Oikos 122: 1167–1176, 2013
doi: 10.1111/j.1600-0706.2012.00220.x

Subject Editor: Dries Bonte. Accepted 4 November 2012

Demographic response of tundra small mammals to a snow fencing experiment

Frédéric Bilodeau, Donald G. Reid, Gilles Gauthier, Charles J. Krebs, Dominique Berteaux and Alice J. Kenney

F. Bilodeau (frederic.bilodeau.4@ulaval.ca) and G. Gauthier, Dept de Biologie and Centre d'Études Nordiques (CEN), Univ. Laval, 1045 Avenues de la Médecine, Québec City, QC, G1V 0A6, Canada. – D. G. Reid, Wildlife Conservation Society Canada, 39 Harbottle Road, Whitehorse, YT, Y1A 5T2, Canada. – C. J. Krebs and A. J. Kenney, Dept of Zoology, Univ. of British Columbia, Vancouver, BC, V6T 1Z4, Canada. – D. Berteaux,Chaire de recherche du Canada en conservation des écosystèmes nordiques and CEN, Univ. du Québec à Rimouski (UQAR), Rimouski, QC, G5L 3A1, Canada.

Snow cover is a key environmental component for tundra wildlife that will be affected by climate change. Change to the snow cover may affect the population dynamics of high-latitude small mammals, which are active throughout the winter and reproduce under the snow. We experimentally tested the hypotheses that a deeper snow cover would enhance the densities and winter reproductive rates of small mammals, but that predation by mustelids could be higher in areas of increased small mammal density. We enhanced snow cover by setting out snow fences at three sites in the Canadian Arctic (Bylot Island, Nunavut, and Herschel Island and Komakuk Beach, Yukon) over periods ranging from one to four years. Densities of winter nests were higher where snow depth was increased but spring lemming densities did not increase on the experimental areas. Lemmings probably moved from areas of deep snow, their preferred winter habitat, to summer habitat during snow melt once the advantages associated with deep snow were gone. Our treatment had no effect on signs of reproduction in winter nests, proportion of lactating females in spring, or the proportion of juveniles caught in spring, which suggests that deep snow did not enhance reproduction. Results on predation were inconsistent across sites as predation by weasels was higher on the experimental area at one site but lower at two others and was not higher in areas of winter nest aggregations. Although this experiment provided us with several new insights about the impact of snow cover on the population dynamics of tundra small mammals, it also illustrates the challenges and difficulties associated with large-scale experiments aimed at manipulating a critical climatic factor.

Climatic conditions in the Arctic are changing rapidly with increasing temperature and shifting precipitation regimes (Solomon 2007, Hannah 2011). These changes will inevitably affect the snow cover, a key environmental component of the tundra for many animals (Chan et al. 2005, Forchhammer et al. 2005, Tyler et al. 2008, Gilg et al. 2009). During the winter, snow provides a vital protective cover for tundra plants and for some wildlife species, most notably small mammals that live under the snow (Callaghan et al. 2004). Arctic small mammal populations are famous for their multi-annual population cycles (Stenseth 1999, Krebs et al. 2002, Ims and Fuglei 2005, Pitelka and Batzli 2007, Gruyer et al. 2008), the causes of which are still far from fully understood (Krebs 2011). Recently, lemming and vole cycles have become less regular, and with a reduced amplitude, in several parts of northern Fennoscandia and Greenland (Hörnfeldt 2004, Hörnfeldt et al. 2005, Ims et al. 2008), a phenomenon that may have far-reaching consequences for the whole tundra food web. Changes in snow cover, including its depth, duration and density, have been invoked to explain these new patterns (Kausrud et al. 2008, Gilg et al. 2009, Ims et al. 2011), but the role played by snow cover in the population dynamics of small mammals is still poorly known and largely based on correlative evidence.

Small mammals are active throughout the long Arctic winter, which can last up to eight months at high latitudes. During this time, they live and even reproduce in the subnivean space (MacLean et al. 1974, Sittler 1995, Duchesne et al. 2011a), which is formed in the depth hoar of the snowpack. Specific conditions are required for the establishment of a low-density snow layer near the ground, which facilitates tunnelling by small mammals and air circulation (McKay and Adam 1981, Marchand 1996, Sanecki et al. 2006). Deeper snow increases the chances of a sub-nivean space forming by providing a higher temperature gradient between the ground and the ambient air (Marchand 1982, Sanecki et al. 2006). Deep snow reduces the probability of ground icing, due to rain or early melting, especially if the snow cover forms quickly in the early winter (Bergsten et al. 2001, Rixen et al. 2004). Deep snow can also restrict access to small mammals by predators such as foxes (Angerbjörn et al. 1999, Gilg et al. 2006), although this may be less applicable to mustelids which can hunt lemmings under the snow (Reid and Krebs 1996). It is thus not surprising that previous studies have reported a preference of lemmings for deep snow areas in winter (Formozov 1969, Sittler 1995, Duchesne et al. 2011b, Reid et al. 2012). However, because mustelids frequently concentrate their hunting effort in areas of high small mammal densities (Klemola et al. 1999, Hellstedt and Henttonen 2006), deep snow areas could potentially attract those predators if lemmings aggregate there. Snow depth is thus a central factor during winter and could affect several demographic parameters of small mammals.

Testing the effect of climatic factors on animal population dynamics is challenging, especially when based on correlations (Krebs and Berteaux 2006). For instance, the possibility of having to deal with chance events such as extreme weather conditions, or our inability to control climate, may seriously hamper our ability to detect meaningful relationships (Cowie 2007). In order to circumvent these problems, we implemented a large-scale snow manipulation experiment to examine the effect of increased snow cover on the population dynamics of arctic small mammals. A strength of our approach was the use of spatial replicates (over several years) at three sites in the Canadian Arctic, two of which were separated by >2000 km. We used rows of snow fence on large grids (>7 ha) to trap drifting snow during winter. In a previous paper, we showed that our manipulation increased snow depth on the experimental grids, created a more favourable sub-nivean temperature regime and influenced the spatial distribution of lemming and vole winter nests (Reid et al. 2012). Therefore, our manipulation improved the winter habitat quality of small mammals.

In this paper, we examine the effects of our snow manipulation on small mammal demographic parameters. Our first two hypotheses were that deeper snow would increase the density and the reproductive rate of small mammals. We thus predicted that winter density (nests) and spring density (individuals), and reproduction in winter (proportion of winter nests with evidence of reproduction) and spring (proportion of reproductive females and of juveniles) would be higher on our snow-manipulated grids than on our control grids. Our third hypothesis was that deeper snow would increase predation rates by mustelids because of increased lemming density. We thus predicted that the intensity of mustelid predation on small mammals in winter nests would be higher on our snow-manipulated grids and higher in aggregated nests.

Material and methods

Study sites

We conducted the study at three sites in the Canadian Arctic. The first is in the Qarlikturvik glacial valley (50 km^2) of Bylot Island, Sirmilik National Park, Nunavut Territory (73°08′N, 80°00′W). The study area consists of tundra polygons, thaw lakes and ponds that form wetlands interspersed with mesic tundra at the bottom of the valley, surrounded by extensive, mesic tundra on the nearby slopes and hills. The second is on Herschel Island, Yukon Territory (69°34′N, 138°54′W). It is a post-glacial island (112 km^2) composed mostly of upland habitats dominated by tussock tundra and dwarf shrub heath. The third is at Komakuk Beach, Ivvavik National Park, on the North Slope of Yukon Territory (69°35′N, 140°11′W). This is a mainland site (12 km^2) mainly composed of wet tundra on a coastal plain (see Reid et al. 2012 for more details).

At all sites the small mammal community is quite simple. On Bylot Island, the only rodent species present are brown and collared lemmings, *Lemmus trimucronatus* and *Dicrostonyx groenlandicus*, and both species exhibit multiannual cycles, although the former species exhibits much stronger fluctuations in abundance (Gruyer et al. 2008). At Herschel, the same lemming species are present and fluctuate with substantial amplitude (Krebs et al. 2011), and the only other rodent species present, in very small numbers, is the tundra vole *Microtus oeconomus*. At Komakuk Beach, brown lemmings and tundra voles are common, collared lemmings are rare, and all species remain at fairly low densities (Krebs et al. 2011); no other rodent species are found at this site. In winter, the main predators are mustelids (ermine, *Mustela erminea*, at Bylot Island, and least weasel, *Mustela nivalis*, in north Yukon) and the Arctic fox *Vulpes lagopus* at all sites. The red fox *Vulpes vulpes* is also present in small numbers at all sites and the wolverine *Gulo gulo* at Herschel Island and Komakuk Beach only.

Snow fence experiment

At all sites we set up two trapping grids at least 600 m apart, one for the experimental treatment and one as a control. Pairs of grids were set up in similar habitats and were dominated by mesic tundra, a habitat used by lemmings during winter (Duchesne et al. 2011b). On Herschel and Komakuk, all trapping grids were 9 ha (300×300 m) and on Bylot the control grid was 10.9 ha (330×330 m) and the experimental one 7.3 ha (270×270 m). In summer 2007 (Bylot and Herschel), and summer 2008 (Komakuk), we installed five parallel rows of 1.5 m high snow fence in the experimental grids to enhance snow depth. Fences were made of orange, UV-resistant plastic. Fence rows were set up perpendicular to the dominant wind and the spacing between rows ranged from 30 to 50 m. On Bylot, we fenced the entire width of the experimental grid, although fenced areas varied between years because 10 to 30% of the fence collapsed every winter but was repaired annually. At Herschel and Komakuk, only half of the experimental grids were fenced (see Reid et al. 2012 for more information about the experimental set up). The experiment lasted four years on Bylot Island (2008–2011), two years on Herschel Island (2008–2009) and one year at Komakuk (2009).

The effect of the fence on snow depth was measured annually on Bylot and on Herschel, either before or at the beginning of snow-melt (end of May to beginning of June on Bylot, late April on Herschel). No measurements could be taken at Komakuk because we could not reach the site before snowmelt. While suitable to compare snow depth among treatments within years, these data should not be used to make inter-annual comparisons due to differences in the timing of snow measurements each year. We measured snow depth at 2 to 5-m intervals along multiple transects perpendicular to the fence on both experimental and control grids. These results have been reported by Reid et al. (2012) but we will briefly summarize here the information relevant to the interpretation of the data that we present.

Lemming winter nests

Most of our information on the winter biology of arctic small mammals comes from winter nests (MacLean et al. 1974, Sittler 1995, Duchesne et al. 2011a). Lemmings and voles build nests for insulation against cold temperatures and to save energy during winter (Casey 1981). These nests are made mainly of grasses and sedges and are easily spotted at close range after snowmelt. It is possible to determine whether brown or collared lemmings used the nest based on the length, form and color of faeces left behind (MacLean et al. 1974, Duchesne et al. 2011a). Collared lemmings have dark reddish faeces about 4–6 mm long, while brown lemmings produce green faeces about 6–10 mm long. Lemmings regularly reproduce under the snow in their winter nests (Millar 2001, Stenseth and Ims 1993). Juveniles have smaller faeces than adults, which allowed us to detect if there was reproduction in a nest following the criteria of Duchesne et al. (2011a). Nests made by voles at Komakuk were differentiated from those of brown lemmings by size of green faeces (<6 mm long and thinner for voles), and the association of nests with typical soil and humus digging and deposits along runways made by *Microtus*.

When weasels prey on small mammals in their winter nests, they often line the nest with their prey's fur and use the nest themselves, or they leave rodent body parts and partially eaten carcasses in the nest (MacLean et al. 1974, Sittler 1995). It is thus possible to obtain an index of weasel predation rate on small mammals during winter by counting nests with fur lining or rodent remains.

Each spring, we systematically counted all winter nests on our control and experimental grids by walking along lines spaced 5 to 10 m apart. Because this distance is less than the effective detection distance of those nests in most habitats (Duchesne et al. 2011b), we assumed a probability of detection of 1 for nests in this census. Revisits of these sites throughout the summer confirmed that $>99\%$ of the nests had been detected by our spring survey. Therefore, our winter nest densities (number of nests per grid/grid size) lacked a variance estimate. All nests on Bylot Island and Komakuk Beach were carefully inspected to determine if reproduction or mustelid predation had occurred using the criteria outlined above. On Herschel Island, winter nests were examined for mustelid predation only. Species using winter nests and winter reproduction could not be determined on Herschel due to time restraints.

Live-trapping

We live-trapped rodents on the control and experimental grids at all sites every year using Longworth traps to obtain mark–recapture estimates of abundance. The trapping grids were laid out in a Cartesian plane of rows and columns, with numbered stakes spaced every 30 m at Bylot Island and every 20 m at the two Yukon sites. At each stake on Bylot, and every second stake in Yukon, we set out a Longworth trap pre-baited with apple near signs of lemming use or burrows (the total number of traps per grid ranged from 100 to 144). We typically had three trapping sessions during the summer but we report here only the first one, which occurred as soon as possible after snow melt (mid-June on Bylot, early to mid-June in north Yukon). Trapping sessions lasted for three days (Bylot) or two days (north Yukon) and traps were checked twice a day on Bylot and four times a day in Yukon. Traps were occasionally closed during inclement weather. This design typically yielded 6–8 trapping occasions and we considered the populations closed during this period, a reasonable assumption considering the short duration of our trapping sessions. All individuals caught were identified to species, sexed, and weighed (± 1 g) with a spring scale. Small mammals were individually marked with ear-tags in Yukon or internal PIT tags on Bylot (Gibbons and Andrews 2004) and all recaptures were noted.

For each female, we assessed reproductive status based on nipple size, vaginal condition, and pelvic separation. The number of pregnant and lactating females divided by the total number of adult females caught gave us an estimate of the proportion of reproductive females in spring just after snowmelt. The weight of each individual provided us with an index of its age (juvenile or adult). All individuals that weighed <33 g for brown lemmings and tundra voles and <40 g for collared lemmings were considered juveniles (Framstad et al. 1993, Gruyer et al. 2010). This gave us an estimate of reproductive activity during late winter based on the proportion of juveniles among all captured individuals in the spring-time population.

Statistical analyses

All density estimates were carried out in DENSITY 4.4 (<www.otago.ac.nz/density>) using Efford's maximum likelihood estimates (Efford et al. 2004, Borchers and Efford 2008), which accounts for the spatial structure of our trapping grids. All parameter settings in DENSITY 4.4 were similar to those used by Krebs et al. (2011). In spring 2010 at Bylot Island, trapping had to be done when snow was still present due to a late snow-melt, which reduced the number of effective traps by 50% in the control and 26% in the experimental grids. Because the effective trapping area had to be corrected, we estimated abundance with program CAPTURE implemented in MARK 4.2 (White and Burnham 1999). To estimate density, we divided abundance by the size of the effective trapping area following Gruyer et al. (2010) (see also Williams et al. 2002). The number of different individuals trapped per grid ranged from 0 to 65 and recapture of previously marked animals was relatively high. When the number of captured individuals was too low for analysis in DENSITY (i.e. <4 individuals), we used the minimum number known to be alive and divided this number by the effective trapping area (Krebs et al. 2011). Density estimates were obtained for each species separately.

The models of Otis et al. (1978) were used to test for variations in capture and movement probabilities. We tested models where capture and movement probabilities were set to vary as a function of time, behavioural response to capture, and individual heterogeneity (see Gruyer et al. 2010 for more details). The best models for our data were selected with Akaike's information criterion (AIC; Burnham and Anderson 2002).

We used general linear models to test for differences between the experimental and control grids (i.e. treatment) in winter nest and spring densities, as well as for an effect of site and interaction between treatment and site. We also tested for a species × treatment interaction separately for the sites where the information was available. Because small mammal densities differed considerably among years (due to their cyclic fluctuations of abundance), and among sites, we first log-transformed density estimates (both winter nests and live trapping data). We then standardized data by subtracting the annual, site-specific mean densities from the individual values of the experimental and control grids. We thus conducted the analyses on the deviations in densities of the control and experimental grids with respect to the annual, site-specific mean. Standardizing the data this way allowed us to use each year and site as replicates in the statistical analysis. We compared reproductive rates (both from winter nests and live-trapping) and predation rates by mustelids between our control and experimental grids using log-linear models. The effects of site, and interactions between site or species and treatment, were also tested. All data from the experimental grids used in the analyses for Herschel and Komakuk were taken from the treated half only (Reid et al. 2012). For statistical analyses, we used R 2.11 (R Development Core Team).

To examine our prediction that predation rate would be higher in aggregated nests, we calculated the local nest density around every nest in a given area. The mean nearest-neighbour distance between winter nests (calculated using the 'spatstat' package in R; Baddeley and Turner 2005) varied between 9.3 and 17.0 m depending on sites and years. Based on that and a visual inspection of the spatial distribution of nests, we chose a 25-m radius zone centered on the nest to calculate density around every individual nest and to assess those nests located in aggregations. To test if mustelid predation was higher in aggregations of nests, we used a logistic regression with local nest density as the independent variable. The model was run separately for each year, site and treatment with sufficient data (nine datasets with individual n ranging from 15 to 176). For these analyses, we applied the sequential Bonferroni correction to maintain the experiment-wise error rate at a reasonable level. We set the significance level as $1 - (1 - 0.05)^{1/9} = 0.0057$, which means that if the smallest probability encountered in our tests exceeded this value, then all other tests would be declared non-significant (Sokal and Rohlf 1995).

Results

Effect of experimental treatment on snow depth

Our experimental enhancement of snow depths on experimental grids was a partial success. On average, the fences increased snow depth by only 5.5 to 13.1 cm (23 to 38% depending of the site and year) over the entire experimental grid. However, fences had a strong local effect within 10 m on either side of each fence row. In these areas, snow was on average 18.2 to 40.2 cm deeper (72 to 108%) on the experimental than on the control grids (Supplementary material Appendix 1 Fig. A1; details in Reid et al. 2012). Consequently, we conducted two separate analyses for winter nest data: one using the entire experimental grid compared to the control, and one using only nests located within 10 m on either side of a fence row (hereafter referred to as the deep snow zone) compared to the control. Monitoring of ground temperature near the snow fences and on the control grids showed that temperature became warmer near the fence during late fall and this difference persisted throughout the winter (Supplementary material Appendix 1 Fig. A2). This suggests that snow accumulated rapidly near the fence rows in early winter and that this effect persisted until spring.

Effect on densities

On Bylot Island, winter nest counts and spring live-trapping density estimates indicate that brown and collared lemmings reached peak densities in 2008, were very low in 2009, increased again to high densities in 2010 and increased further in 2011. On Herschel Island, live trapping showed that brown lemmings reached peak densities in 2008 whereas collared lemmings reached their highest densities in 2007 and 2010 (i.e. pre- and post-treatment years; Krebs et al. 2011). No clear cyclic fluctuations could be detected for any small mammal species at Komakuk (Krebs et al. 2011). Voles were in very low densities at Herschel compared to lemmings but were the dominant species at Komakuk.

The treatment affected winter nest densities ($F_{1,18} = 5.46$, $p = 0.031$) and despite a significant interaction between site and treatment ($F_{2,18} = 10.47$, $p < 0.001$), the treatment effect was present at all three sites; only its magnitude varied (Fig. 1). Density of small mammal winter nests was on average 1.5 times higher on the experimental than on the control grids for the same years. When we repeated the analysis by restricting the experimental grid data to the deep snow zone, results were similar but the treatment effect was much stronger as nest densities were on average 3.3 times higher in this deep snow zone than on the control grids (treatment: $F_{1,18} = 26.63$, $p < 0.001$; site × treatment: $F_{2,18} = 10.88$, $p < 0.001$). On Bylot Island and Komakuk, all species reacted similarly to the treatment over the entire grids (species × treatment: $F_{2,12} = 2.57$, $p = 0.118$) and, although a significant interaction was found for the deep snow zone ($F_{2,12} = 7.71$, $p = 0.007$), all species reacted positively to the treatment and only the magnitude of the reaction varied among them, with a much stronger effect on brown lemming, the most abundant species on Bylot Island.

The previous patterns were not repeated in the mark–recapture estimates of rodent density in spring, soon after snow melt (Fig. 2). Overall, there was no treatment effect ($F_{1,24} = 0.02$, $p = 0.894$) but we found a significant site × treatment interaction ($F_{1,24} = 3.92$, $p = 0.034$). This

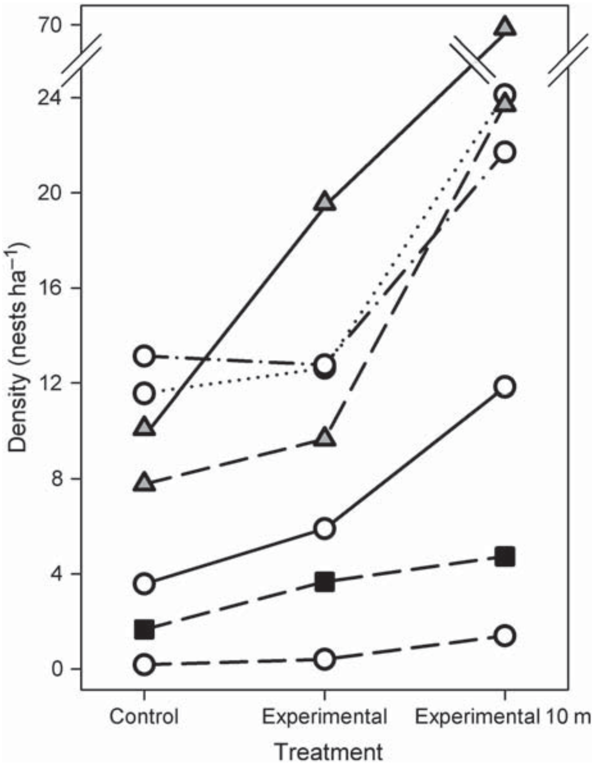

Figure 1. Small-mammal winter nests densities in our experimental and control grids at Bylot Island (white circles), Herschel Island (gray triangles) and Komakuk Beach (black squares) in 2008 (solid lines), 2009 (dashed lines), 2010 (dotted line) and 2011 (dash-dot line). 'Experimental 10 m' stands for the 10-m strip on either side of each fence row where snow accumulation was deepest. Species were not distinguished on the figure because all species reacted positively to our treatment (Results).

interaction shows conflicting results between sites and thus a conservative approach would be to say that we cannot detect an effect of treatment. Therefore, we found partial support for our first hypothesis because, although density of winter nests was increased by our experimental treatment, it had no effect on spring density.

Effect on reproduction

The proportion of winter nests showing signs of reproduction did not differ between the experimental and control grids ($\chi^2 = 0.900$, DF = 1, $p = 0.343$; Fig. 3), and there were no site × treatment ($\chi^2 < 0.001$, DF = 1, $p = 0.988$) or species × treatment interactions ($\chi^2 = 0.644$, DF = 2, $p = 0.725$). Results were similar for the analysis restricted to the deep snow zone of the fences (treatment: $\chi^2 = 0.807$, DF = 1, $p = 0.369$; site × treatment: $\chi^2 = 0.146$, DF = 1, $p = 0.702$; species × treatment: $\chi^2 = 1.796$, DF = 2, $p = 0.407$).

Spring live-trapping revealed the same patterns. Proportion of reproducing females in spring did not differ between experimental and control grids (treatment: $\chi^2 = 1.124$, DF = 1, $p = 0.289$; site × treatment: $\chi^2 = 0.169$, DF = 2, $p = 0.919$; species × treatment: $\chi^2 = 0.007$, DF = 2, $p = 0.997$; Fig. 4). Similar results were obtained for the proportion of juveniles among individuals caught in spring (treatment: $\chi^2 = 0.008$, DF = 1, $p = 0.930$; site × treatment: $\chi^2 = 1.775$, DF = 2, $p = 0.412$; species × treatment: $\chi^2 = 1.528$, DF = 2, $p = 0.466$; Fig. 5). Therefore, we found no support for our hypothesis of an enhanced reproductive rate on the experimental grids.

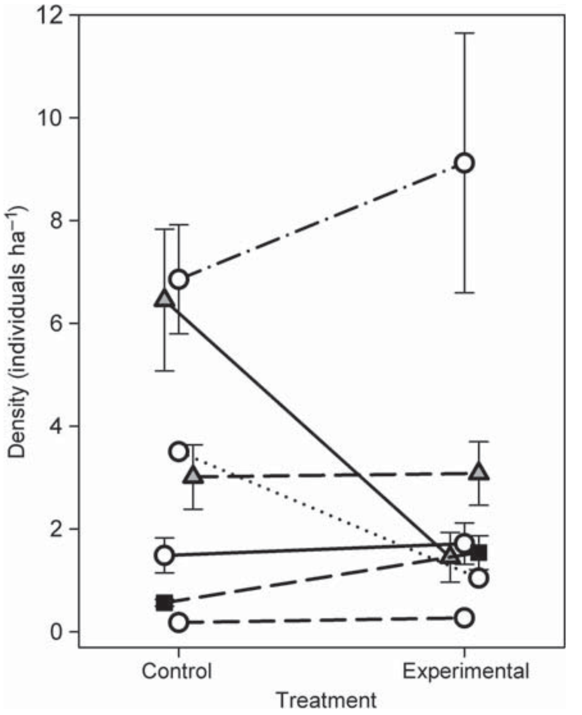

Figure 2. Small-mammal spring densities at Bylot Island (white circles), Herschel Island (gray triangles) and Komakuk Beach (black squares) from 2008 (solid lines), 2009 (dashed lines), 2010 (dotted line) and 2011 (dash-dot line). Species were not distinguished on the figure because they all responded similarly to our treatment. Error bars represent SE. Some data points were dithered horizontally to avoid superposition.

Effect on predation

The proportion of small mammal winter nests predated and used by mustelids tended to be lower in the experimental than in the control grids at Bylot and Komakuk but the opposite trend was detected at Herschel (site × treatment: $\chi^2 = 6.85$, DF = 2, $p = 0.033$; Fig. 6). The same pattern was detected when we compared the deep snow zone of experimental grids to the control (site × treatment: $\chi^2 = 10.26$, DF = 2, $p = 0.006$). On Bylot and Komakuk, the effect of the treatment on predation rates was similar for all species (treatment × species, entire grid: $\chi^2 = 1.106$, DF = 2, $p = 0.575$; deep snow zone: $\chi^2 = 0.395$, DF = 2, $p = 0.821$). Therefore, as two sites out of three did not show higher predation rates on the experimental grid, our prediction that winter predation should increase on our snow-manipulated grids was not supported.

Across all sites, grids and years with sufficient data, only Herschel showed a trend for a negative effect of nest density on predation rate by mustelids in the control grid in 2008 ($\beta = -0.71 \pm 0.42$; $F_{1,89} = 5.90$, $p = 0.017$) and 2009 ($\beta = -0.75 \pm 0.55$; $F_{1,51} = 6.88$, $p = 0.011$). However, these tests were not significant based on the Bonferroni-corrected significance level ($\alpha = 0.0057$). Our initial prediction that

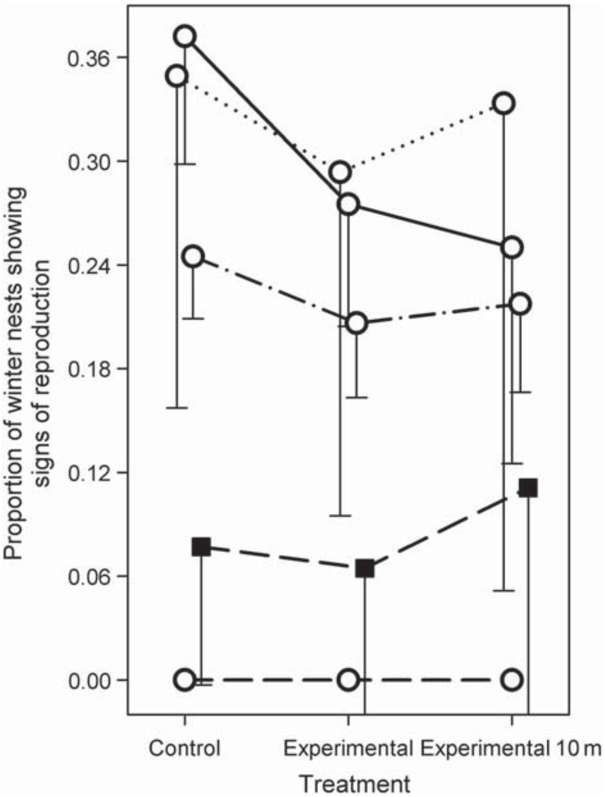

Figure 3. Proportion of small-mammal winter nests showing signs of reproduction at Bylot Island (white circles) and Komakuk Beach (black squares) from 2008 (solid lines), 2009 (dashed lines), 2010 (dotted line) and 2011 (dash-dot line). 'Experimental 10 m' stands for the 10-m strip on either side of each fence row where snow accumulation was deepest. Species were not distinguished on the figure because they all responded similarly to our treatment. Error bars represent SE. Some data points were dithered horizontally to avoid superposition.

predation would be higher in aggregated nests, such as those found on the snow-manipulated grid, was thus not supported.

Discussion

Population densities

Previous studies showed that lemmings tend to aggregate in areas of deeper snow (Duchesne et al. 2011b, Reid and Krebs 1996). Our experimental manipulation clearly demonstrated a cause–effect relationship between snow depth and lemming habitat use in winter as the density of winter nests increased on our experimental grids, with the greatest increase found in areas of deepest snow along the fence. This suggests that normal snow conditions on the widespread mesic tundra habitats at our three sites offer less than optimal conditions for wintering lemmings. Greater snow depth provides benefits to lemmings, potentially as superior protection against cold temperatures, and improves the quality of the snowpack compared to adjacent areas with shallower snow depth (Marchand 1982, Duchesne et al. 2011b, Reid et al. 2012). Although all rodent species reacted positively to the treatment, the effect was apparently greatest on brown lemmings in the deepest snow areas near the fence. One possibility is that this species showed a stronger preference for deep snow areas than the collared lemming or tundra vole. Alternatively, because the brown lemming is behaviourally dominant over the collared lemming (Morris et al. 2000), it is also possible that it limited occupation of those areas by the latter species through interspecific competition.

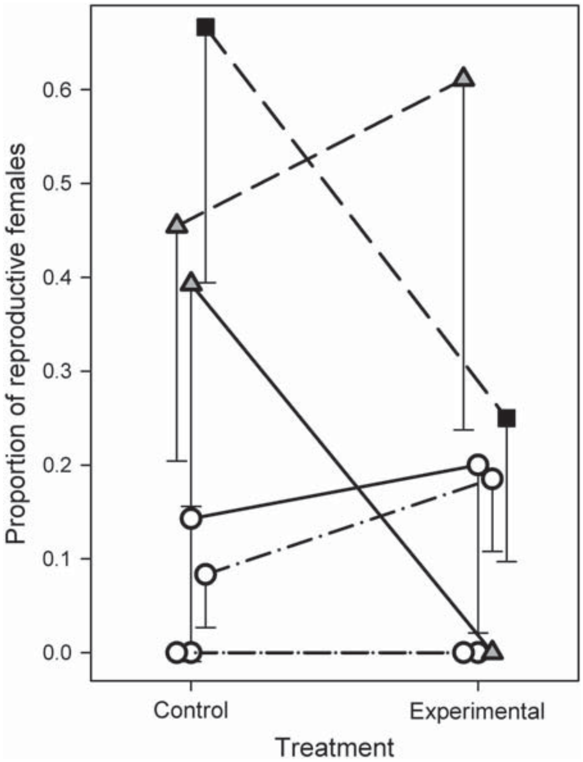

Figure 4. Proportion of small-mammal females caught in spring and showing signs of reproduction at Bylot Island (white circles), Herschel Island (gray triangles) and Komakuk Beach (black squares) from 2008 (solid lines), 2009 (dashed lines), 2010 (dotted line) and 2011 (dash-dot line). Species were not distinguished on the figure because they all responded similarly to our treatment. Error bars represent SE. Some data points were dithered horizontally to avoid superposition.

It is unclear if the increase in winter nest density that we observed is a genuine population increase or simply the consequence of a redistribution of individuals from areas surrounding our grids due to improved overwintering habitat quality near the snow fences (i.e. aggregative numerical response). Small rodents probably redistribute themselves in autumn in the process of finding the areas with the earliest accumulations of deeper snow (Reid et al. 2012). However, the absence of an increase in reproductive rate on our experimental grids does not support the hypothesis that our manipulation caused a real population increase in winter (i.e. a reproductive numerical response).

The lack of consistently higher spring densities on treatment grids compared to controls, despite an increase in winter nests, suggests that some individuals composing the winter rodent population on our grids may have moved away before or at snowmelt. In conjunction with this study,

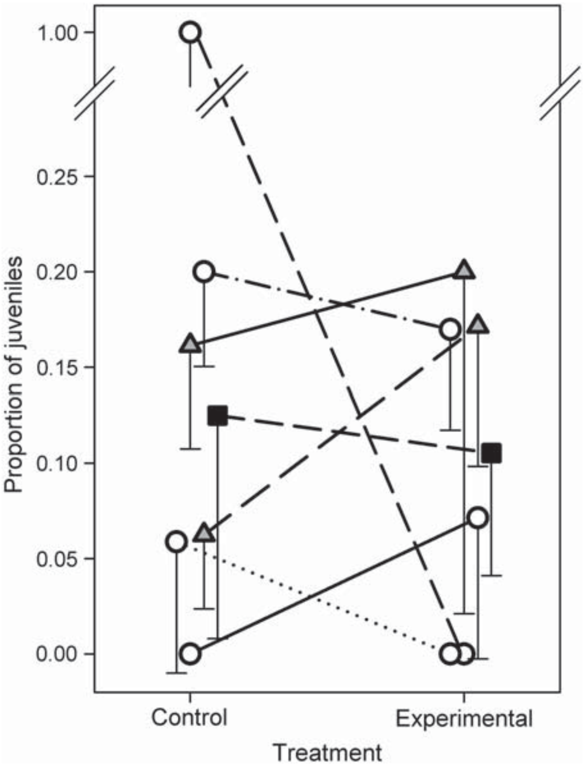

Figure 5. Proportion of small-mammal juveniles caught in spring at Bylot Island (white circles), Herschel Island (gray triangles) and Komakuk Beach (black squares) from 2008 (solid lines), 2009 (dashed lines), 2010 (dotted line) and 2011 (dash-dot line). Species were not distinguished on the figure because they all responded similarly to our treatment. Error bars represent SE. Some data points were dithered horizontally to avoid superposition.

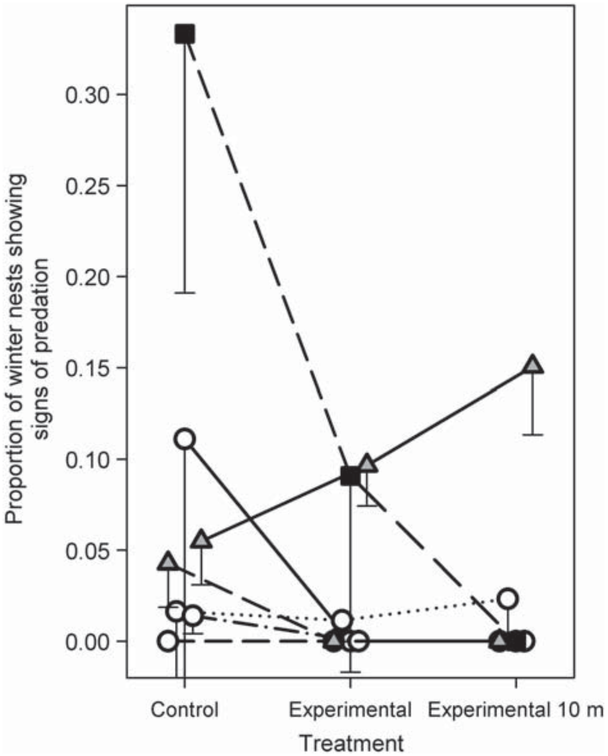

Figure 6. Proportion of small-mammal winter nests showing signs of predation by mustelids at Bylot Island (white circles), Herschel Island (gray triangles) and Komakuk Beach (black squares) from 2008 (solid lines), 2009 (dashed lines), 2010 (dotted line) and 2011 (dash-dot line). 'Experimental 10 m' stands for the 10 m strip on either side of each fence row where snow accumulation was deepest. Species were not distinguished on the figure because they all responded similarly to our treatment. Error bars represent SE. Some data points were dithered horizontally to avoid superposition.

we have discovered that, even though winter nest densities explain up to 64% of the variance in mark–recapture population estimates in the subsequent spring, a sizeable amount of variation remains unexplained, suggesting a role for other ecological factors in re-distributing the population between seasons (Krebs et al. 2012). It is possible that the scale of our treatment may not have been sufficiently large to account for small mammal inter-seasonal movements though the distance moved by lemmings between seasons remain unknown. During the process of snow melt, the sub-nivean space generally becomes colder than the ambient air (Bilodeau et al. 2012); basal ice frequently forms with the re-freezing of melt water at the ground, and melt water puddles develop in hollows (Pomeroy and Brun 2001). Therefore, at snow melt, areas of deep snow may offer a poorer environment for lemmings than areas with a thinner snow pack. Lemmings probably disperse from these poorer quality areas to better drained sites or even to the first areas that become snow free (Batzli et al. 1983, Pitelka and Batzli 1993). These movements may also be stimulated by seasonal changes in other habitat conditions such as food quality because food plants will grow earlier on snow-free sites.

Higher winter density on the treatment area could have increased density-dependent effect through food depletion compared to the control, hence favouring dispersal of small mammals away of these areas in spring. However, we found little support for this hypothesis as we did not detect any obvious signs of lemming overgrazing after snow-melt in our areas of highest winter nest density contrary to what has been reported elsewhere under high lemming density (Moen et al. 1993). Moreover, monitoring of the impact of lemming winter grazing on vegetation with exclosures on Bylot Island showed little effect in their preferred wintering habitat (snowbeds) even during years of peak lemming abundance (F. Bilodeau et al. unpubl. data).

Reproduction

It is surprising that our manipulation did not enhance winter reproduction, at least based on the indices that we used, considering that it had a strong effect on the local abundance of winter nests. The increase in winter nest abundance we observed near the fence, where snow accumulation started early during the winter and was greatest, was likely due to an increase in the sub-nivean temperature (on average, sub-nivean temperature were 1.5 to 4.5°C warmer near the fence than on the control areas; Reid et al. 2012). Chappell (1980) estimated an energy savings for lemmings in the subnivean space of about 30 kJ d^{-1} for a 10°C increase in temperature (equivalent to about 50% of basal metabolic rate), and daily energy expenditures of between about 135 and 240 kJ at the height of winter.

Thus, although the increases in subnivean temperature that we observed near the fences would have meant some energy savings for lemmings, this energetic advantage may not have been large enough to enhance reproduction. Our results are also consistent with Duschesne et al. (2011b) who found a negligible effect of enhanced thermal protection due to higher snow depth on probability of reproduction in winter nests. However, Duchesne et al. (2011b) also found an association between the presence of some vascular plants and the probability of winter reproduction in brown lemmings. Thus, it is possible that the low abundance of some plant species, and especially graminoids, may have hindered reproduction on our experimental plots.

The timing of snow accumulation in fall may be a critical factor determining the intensity of winter reproduction. If snow accumulation is too small before the onset of the coldest winter months, it is possible that reproduction will be delayed until temperatures begin increasing toward the end of winter and become more clement across an entire region, regardless of the difference in snow accumulation between our treated and control grids. Reid and Krebs (1996) found that the intensity of cold stress experienced by collared lemmings during the September and October period of photoperiod-induced changes in body morphology and, before the onset of deeper winter snow, explained the majority of the variance in rate of population growth during the entire winter. In areas where snow accumulates rapidly early in winter, individuals under a deeper snow cover may start reproducing earlier and have more or larger litters. Also, warmer temperatures on the experimental grid may have enhanced survival or growth rates of juveniles, although the absence of an increase in the proportion of juveniles caught at snow-melt does not support this hypothesis. The lack of an effect of our experiment on the proportion of reproductive females in spring, soon after snow-melt, is less surprising because reproductive activity is usually reduced or nil during the snow melt period (Negus and Berger 1998, Millar 2001).

Predation

Contrary to what we predicted, experimental areas where snow depth was enhanced did not have a higher predation index by mustelids despite a higher density of lemming nests and, at a finer scale, aggregations of winter nests did not increase the probability of being predated on our grids. A winter nest lined with fur by a weasel is a clear indication that the weasel killed lemming(s) using that nest. However, if the weasel subsequently used that nest as a starting point to forage in the surrounding area, it may encounter other winter nests and kill their occupants without necessarily using their nests. Therefore, the number of nests used by weasels may provide an underestimation of the true predation rate, and possibly a variable estimate of the predation rate depending on the degree of nest aggregation. It is also possible that the increase in winter nest density near the fence was not high enough to elicit a response by weasles but we believe that it is unlikely because the density of winter nests recorded near the fence was comparable to the density measured in preferred lemming winter habitat at our study sites (Duchesne et al. 2011b, F. Bilodeau et al. unpubl. data).

Another potential issue is the scale of our experiment. It is noteworthy that the proportion of winter nests predated by weasel for most of our site by year combinations were low (< 5% of nests), and often nil. This suggests that weasels were at very low densities, or that they did not visit and establish themselves on our grids. In choosing our grids, we avoided the highest quality winter habitats for lemmings, where snow was known to form deeper drifts because of large-scale landscape topography. So, the search pattern of weasels for areas of deeper snow, and therefore higher likelihood of lemmings, may have easily missed our relatively small scale snow depth enhancements. The home ranges of Arctic weasels in winter are not documented, but based on published information on summer ranges, are likely to be larger than our study grids and dependent on the probability of finding high concentrations of prey (Klemola et al. 1999, King and Powell 2007).

Other studies, also relying on winter nest sampling, have found that probability of predation by mustelids increased in areas of high lemming nest densities at the landscape level (Sittler 1995), including at one of our study sites (Bylot Island; Duchesne et al. 2011b). Data from Bylot also show that predation is highest in riparian habitat (Bilodeau et al. unpubl.), suggesting that weasels forage more in such habitats where snow is consistently deeper than elsewhere. Thus, habitat may be more important in affecting weasel foraging decisions than lemming density or snow depth per se.

The challenges of experimental climate manipulations

Several aspects of the snow cover such as its duration, density or depth could affect the population dynamic of tundra small mammals (Kausrud et al. 2008, Gilg et al. 2009, Ims et al. 2011). Our experiment, which was designed to manipulate only one of them, has provided us with several new insights about the impact of snow depth on the demography of small mammals. However, it also illustrates the difficulties associated with an experiment aimed at manipulating a key climatic factor and the experiment's relevance for assessing the impact of climate change on animal populations. We were able to experimentally manipulate snow depth, a key climate-related factor, but at a relatively local scale. The treatment affected the spatial distribution of small mammals, as evident in the changing densities of their winter nests, but apparently had little effect on other demographic parameters such as reproduction and predation rate. This raises the important issue of spatial scale of ecological experimentation in the Arctic. Although fairly large and logistically difficult to accomplish, our snow depth experiment perhaps still covered too small an area to encompass some of the inter-seasonal movements of small rodents and, most likely, the within-winter movements of one of their chief predators, weasels. The question of scale may be too logistically difficult to overcome, and we may have to be satisfied in some situations with mensurative assessments of relationships between demographic parameters and possible causative factors at more appropriate landscape scales. Our experiment also stresses the need to develop additional and potentially more sensitive indices of winter demographic parameters of lemmings and their predators, such as live-trapping through the snow-pack or remote sensing of lemming and weasel movements in the subnivean (e.g. radio-telemetry).

Climate change is not only characterised by changes in average weather conditions, but also by increased variability which provides even greater difficulties for experiments trying to simulate future weather conditions. An experiment such as ours, ranging for up to four years, is suitable to measure average conditions and provide some annual variability. However, it is not long enough to account for extreme events that can have profound and lasting effects on the dynamics of animal populations and which are bound to be more frequent in the future (Callaghan et al. 2004). Examples include exceptional icing events having catastrophic impact on reindeer populations (Miller and Gunn 2003, Chan et al. 2005) or a very early onset of winter affecting the wolf–muskox–hare dynamic (Mech 2004). Future experiments similar to ours should be run over longer time periods encompassing greater climatic variability. We conclude that, although experiments aimed at manipulating climatic variables may be useful in testing hypotheses at some spatial scales, long-term, non-manipulative but spatially replicated experiments with clear hypotheses may be a better approach to address these questions at the larger spatial scales typical of population processes.

Acknowledgements – Building and dismantling the fences was a huge task and we thank G.-O. Cimon, S. Gilbert, M. Müller, E. McLeod, A. Fehr, E. Hofer, D. Duchesne, J.-B. Lambert, P. Morissette, H. Mailhot-Couture, V. Lamarre, J.-F. Guay, P. Bouchard, J. Rosa-Francoeur, G. Souchay, C. Morin, J.-F. Therrien, N. Perreault, P. Bertrand, S. Pellerin, M.-A. Valiquette, M. Sirois, P.-Y. L'Hérault, É. D'Astous, L. Mercier, V. Duclos and students of the Renewable Resources Management Program (2008) at Yukon College for the help they provided. We also thank M. Leung, A. Fehr, D. Fehr, S. McLeod, J.-B. Lambert, S. Pellerin, V. Duclos, H. Mailhot-Couture and P. Morissette for help in mapping winter nests. The research relied on the logistic assistance of the staff of the Polar Continental Shelf Program (PCSP, Natural Resources Canada), the Rangers of Yukon's Qikiqtaruk Territorial Park, the staff of Ivvavik and Sirmilik National Parks, and the staff of the Aurora Research Institute in Inuvik, Northwest Territories. The research was funded by the Natural Sciences and Engineering Research Council International Polar Year program, the Canadian federal government's International Polar Year program (Project MD-021) and the Northern Student Training Program, both administered by Indian and Northern Affairs Canada, the Canadian Network of Centres of Excellence ArcticNet, the PCSP, and Wildlife Conservation Society Canada.

References

Angerbjörn, A. et al. 1999. Predator–prey relationships: arctic foxes and lemmings. – J. Anim. Ecol. 68: 34–49.

Baddeley, A. and Turner, R. 2005. Spatstat: an R package for analysing spatial point patterns. – J. Stat. Softw. 12: 1–42.

Batzli, G. O. et al. 1983. Habitat use by lemmings near Barrow, Alaska. – Holarctic Ecol. 6: 255–262.

Bergsten, U. et al. 2001. Frost heaving in a boreal soil in relation to soil scarification and snow cover. – Can. J. For. Res. 31: 1084–1092.

Bilodeau, F. et al. 2012. Evaluation of a technique to trap lemmings under the snow. – Arctic 66: 32–36.

Borchers, D. L. and Efford, M. G. 2008. Spatially explicit maximum likelihood methods for capture–recapture studies. – Biometrics 64: 377–385.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. – Springer.

Callaghan, T. V. et al. 2004. Responses to projected changes in climate and UV-B at the species level. – Ambio 33: 418–435.

Casey, T. M. 1981. Nest insulation: energy savings to brown lemmings using a winter nest. – Oecologia 50: 199–204.

Chan, K.-S. et al. 2005. Continuous and discrete extreme climatic events affecting the dynamics of a high-Arctic reindeer population. – Oecologia 145: 556–563.

Chappell, M. A. 1980. Thermal energetic and thermoregulatory costs of small arctic mammals. – J. Mammal. 61: 278–291.

Cowie, J. 2007. Climate change: biological and human aspects. – Cambridge Univ. Press.

Duchesne, D. et al. 2011a. Evaluation of a method to determine the breeding activity of lemmings in their winter nests. – J. Mammal. 92: 511–516.

Duchesne, D. et al. 2011b. Habitat selection, reproduction and predation of wintering lemmings in the Arctic. – Oecologia 167: 967–980.

Efford, M. G. et al. 2004. DENSITY: software for analysing capture-recapture data from passive detector arrays. – Anim. Biodivers. Conserv. 27: 217–228.

Forchhammer, M. et al. 2005. Local-scale and short-term herbivore–plant spatial dynamics reflect influences of large-scale climate. – Ecology 86: 2644–2651.

Formozov, A. N. 1969. Snow cover as an integral factor of the environment and its importance in the ecology of mammals and birds. – No. 1 Occas. Publ., Boreal Inst., Univ. of Alberta, Edmonton.

Framstad, E. et al. 1993. Demography of *Lemmus lemmus* through five population cycles. – In: Stenseth, N. C. and Ims, R. A. (eds), The biology of lemmings. Academic Press, pp. 117–134.

Gibbons, J. W. and Andrews, K. M. 2004. PIT tagging: Simple technology at its best. – Bioscience 54: 447–454.

Gilg, O. et al. 2006. Functional and numerical responses of four lemming predators in high arctic Greenland. – Oikos 113: 193–216.

Gilg, O. et al. 2009. Climate change and cyclic predator–prey population dynamics in the high Arctic. – Global Change Biol. 15: 2634–2652.

Gruyer, N. et al. 2008. Cyclic dynamics of sympatric lemming populations on Bylot Island, Nunavut, Canada. – Can. J. Zool. 86: 910–917.

Gruyer, N. et al. 2010. Demography of two lemming species on Bylot Island, Nunavut, Canada. – Polar Biol. 33: 725–736.

Hannah, L. 2011. Climate change biology. – Academic Press.

Hellstedt, P. and Henttonen, H. 2006. Home range, habitat choice and activity of stoats (*Mustela erminea*) in a subarctic area. – J. Zool. 269: 205–212.

Hörnfeldt, B. 2004. Long-term decline in numbers of cyclic voles in boreal Sweden: analysis and presentation of hypotheses. – Oikos 107: 376–392.

Hörnfeldt, B. et al. 2005. Fading out of vole and predator cycles? – Proc. R. Soc. B 272: 2045–2049.

Ims, R. A. and Fuglei, E. 2005. Trophic interaction cycles in tundra ecosystems and the impact of climate change. – Bioscience 55: 311–322.

Ims, R. A. et al. 2008. Collapsing population cycles. – Trends Ecol. Evol. 23: 79–86.

Ims, R. A. et al. 2011. Determinants of lemming outbreaks. – Proc. Natl Acad. Sci. 108: 1970–1974.

Kausrud, K. L. et al. 2008. Linking climate change to lemming cycles. – Nature 456: 93–97.

King, C. M. and Powell, R. A. 2007. The natural history of weasels and stoats: ecology, behavior, and management, 2nd edn. – Oxford Univ. Press.

Klemola, T. et al. 1999. Mobility and habitat utilization of small mustelids in relation to cyclically fluctuating prey abundances. – Ann. Zool. Fenn. 36: 75–82.

Krebs, C. J. 2011. Of lemmings and snowshoe hares: the ecology of northern Canada. – Proc. R. Soc. B 278: 481–489.

Krebs, C. J. and Berteaux, D. 2006. Problems and pitfalls in relating climate variability to population dynamics. – Clim. Res. 32: 143–149.

Krebs, C. J. et al. 2002. Synchrony in lemming and vole populations in the Canadian Arctic. – Can. J. Zool. 80: 1323–1333.

Krebs, C. J. et al. 2011. Fluctuations in lemming populations in north Yukon, Canada, 2007–2010. – Can. J. Zool. 89: 297–306.

Krebs, C. J. et al. 2012. Are lemming winter nest counts a good index of population density? – J. Mammal. 93: 87–92.

MacLean, S. F. et al. 1974. Population cycles in arctic lemmings: winter reproduction and predation by weasels. – Arct. Alpine Res. 6: 1–12.

Marchand, P. J. 1982. An index for evaluating the temperature stability of a subnivean environment. – J. Wildlife Manage. 46: 518–520.

Marchand, P. J. 1996. Life in the cold: an introduction to winter ecology. – Univ. Press of New England, Hanover.

McKay, G. A. and Adam, W. P. 1981. Snow and living things. – In: Gray, D. M. and Male, D. H. (eds), Handbook of snow: principles, processes, management and use. Pergamon Press, pp. 3–31.

Mech, L. D. 2004. Is climate change affecting wolf populations in the high Arctic? – Climatic Change 67: 87–93.

Millar, J. 2001. On reproduction in lemmings. – Ecoscience 8: 145–150.

Miller, F. L. and Gunn, A. 2003. Catastrophic die-off of Peary caribou on the Western Queen Elizabeth Islands, Canadian high Arctic. – Arctic 56: 381–390.

Moen, J. et al. 1993. Lemming grazing on snowbed vegetation during a population peak, northern Norway. – Arctic Alpine Res. 25: 130–135.

Morris, D. W. et al. 2000. Measuring the ghost of competition: insights from density-dependent habitat selection on the co-existence and dynamics of lemmings. – Evol. Ecol. Res. 2: 41–67.

Negus, N. C. and Berger, P. J. 1998. Reproductive strategies of *Dicrostonyx groenlandicus* and *Lemmus sibiricus* in high-arctic tundra. – Can. J. Zool. 76: 391–400.

Otis, D. L. et al. 1978. Statistical inference from capture data on closed animal populations. – Wildlife Monogr. 62: 3–135.

Pitelka, F. A. and Batzli, G. O. 1993. Distribution, abundance and habitat use by lemmings on the north slope of Alaska. – In: Stenseth, N. C. and Ims, R. A. (eds), The biology of lemmings. Academic Press, pp. 213–236.

Pitelka, F. A. and Batzli, G. O. 2007. Population cycles of lemmings near Barrow, Alaska: a historical review. – Acta Theriol. 52: 323–336.

Pomeroy, J. W. and Brun, E. 2001. Physical properties of snow. – In: Jones, H. E. et al. (eds), Snow ecology: an interdisciplinary examination of snow-covered ecosystems. Cambridge Univ. Press, pp. 45–126.

Reid, D. G. and Krebs, C. J. 1996. Limitations to collared lemming population growth in winter. – Can. J. Zool. 74: 1284–1291.

Reid, D. G. et al. 2012. Lemming winter habitat choice: a snow-fencing experiment. – Oecologia 168: 935–946.

Rixen, C. et al. 2004. Ground temperatures under ski pistes with artificial and natural snow. – Arct. Antarct. Alp. Res. 36: 419–427.

Sanecki, G. M. et al. 2006. The characteristics and classification of Australian snow cover: an ecological perspective. – Arct. Antarct. Alp. Res. 38: 429–435.

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. – Ann. Zool. Fenn. 32: 79–92.

Sokal, R. R. and Rohlf, F. J. 1995. Biometry: the principles and practice of statistics in biological research, 3rd edn. – W. H. Freeman.

Solomon, S. 2007. Climate change 2007: the physical science basis. Contrib. Working Group I to the 4th Assess. Rep. of the Intergovernmental Panel on Climate Change. – Cambridge Univ. Press.

Stenseth, N. C. 1999. Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. – Oikos 87: 427–461.

Stenseth, N. C. and Ims, R. A. 1993. Population dynamics of lemmings: temporal and spatial variation – an introduction. – In: Stenseth, N. C. and Ims, R. A. (eds), The biology of lemmings. Academic Press, pp. 61–96.

Tyler, N. J. C. et al. 2008. Nonlinear effects of climate and density in the dynamics of a fluctuating population of reindeer. – Ecology 89: 1675–1686.

White, G. C. and Burnham, K. P. 1999. Program MARK: survival estimation from populations of marked animals. – Bird Study 46: 120–139.

Williams, B. K. et al. 2002. Analysis and management of animal populations. – Academic Press.

Supplementary material (available online as Appendix Oik-00220 at <www.oikosoffice.lu.se/appendix>). Appendix 1.