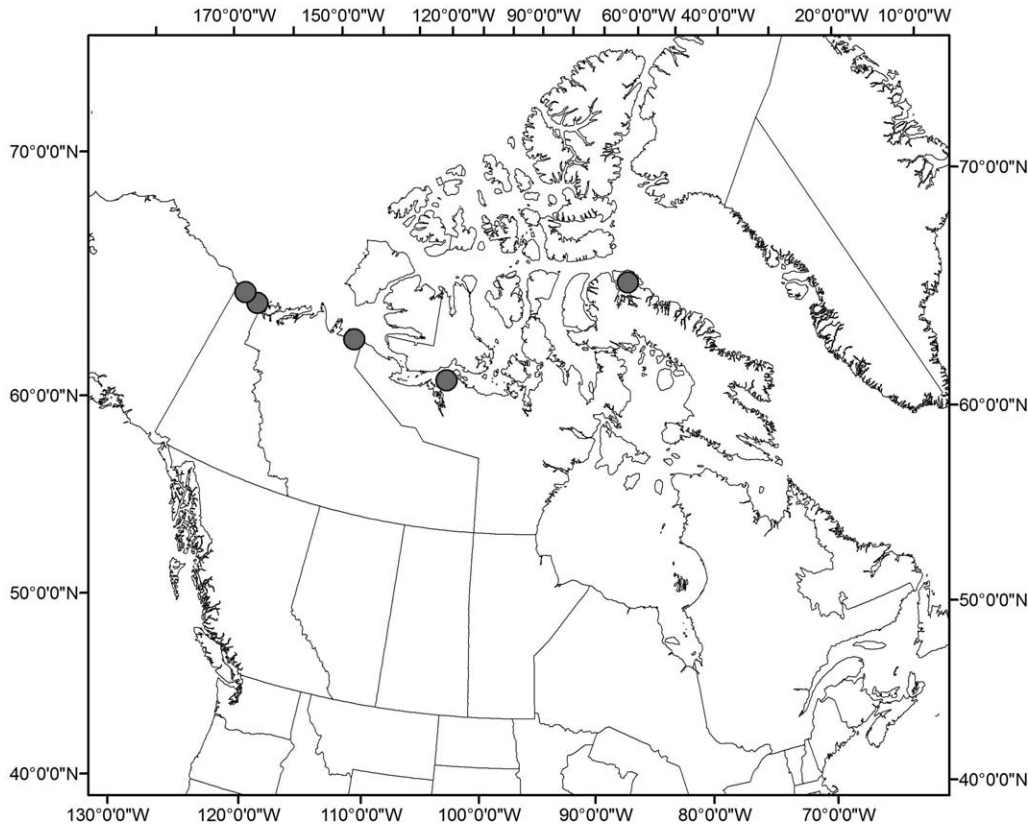


FIG. 1.—Location of the 5 study areas in the Canadian Arctic. From west to east, Komakuk Beach, Herschel Island, Pearce Point, Walker Bay, and Bylot Island.

($69^{\circ}34.2'N$, $138^{\circ}54.1'W$) off the north Yukon coast; at Pearce Point, Northwest Territories ($69^{\circ}48'N$, $122^{\circ}40'W$), on the south shore of the Amundsen Gulf; at Walker Bay, Nunavut ($68^{\circ}21'N$, $108^{\circ}05'W$), on the Kent Peninsula; and on Bylot Island, Sirmilik National Park, Nunavut ($73^{\circ}N$, $80^{\circ}W$). All these areas are treeless tundra and contain a mixture of mesic tundra and wet sedge meadows. Details of vegetation at these sites have been presented in Gruyer et al. (2010), Krebs et al. (2011), Reid et al. (1997), and Wilson et al. (1999). Herschel Island and Komakuk Beach are in Circumpolar Arctic Bioclimate Zone E, Pearce Point and Walker Bay are in Zone D, and Bylot Island is in Zone C (Walker et al. 2005).

We did a complete census of all winter nests on our permanent livetrapping grids immediately after snow melt each spring and at the same time we carried out mark–recapture to estimate spring density (see below for details of the mark–recapture census). Nest counts were completed by walking transects spaced every 3–5 m, recording the position of each nest on a global positioning system, and shredding or removing each nest so that it could not be counted twice. We are confident that we have a complete count, and any additional nests found during subsequent livetrapping of the grid were added later to the data (<2% of the total). The total number of nests tallied was divided by the area searched to determine the number of winter nests per hectare. When most of these data were collected we did not have the ability to differentiate the species of tundra rodent that constructed the

winter nest at 4 of our sites. Duchesne et al. (2011a, 2011b) have subsequently validated a good procedure for doing this on Bylot Island, and nests could be assigned to either brown or collared lemmings at that site. In most grids in the central and western Arctic our data come from livetrapping areas dominated by collared lemmings so that our results in these sites are not greatly affected by this lack of species specificity.

To estimate autumn (late August or September) and spring (June) rodent densities, we livetrapped brown lemmings, collared lemmings, and tundra voles on all sites in the same manner. Most livetrapping grids were 7–9 ha in area, and only 1 on Herschel Island was in restricted habitat and as small as 1.8 ha. At Pearce Point where densities were low, grids ranged from 18 to 25 ha in area. Details of livetrapping are given in Gruyer et al. (2010), Krebs et al. (2011), Reid et al. (1997), and Wilson et al. (1999). Grids were placed in habitats that were typical of the local landscapes. On Bylot Island grids were set in homogeneous wet or mesic tundra. We did not select areas that were particularly rich or productive but attempted at all sites to use areas that were typical of the landscape. Most grids were checkerboards with live traps spaced 20–30 m apart in 10×10 , 12×12 , or 16×16 arrays with 100–144 Longworth live traps (Alana Ecology Ltd., Shropshire, United Kingdom, <http://www.alanaecology.com/wildlife>). A smaller 1.8-ha grid on Herschel Island was set up as a 10×10 array with 15-m spacing in good brown lemming habitat. All rodents were captured in Longworth live traps. Traps were prebaited with

TABLE 1.—Descriptive data for the 5 study areas in the Canadian Arctic. The number of years sampled includes only years for which both winter nest counts and mark–recapture data were carried out on the same grids.

Area	Dominant species	No. grids sampled ^a	No. years sampled ^a	Average density of all rodents combined (<i>n</i> /ha)	Range of rodent densities (<i>n</i> /ha)
Herschel Island	Collared lemming	2	4	4.5 ^b	1.2–11.2
Herschel Island	Brown lemming ^c	1	4	17.2 ^d	2.2–64.5
Komakuk Beach	Tundra vole, brown lemming	2	3	3.3	1.2–5.3
Pearce Point	Collared lemming	4	2	0.6	0.2–2.1
Walker Bay	Collared lemming	5	4	5.2	0.1–34.1
Bylot Island	Collared lemming	3	4	0.3 ^b	0–3.0
Bylot Island	Brown lemming	3	4	1.6 ^d	0–8.7

^a Not all grids sampled every year.

^b Only collared lemmings.

^c One small grid dominated by brown lemmings (1.8 ha).

^d Only brown lemmings.

apples for 3–6 days before livetrapping. Traps were left in place and locked open all summer. When set, traps were checked every 4–12 h, and in most cases a trapping session involved 5 or 6 checks over 2–3 days, with 1–4 trapping sessions each summer. We trapped in spring as soon as the snow melted, and in autumn typically in mid- to late August or on occasion at Herschel Island in early September. Traps were occasionally closed down in inclement weather. Our approach was to have an excess of traps to prevent trap competition and to space the intertrap distance on the trapping grids in such a way as to catch a high proportion of the animals present. The average probability of capturing an individual in each of the 5 or 6 trapping checks was high so that recaptures were frequent within 1 trapping session. Individuals caught were identified as to species, ear-tagged with numbered fingerling fish tags (National Band and Tag Company, Newport, Kentucky) or tagged with passive integrated transponder electronic tags (Biomark, Boise, Idaho), sexed, weighed, and immediately released at the point of capture.

In earlier studies at Pearce Point we used the Jolly–Seber model to estimate rodent numbers, and at Walker Bay we used Program CAPTURE or Program MARK (White and Burnham 1999; Williams et al. 2002) to estimate numbers. For both of these sites we added a boundary strip to estimate density. In later studies at Herschel Island, Komakuk Beach, and Bylot Island we used Efford's maximum-likelihood spatial model (Borchers and Efford 2008) to estimate density when more than 4 individuals were captured in a trapping session. When fewer than 4 animals were present none of the methods of estimation can be solved and we reverted to the minimum number known to be alive (MNA) as the best estimate of population size. Details of the density estimations may be found in the previously cited papers.

All livetrapping of rodents was carried out in accord with the animal care principles of the American Society of Mammalogists (Sikes et al. 2011) and all our protocols were approved by the University of British Columbia Animal Care Committee and the University of Laval Animal Care Committee.

Statistical analysis.—All statistical analyses were done in NCSS (Number Crunching Statistical System, Kay, Utah, www.ncss.com). For linear regression and analysis of

covariance (ANCOVA) we checked the normality assumption with the Shapiro–Wilk test, and we checked the equality of slopes assumption for ANCOVA.

RESULTS

Table 1 gives the descriptive statistics for the data collected from the 5 study sites. For the 2 upland grids on Herschel Island, 58% of the individuals captured were collared lemmings and 39% were brown lemmings. For the lowland grid on Herschel Island, 87% of the animals captured were brown lemmings and 12% were tundra voles. For Komakuk Beach, 70% were tundra voles and 28% were brown lemmings. For Pearce Point, all the animals captured were collared lemmings. For Walker Bay 87% were collared lemmings and 13% were brown lemmings. For Bylot Island, the mesic grids had 79% brown lemmings overall, and the wet grid had 94% brown lemmings, with collared lemmings comprising the remainder. The highest proportion of our data at central and western sites thus refers to collared lemming populations, whereas that on Bylot Island are weighted toward brown lemmings.

To gain an appreciation of the value of winter nest counts, we tested the ability of autumn lemming density estimates to predict density in the following spring. A log transformation of both density estimates was used to stabilize the variances, and the log-transformed linear regression was significant but a poor fit ($r^2 = 0.33$, $n = 56$, $F_{1,54} = 26.57$, $P < 0.001$) so that only 33% of the variation in spring density could be predicted from the previous autumn density. This reflects the fact that depending on the stage of the population cycle, densities could be rising or falling overwinter. Winter nest counts could be useful to monitor these differences in cyclic phase.

The relationships between winter nest counts and lemming density in the previous autumn and the following spring are nonlinear. Spearman rank-correlation coefficients for winter nests were higher with densities the following spring ($r_s = 0.80$, $n = 60$, $P < 0.001$), and lower with densities the previous autumn ($r_s = 0.55$, $n = 56$, $P < 0.001$). Pearson correlation coefficients between nest counts and lemming density are much lower (spring, $r = 0.55$, autumn $r = 0.32$),

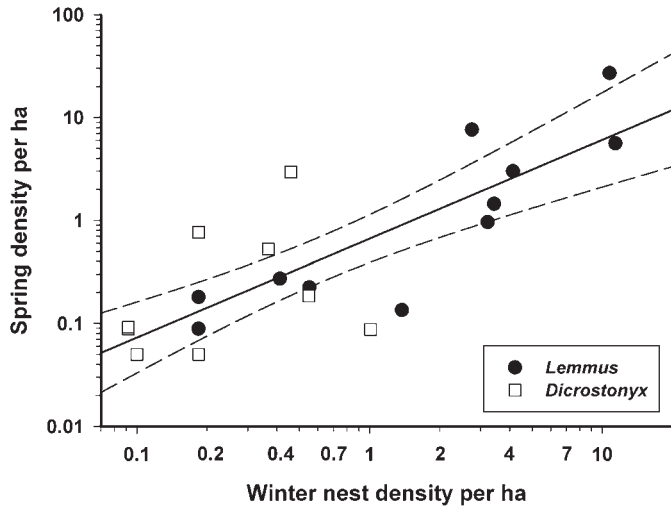


FIG. 2.—Log-log plot of spring lemming density on winter nest density per hectare for Bylot Island, 2007–2010. A single regression for both lemming species fits these data. $\text{Log}(\text{spring density}) = -0.2112 + 0.9325 \text{ log}(\text{nest density})$, with $r^2 = 0.65$, variance about regression = 0.2412, standard error of slope = 0.1574, $n = 21$. Dashed lines show 95% confidence limits.

indicating a transformation was required. The variance increased with the mean winter nest count. Consequently we took logarithms base-10 for both density and winter nest counts in order to stabilize the variance. All further statistical analyses were carried out with log-transformed data.

To determine if there was any evidence that the 2 lemming species had different regression lines we used the Bylot Island density data for spring, which was the only site in which winter nests were identified to species and where there were no *Microtus*. An ANCOVA for these data showed that species was not a significant covariate ($F_{1,18} = 0.05$, $P = 0.68$). We proceeded with the analysis on the assumption that a single regression line could describe the 2 lemming species combined (Fig. 2).

Two potential sources of variation in the relationship between spring density and winter nest counts are the phase of the cycle (low, increase, peak, or decline) and the geographic location. We carried out an ANCOVA using a general linear model to test whether these 2 factors had a significant effect on the spring density–winter nest regression. Geographic location had no significant effect on the slope of this regression ($F_{4,50} = 1.96$, $P = 0.12$), and phase of the cycle also was not significant ($F_{2,45} = 1.91$, $P = 0.16$). The result of this analysis was that we could use 1 regression to describe the data from all areas and all cyclic phases. Fig. 3 shows the best predictive plot from our data across all 5 areas with a log-log transformation. The prediction interval is moderately wide, with the regression explaining statistically 64% of the variability in spring densities.

Because cyclic phase approached significance in the general linear model, we checked the residuals of the regression in Fig. 3 to determine if the phase of the population cycle might affect deviations from the regression. We classified each year as low, increase, peak, or decline phase from data we had from

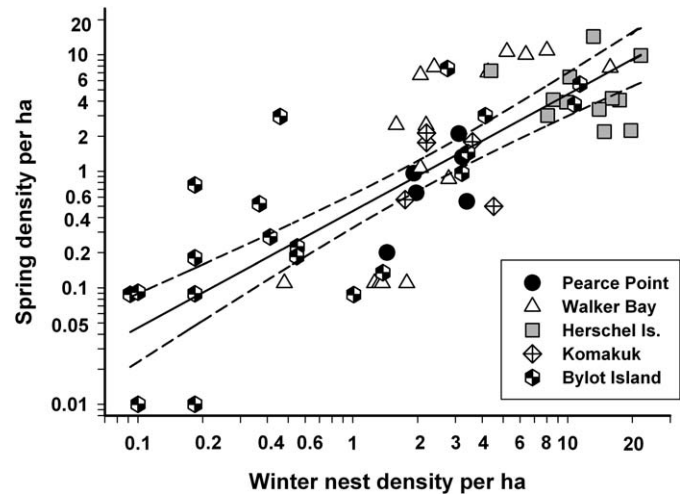


FIG. 3.—Log-log regression of spring microtine density versus winter nest density from the previous winter, with 95% confidence band for predicted mean density. The regression is $\text{log}(\text{spring density}) = -0.3416 + 1.0013 \text{ log}(\text{winter nest density})$, with $r^2 = 0.64$, variance about regression = 0.2465, standard error of slope = 0.0994, $n = 60$. Dashed lines show 95% confidence limits.

mark–recapture estimates. There was significant variation among the residuals in relation to cycle phase. Two phases differed when examined in a Tukey–Kramer multiple comparison test. Residuals from the low phase ($\bar{X} = -0.52 \pm 0.20 \text{ SE}$, $n = 22$) were significantly different ($F_{3,56} = 5.45$, $P = 0.002$) from those of the peak phase ($\bar{X} = 0.75 \pm 0.26 \text{ SE}$, $n = 12$). These results confirm that winter nest counts in a phase of low numbers will tend to overestimate spring density, whereas those in peak phase will tend to underestimate spring density.

DISCUSSION

Many species of voles and lemmings construct nests of grass either below the ground in burrows or particularly in winter at the ground surface where animals can avoid flooded burrows (Lambin 1994) or icing. In polar areas snow insulates these nests from cold air temperatures and several studies have documented the high value of winter nests for lemming energetics (Casey 1981; Chappell 1980). In tundra areas these grass nests are highly visible in spring just after snow melt, and can be easily counted (Duchesne et al. 2011b; Maher 1967).

Winter nest counts were significantly related to spring densities of tundra small mammals, and they explained 64% of the variation in winter nest density, leaving about 36% of the variability unexplained. Prairie (1996) pointed out that regression models with R^2 values around 0.65 are able to resolve only 2 classes of events, and in our case this means we can use the regression in Fig. 3 to clearly separate low and high spring densities of lemmings. The key point is that we can achieve only a low level of resolution of lemming density by the use of winter nest counts unless we can obtain additional predictive variables.

There are many possible sources of variation for winter nest counts of lemmings and tundra voles. We do not know how many winter nests a single individual lemming or vole builds during winter, but duration of occupancy could vary with local food abundance or predation risk. Species could differ in their duration of use of individual nests, although this was probably a minor effect at least among lemmings because our evidence from Bylot Island does not suggest any difference between the 2 lemming species. Habitat could be important because in tussock tundra lemmings and voles can build winter nests inside *Eriophorum* tussocks. These winter nests are typically not visible to an observer and could be counted only by destroying the habitat and possibly underestimating the numbers of winter nests in tussock habitat. However, tussock nests were very rare at our highest-latitude site (Bylot Island) and the proportion of variation in spring densities explained by winter nests was virtually identical at this site. In dry habitats some underground burrows could be utilized in early winter if they are not choked by ice crystals or flooded.

Winter is a long period with numerous potential changes in density at these high latitudes, and nest counts represent some integration of those changes. If populations are rising and population growth occurs mainly in late winter or spring (before melt), the number of winter nests could be relatively low in relation to spring density, and this would inflate the residuals in the peak year, as we found in our analysis. Similarly, in a declining population winter nests could be abundant yet few lemmings survive the winter, and this would tend to deflate the residuals. An example of this effect was reported by Pitelka and Batzli (2007) for brown lemmings at Barrow, Alaska, where many winter nests were found coincident with very few lemmings in spring.

Even though our trapping grids were relatively large (>7 ha in most cases), differences in habitat use by small mammals between summer and winter may be a significant source of variability when relating winter and spring densities at the grid scale. In winter, lemmings show a strong preference for areas with deep snow, which are typically snow-drift areas along ridges in the tundra (Duchesne et al. 2011b; Reid and Krebs 1996). At snow melt, when many areas are flooded, individuals presumably move to different habitats, especially those where the ground is suitable to dig burrows.

If lemmings move from summer to winter habitats and if the scale of these movements is large relative to the trapping grid area, biased estimates of this regression will result. If the trapping area is largely summer habitat, the observed winter nest density would be too small in these situations. Because most trapping grids are chosen in summer, this could be a significant source of bias. In the extreme case, all winter nests will be found in a habitat with no lemmings in spring, and no winter nests will be found in the habitat where all the lemmings occur in summer. But if these habitats are fine grained, as they seem to be on most of our Canadian sites, this potential bias will be small or negligible.

Although counts of winter nests can give a general estimate of lemming abundance, examination of our data suggests that

they cannot be used for precise density estimation at least at our Canadian sites. Although spring densities can be estimated approximately ($R^2 = 0.64$), density in the previous autumn was predicted rather poorly from winter nest counts the following spring ($R^2 = 0.34$). Winter nest counts were more strongly correlated with spring than autumn rodent densities, probably because the span of time between likely nest occupancy and our livetrapping was generally shorter in spring than in autumn.

Only 1 other study of lemmings has related winter nest counts to lemming density. Gilg et al. (2003) also used winter nests of collared lemmings in eastern Greenland to estimate spring densities of lemmings for years in which they had no direct mark–recapture data. They found that winter nests could explain 99% of the variation in their livetrapping estimates of density of lemmings in spring, a surprisingly high value compared to our study. The regression of Gilg et al. (2003) ($\log_e[\text{spring density}] = 1.15 + 1.35 \log_e[\text{winter nests}]$, all units per hectare) differs dramatically from that derived here. The differences in estimates for lemming density in spring varies 4-fold for nest densities of 0.1 nest/ha and 10-fold for nest densities of 3 nests/ha, with our lemming density estimates substantially lower than those estimated from the regression of Gilg et al. (2003) from Greenland. We believe that methodological differences may explain the discrepancies between our regression and that of Gilg et al. (2003). Gilg et al. (2003) related winter nest densities estimated over a very large area (15 km²) to lemming densities estimated on extremely small plots (0.3–0.8 ha—Gilg 2002), which raised potential scaling issues. Gilg (2002) may have underestimated winter nest densities because the nests were counted along transects spaced 20–30 m apart (Sittler 1995), which is beyond the effective detection distance for winter nests on Bylot Island (Duchesne et al. 2011b); however, Sittler (1995) claimed that nests were readily seen at these longer distances. Gilg (2002) may also have overestimated lemming densities, especially in years of high abundance, if the small livetrapping plots in that study were located in prime lemming habitat. The result might be that the regression of Gilg (2002) results from comparing lemming densities in favorable habitat patches of polar desert to nest densities averaged over large areas of unfavorable lemming habitat. It is important to note that only 1 of our Canadian sites is located in high arctic tundra (Bylot Island), although polar desert or cryptogram–herb barrens (cf. Walker et al. 2005), the type of largely barren habitat found in the study area of Gilg et al. (2003) in eastern Greenland, was not dominant at that site. The issue raised here is how general the regressions discussed here may be applied to the circumpolar tundra regions. We do not know the answer to this question, and we encourage the gathering of additional data from different tundra habitats.

We have very limited data on tundra areas dominated by tundra voles. Examination of our limited data suggests their winter nest regression may be similar to that of the 2 lemmings, but we urge caution in applying the regression used here without further validation for tundra voles.

We conclude that although counts of lemming winter nests on tundra areas can give a good general picture of lemming densities, their precision as an estimate of lemming density in spring is low and that nest counts should be primarily used to classify spring densities as low, moderate, or high. If accurate estimates of lemming densities are required for predator–prey models or models of tundra ecosystem dynamics, it is essential to utilize mark–recapture methods.

Winter nest counts do have several merits. They are a simple, low-cost method that does not require capture of animals, and they could be deployed over a large area to map spatial synchrony of cycles. They provide some insights into the winter ecology of small mammals such as habitat use, and provide additional information on reproduction (Duchesne et al. 2011a, 2011b) during winter. They also give a qualitative measure of the impact of weasel predation on lemmings during winter (Maher 1967; Sittler 1995). The qualitative values of winter nest counts are important for helping to understand tundra small mammal ecology, but nest counts should not be used as precise estimates of density of tundra rodents.

ACKNOWLEDGMENTS

We thank the Natural Science and Engineering Research Council of Canada, the International Polar Year Program of Indian and Northern Affairs Canada (project MD-021, Arctic WOLVES), the Canadian Network of Centres of Excellence ArcticNet, and Parks Canada for their long-term support of this research and the Polar Continental Shelf Program for aircraft charter support. We acknowledge the hard work of numerous field staff employed counting nests and livetrapping in the various sites and we thank them. We thank the 2 referees for suggestions that improved the manuscript.

LITERATURE CITED

- ANGERBJÖRN, A., M. TANNERFELDT, AND H. LUNDBERG. 2001. Geographical and temporal patterns of lemming population dynamics in Fennoscandia. *Ecography* 24:298–308.
- BORCHERS, D. L., AND M. G. EFFORD. 2008. Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics* 64:377–385.
- CASEY, T. M. 1981. Nest insulation: energy savings to brown lemmings using a winter nest. *Oecologia* 50:199–204.
- CHAPPELL, M. A. 1980. Thermal energetics and thermoregulatory costs of small arctic mammals. *Journal of Mammalogy* 61:278–291.
- DUCHESNE, D., G. GAUTHIER, AND D. BERTEAUX. 2011a. Evaluation of a method to determine the breeding activity of lemmings in their winter nests. *Journal of Mammalogy* 92:511–516.
- DUCHESNE, D., G. GAUTHIER, AND D. BERTEAUX. 2011b. Habitat selection, reproduction and predation of wintering lemmings in the Arctic. *Oecologia* 167:967–980.
- GILG, O. 2002. The summer decline of the collared lemming, *Dicrostonyx groenlandicus*, in high arctic Greenland. *Oikos* 99:499–510.
- GILG, O., I. HANSKI, AND B. SITTLER. 2003. Cyclic dynamics in a simple vertebrate predator–prey community. *Science* 302:866–868.
- GRUYER, N., G. GAUTHIER, AND D. BERTEAUX. 2008. Cyclic dynamics of sympatric lemming populations on Bylot Island, Nunavut, Canada. *Canadian Journal of Zoology* 86:910–917.
- GRUYER, N., G. GAUTHIER, AND D. BERTEAUX. 2010. Demography of two lemming species on Bylot Island, Nunavut, Canada. *Polar Biology* 33:725–736.
- KREBS, C. J., D. REID, A. J. KENNEY, AND S. GILBERT. 2011. Fluctuations in lemming populations in north Yukon, Canada, 2007–2010. *Canadian Journal of Zoology* 89:297–306.
- LAMBIN, X. 1994. Natal philopatry, competition for resources, and inbreeding avoidance in Townsend's voles (*Microtus townsendii*). *Ecology* 75:224–235.
- MAHER, W. J. 1967. Predation by weasels on a winter population of lemmings, Banks Island, Northwest Territories. *Canadian Field-Naturalist* 81:248–250.
- PITELKA, F. A., AND G. O. BATZLI. 2007. Population cycles of lemmings near Barrow, Alaska: a historical review. *Acta Theriologica* 52:323–336.
- PRAIRIE, Y. T. 1996. Evaluating the predictive power of regression models. *Canadian Journal of Fisheries and Aquatic Sciences* 53:490–492.
- REID, D. G., AND C. J. KREBS. 1996. Limitations to collared lemming population growth in winter. *Canadian Journal of Zoology* 74:1284–1291.
- REID, D. G., C. J. KREBS, AND A. J. KENNEY. 1997. Patterns of predation on noncyclic lemmings. *Ecological Monographs* 67:89–108.
- SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235–253.
- SITTLER, B. 1995. Response of stoats (*Mustela erminea*) to a fluctuating lemming (*Dicrostonyx groenlandicus*) population in north east Greenland: preliminary results from a long-term study. *Annales Zoologici Fennici* 32:79–92.
- WALKER, D. A., ET AL. 2005. The Circumpolar Arctic vegetation map. *Journal of Vegetation Science* 16:267–282.
- WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46, supplement:120–138.
- WILLIAMS, B. K., J. D. NICHOLS, AND M. J. CONROY. 2002. Analysis and management of animal populations. Academic Press, San Diego, California.
- WILSON, D. J., C. J. KREBS, AND A. R. E. SINCLAIR. 1999. Limitation of collared lemming populations during a population cycle. *Oikos* 87:382–398.

Submitted 12 April 2011. Accepted 6 July 2011.

Associate Editor was Bradley J. Swanson