Variation in snowshoe hare density near Churchill, Manitoba estimated using pellet counts

Courtney E. Freeth[1], Matthew R. E. Teillet[1] and James D. Roth[1]

[1]Department of Biological Sciences, University of Manitoba, Winnipeg, MB, Canada R3T 2N2

contact author:Jim.Roth@umanitoba.ca

Abstract

Snowshoe hares (Lepus americanus) are a keystone species in the Boreal Forest of Canada and their well-characterized population cycles can strongly influence the abundance of their predators. We examined annual variation in snowshoe hare density near Churchill, Manitoba, using counts of hare fecal pellets from 2012 to 2015. We used a regression formula to estimate the density of snowshoe hares based on fecal pellet density. Our estimates of snowshoe hare densities were highest in the first year of study, which may reflect a bias due to pellets accumulating from previous years, and we found no difference in hare density estimates in the subsequent three years. These results suggest the forest-tundra ecozone may be marginal habitat for snowshoe hares, precluding rapid increases in hare density, so population densities of snowshoe hares in Churchill may not cycle in their historic 10-year intervals. However, the northward advancement of the tree line with climate warming may improve habitat conditions for snowshoe hares, and thus the predator populations they typically support.

Keywords: Lepus americanus, population cycles, boreal forest, northern tree line, fecal pellet counts, forest-tundra ecozone

1. Introduction

Species diversity in the North is relatively low, which magnifies the importance of interactions between species (C. J. Krebs, 2011). Snowshoe hares (*Lepus americanus*) are a keystone species in the boreal forests of Canada because they have a large impact on their environment compared to their abundance through their 10-year cyclic population fluctuations, which strongly influences the density of their predators (Keith, 1990, C. Krebs et al., 2001, McCann, Moen, & Niemi, 2008, C. J. Krebs, 2011). Estimating snowshoe hare density, therefore, can be important for conservation and management because snowshoe hares are an integral part of the boreal ecosystem (C. J. Krebs et al., 1995).

Snowshoe hare cycles have been observed in Canada as early as the 18th century, but the reasons for the fluctuations have not always been clear (C. J. Krebs, Boonstra, Boutin, & Sinclair, 2001, Tyson, Haines, & Hodges, 2010). In northern Canada, snowshoe hare cycles stem from complicated interactions between food supplies and several predator species (C. J. Krebs et al., 2001, Tyson et al., 2010). The relationship between snowshoe hares and one of their predators, the Canada lynx (*Lynx canadensis*) has been examined extensively for management and conservation purposes (C. Krebs et al., 2001;Tyson et al., 2010,Lewis, Hodges, Koehler, & Mills, 2011). Population estimates may also be useful for determining number of individuals that can be sustainably harvested without disturbing the natural dynamics of the population. Populations of snowshoe hare at the northern edge of the boreal forest may be more greatly impacted by climate warming as the tree line extends northward (Grace, Berninger, & Nagy, 2002, Gamache & Payette, 2005, Harsch, Hulme, McGlone, & Duncan, 2009). The northward advancement of the tree line will change the structure of the forest-tundra ecozone and allow for larger tree and shrub species to inhabit the region, such as willow, alder, and dwarf birch (Starfield & Chapin, 1996, Tape, Sturm, & Racine, 2006, Ewacha, Roth, & Brook, 2014). The larger vegetation that accompanies the moving tree line could alter the ability of a predator to find snowshoe hares (Ewacha et al., 2014). Changes in the ecosystem structure could also affect the woody plant species that make up the diet of snowshoe hares in the winter and the leafy plant species that make up their diet in the summer, therefore impacting the dynamics of snowshoe hare populations (Hodges, 2000, Hart & Chen, 2006, Ewacha et al., 2014). The vegetation changes that accompany a moving tree line and the unique habitat found in the forest-tundra ecotone account for large variability in the boreal habitat of the Churchill region (Elliot-Fisk, 1983, Ewacha et al., 2014). As the tree line moves northward, we predict that snowshoe hares may adjust their distribution according to their habitat preferences within the boreal forest. The objective of our study was to use fecal pellet counts to estimate the density of snowshoe hares in the Churchill, Manitoba region from 2012 to 2015 to determine if snowshoe hare density varied annually. Pellet counts have been used to estimate mammal population densities for many years although they often vary in quadrat size and shape (C. J. Krebs, Gilbert, Boutin, & Boonstra, 1987, C. Krebs et al., 2001, Murray, Roth, Ellsworth, Wirsing, & Steury, 2002, Mills et al., 2005, McCann et al., 2008, Berg & Gese, 2010). Snowshoe hare densities were first estimated using pellet counts in Yukon Territory in 1986 (C. J. Krebs et al., 1987). Estimating snowshoe hare density with pellet counts has since become a popular method and has been used across North America (Mills et al., 2005, McCann et al., 2008). These past successes with the pellet count method justified its use in the Churchill region (C. J. Krebs et al., 1987). We predicted that hare densities would differ from 2012 to 2015 as snowshoe hare populations fluctuate within their observed 10-year cycle (Keith, 1990, Hodges, 2000). We also predicted that hare densities in different regions of the forest would be consistent over time due to the habitat preferences of hares.

2. Methods

We estimated snowshoe hare density using fecal pellet counts on transects located within treed bog habitat outside Churchill, Manitoba (58.77°N, 94.26°W; Ewacha et al., 2014). Eight 300-metre transects were placed at least 1-km apart in continuous boreal forest (near tree line), and each transect included ten $1-m^2$ circular plots, 30 metres apart. Transects were established semi-randomly due to lack of continuous boreal forest in the region. Transects were established in August 2012 and snowshoe hare pellets were counted once per year. Pellets were counted in each plot and subsequently removed so that they would not be counted in following years (C. Krebs et al., 2001). Pellets were also counted and removed from each plot every June from 2013-2015. One plot in 2014 and one in 2015 could not be located because the marking stake disappeared over winter, so new stakes were installed and those data were excluded for that year.

McCann et al. (2008) used an experimental design that was comparable to our protocol with circular plots that were $1-m^2$ at 25-metre intervals on each transect. We assumed that the relationship between pellet density and hare density in Minnesota was the same in northern Manitoba due to similar climates. We averaged the pellet counts across eight plots for each transect. The mean pellet counts (x) were then converted into hare density (y) using a linear regression formula ($y = 0.398 + 0.060x$). This formula was developed by comparing mark-recapture estimates of snowshoe hares and fecal pellet counts at the same sites in Minnesota (McCann et al., 2008). The equation we used to convert pellet counts into hare density estimates (McCann et al. 2008) was developed using quadrats of similar size and shape as our study, whereas other studies such as Krebs et al. (1987) and Krebs et al. (2001a) used rectangular plots. Mills et al. (2005) found that the regression equations converting pellet densities to hare densities are different whether circular plots were used or rectangular plots were used. Other studies with a similar experimental design, such as Berg and Gese (2010) and Murray et al. (2002), differed substantially in climate and geographic location. Therefore, we considered the conversion equation developed by McCann et al. (2008) to be the most appropriate for our study area.

We averaged hare densities across the eight transects to provide an estimate of mean annual snowshoe hare density. To determine if habitat preferences remain consistent over time, we also compared pellet densities among transects. We analyzed our data using JMP 10.0.1. We used a Log_{10} transformation of the hare densities in each transect to normalize the distribution and improve homogeneity of variance. To detect differences in mean annual hare density we used a two-way ANOVA, blocking on transect, followed by a Tukey-Kramer HSD test to determine which years differed. We also used a two-way ANOVA to determine differences among the mean hare densities per transect over the four years of the study, followed by a Tukey-Kramer HSD to determine which transects differed.

3. Results

The mean pellet count was highest in 2012 with 12.4 pellets/m^2 and lowest in 2015 with 3.9 pellets/m^2 (overall range 0 – 34.9 pellets per plot). These pellet densities translate to estimated hare densities of 1.14 hares per hectare in 2012 and 0.63 hares per hectare in 2015 (Figure 1). The mean pellet counts for 2013 and 2014 were 4.0 pellets/m^2 and 5.6 pellets/m^2 respectively. These pellet counts translate to estimated hare densities of 0.63 hares per hectare in 2013 and 0.72 hares per hectare in 2014 (Figure 1). Hare density varied over time, $F_{3,21} = 4.611$ and $P = 0.0125$ (Figure 1). Hare density was higher in 2012 than 2013 (P = 0.0169) and 2015 (P = 0.0240), but hare densities did not differ between any other years (all P > 0.122, Figure 1).

Transect 4 contained the most hare activity, with the highest mean pellet count (17.5 pellets per plot) throughout the four years of the study. Transects differed in hare density, $F_{7,21} = 17.25$ and $P < 0.0001$ (Figure 2). Hare density was consistently higher on Transects 1, 3, and 4 than on 2, 5, 6, 7, and 8 (P < 0.0443, Figure 2). Hare densities did not differ between any high-density transects (Transects 1, 3, and 4; P > 0.95) and likewise did not differ between any low-density transects (Transects 2, 5, 6, 7, and 8; P > 0.47).

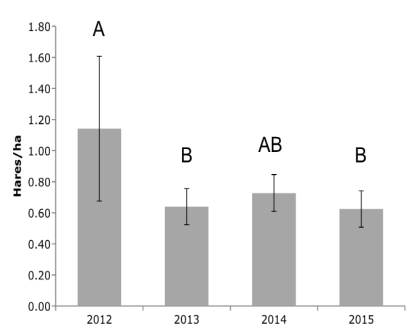

Figure 1: *Estimated hare densities per hectare (± S.E) for the study period. Letters above error bars represent significant differences (P < 0.05). Hare densities that are not sharing a letter are significantly different.*

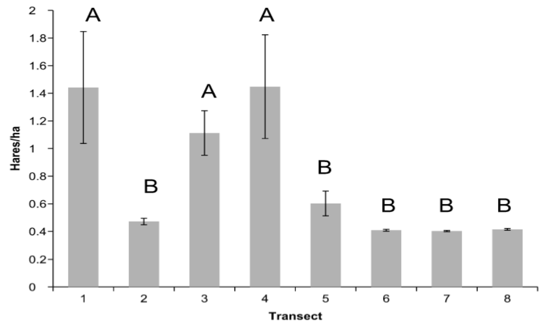

Figure 2: *Estimated mean hare densities per transect (± S.E.) over the four years of study. Letters above error bars represent significant differences (P < 0.05). Hare densities that are not sharing a letter are significantly different.*

4. Discussion

Hodges (2000) found that during a snowshoe hare population cycle, annual changes in density could be as high as a three-fold increase in the growing phase of the cycle and up to a 90% decrease in the decline phase. After controlling for the variance in density among transects, our results show a significant difference among years. Specifically, snowshoe hare densities in 2012 differed from 2013-2015. This trend may suggest snowshoe hare populations in Churchill could be fluctuating over time. The largest mean pellet count and the largest estimated hare density was from the first year of data collection, when pellets from previous years had not been removed from the plots. Snowshoe hare pellets can last up to 20 years in the boreal forest (C. Krebs et al., 2001), and therefore excess pellets could have added a bias to the first year pellet counts, which would have skewed our results. Hare density estimates did not differ from 2013-2015, so because of the potential bias in 2012 we cannot necessarily conclude that snowshoe hare populations are fluctuating in our study area. Krebs et al. (2001a) conducted a similar study in Yukon Territory and found a low of 0.2 hares per hectare and a high of 10.5 hares per hectare over nine consecutive years. Snowshoe hares were still found to be cycling in their normal 10-year cycle in the Yukon according to a recent study conducted in 2010 (C. J. Krebs, 2011). Based on our estimated hare densities of 0.63 – 1.14 hares per hectare, snowshoe hare numbers are similar to the low densities experienced in the Yukon.

We expected to find snowshoe hare densities fluctuating in their typical 10-year cycle (Keith, 1990, Hodges, 2000). Keith (1990) and Murray (2000) found that populations in southern Canada and the northern United States do not follow a typical 10-year cycle. Instead, hares near the southern edge of their distribution experience more stable population levels at lower densities, likely due to an increased density and diversity of predators and alternative prey. Abundant alternative prey could support hare predators when hare densities start to decline, buffering the impact of changing prey abundance and stabilizing the population dynamics of predators and their prey. Greater stabilization could also occur at the northern edge of the hares' range, such as in the Churchill area, but through a different mechanism. Populations at the periphery of a species' distribution may experience more marginal conditions and fragmented or lower-quality habitat that precludes high population densities. However, climate change, which promotes the northward advancement of the tree line (Grace et al., 2002, Gamache & Payette, 2005, Harsch et al., 2009), in this case could provide more habitat and greater habitat range for hares. Since this study only included three years of unbiased data, we cannot conclude whether or not hare populations are fluctuating in a 10-year cycle, as we may have missed any significant fluctuations in the population level. Continuing to monitor hare population densities in Churchill could further our understanding of the underlying mechanisms of hare density fluctuations at the edge of the species' distribution, possibly due to a lack of food and low diversity of alternative prey for their predators.

Three transects (6, 7 and 8) consistently had the lowest mean pellet counts. Ewacha et al. (2014) suggested that the type of vegetation might impact snowshoe hare activity, which could explain the low densities on these three transects. Future vegetation sampling conducted simultaneously with pellet counts would be useful for examining the response of hares to vegetation changes and could also supplement climate change research in the area by monitoring the dynamics of different species of plants on our plots. The equation we used to convert pellet counts into hare density estimates published by McCann et al. (2008) was developed using quadrats of similar size and shape as our study, whereas other studies such as Krebs et al. (1987) and Krebs et al. (2001a) used rectangular plots. Mills et al. (2005) found that the regression equations converting pellet densities to hare densities are different whether circular plots were used or rectangular plots were used. Other studies with a similar experimental design, such as Berg and Gese (2010) and Murray et al. (2002), differed substantially in climate and geographic location. Therefore, we considered the conversion equation developed by McCann et al. (2008) to be the most appropriate for our study area.

In conclusion, our results suggest that snowshoe hare population densities near Churchill during our study period appear to be low and non-cyclic. This information may be useful to determine the number of hares that may be harvested each year without dramatically reducing the population. These data could also be compared to furbearer harvest records to understand how much of the variability in abundance of local predators that prey on hares can be explained by variation in hare abundance. Furthermore, climate change may influence snowshoe hare populations in the future, as the northward advancement of the tree line may expand the range of favourable habitat and allow populations to grow.

Subsequent studies that span a longer period of time are needed to determine conclusively whether snowshoe hare populations near Churchill are fluctuating in a 10-year cycle. Future studies should also include a larger number of transects, if sufficient blocks of continuous forest can be located, in order to obtain a larger sample size and gain a better understanding of the current population dynamics of snowshoe hares and the impact this has on their predators, near the northern edge of their distribution.

5. Acknowledgements

We thank Michelle Ewacha, Jill Larkin and students from the University of Manitoba's Arctic Field Ecology course in 2014 and 2015 for help with data collection. Parks Canada and the Churchill Northern Studies Centre provided additional logistical support. Funding for this research was provided by the University of Manitoba Faculty of Science Field Work Support Program and a National Science and Engineering Research Council of Canada Discovery Grant.

References

Berg, N. D., & Gese, E. M. (2010). Relationship between fecal pellet counts and snowshoe hare density in western wyoming. *The Journal of Wildlife Management*, *74*, 1745-1751.

Elliot-Fisk, D. L. (1983). The stability of the northern canadian tree limit. *Annals of the Association of American Geographers*, *73*(4), 560-576.

Ewacha, M. V. A., Roth, J. D., & Brook, R. K. (2014). Vegetation structure and composition determine snowshoe hare (lepus americanus) activity at arctic tree line. *Canadian Journal of Zoology*, *92*, 789-794.

Gamache, I., & Payette, S. (2005). Latitudinal response of subarctic tree lines to recent climate change in eastern canada. *Journal of Biogeography*, *32*, 849-862.

Grace, J., Berninger, F., & Nagy, L. (2002). Impacts of climate change on the tree line. *Annals of Botany*, *90*, 537-544.

Harsch, M. A., Hulme, P. E., McGlone, M. S., & Duncan, R. P. (2009). Are treelines advancing? a global meta-analysis of treeline response to climate warming. *Ecology Letters*, *12*, 1040-1049.

Hart, S. A., & Chen, H. Y. H. (2006). Understory vegetation dynamics of north American boreal forests. *Critical Reviews in Plant Science*, *25*, 381-397.

Hodges, K. E. (2000). Ecology of snowshoe hares in southern boreal and montane forests. In *Ecology and conservation of lynx in the united states.* L.F.

Keith, L. B. (1990). Dynamics of snowshoe hare populations. In H. H. Genoways (Ed.), *Current mammalogy* (p. 199-195). NY: Plenum.

Krebs, C., Boonstra, R., Nams, V., O'Donoghue, M., Hodges, K. E., & Boutin, S. (2001). Estimating snowshoe hare population density from pellet plots: a further evaluation. *Canadian Journal of Zoology*, *79*, 1-4.

Krebs, C. J. (2011). Of lemmings and snowshoe hares: the ecology of northern canada. In *Proceedings of the royal society b 278* (p. 481-489).

Krebs, C. J., Boonstra, R., Boutin, S., & Sinclair, A. R. E. (2001). What drives the 10-year cycle of snowshoe hares? *Bioscience*, *51*, 25-35.

Krebs, C. J., Boutin, S., Boonstra, R., Sinclair, A. R. E., Smith, J. N. M., Dale, M. R. T., ... Turkington, R. (1995). Impact of food and predation on the snowshoe hare cycle. *Science*, *269*, 1112-1115.

Krebs, C. J., Gilbert, B. S., Boutin, S., & Boonstra, R. (1987). Estimation of snowshoe hare population density from turd transects. *Canadian Journal of Zoology*, *65*, 565-567.

Lewis, C. W., Hodges, K. E., Koehler, G. M., & Mills, L. S. (2011). Influence of stand and landscape features on snowshoe hare abundance in fragmented forests. *Journal of Mammology*, *92*(3), 561-567.

McCann, N. P., Moen, R. A., & Niemi, G. J. (2008). Using pellet counts to estimate snowshoe hare numbers in minnesota. *Journal of Wildlife Management*, *72*, 955-958.

Mills, S., Griffin, P. C., Hodges, K. E., McKelvey, K., Ruggiero, L., & Ulizio, T. (2005). Pellet count indices compared to mark-recapture estimates for evaluating snowshoe hare density. *Journal of Wildlife Management*, *69*, 1053-1062.

Murray, D. L. (2000). A geographic analysis of snowshoe hare population demography. *Canadian Journal of Zoology*, *78*, 1207-1217.

Murray, D. L., Roth, J. D., Ellsworth, E., Wirsing, A. J., & Steury, T. D. (2002). Estimating low-density snowshoe hare populations using fecal pellet counts. *Canadian Journal of Zoology*, *80*, 771-781.

Ruggiero, K. B. A., Buskirk, S. W., Koehler, G. M., Krebs, C. J., McKelvey, K. S., & Squires, J. R. (n.d.). (Tech. Rep.). Denver, CO: University Press of Colorado.

Starfield, A. M., & Chapin, F. S. (1996). Model of transient changes in arctic and boreal vegetation in response to climate change and land use change. *Ecological Applications*, *6*(3), 842-864.

Tape, K., Sturm, M., & Racine, C. (2006). The evidence for shrub expansion in northern alaska and the pan-arctic. *Global Change Biology*, *12*(4), 686-702.

Tyson, R., Haines, H., & Hodges, K. E. (2010). Modelling the canada lynx and snowshoe hare population cycle: the role of specialist predators. *Theoretical Ecology*, *3*(2), 97-111.