Chapitre 2

The effect of snow cover on lemming population cycles in the Canadian High Arctic

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Résumé

L'augmentation des températures et les changements dans le régime des précipitations vont avoir un puissant impact sur la qualité du couvert nival dans l'Arctique. Un couvert nival de bonne qualité, protégeant les lemmings des températures froides et des prédateurs serait un facteur important pour maintenir la dynamique cyclique de leurs populations dans la toundra. Nous avons examiné si les caractéristiques des fluctuations annuelles (amplitude et forme des phases) de densité du lemming brun (*Lemmus trimucronatus*) pouvaient être déterminées par l'épaisseur de neige, la densité de la neige, la température sous-nivale et la persistance de la neige. En utilisant une série temporelle s'étalant sur 18 ans d'abondance de lemming brun à l'île Bylot, dans l'Arctique Canadien, nous avons testé si les variables associées à la neige pouvaient expliquer la variation résiduelle entre les densités de lemming observées et celles prédites par des modèles où la cyclicité est expliquée. Nos analyses supportent l'hypothèse que le couvert nival peut affecter l'amplitude et possiblement la périodicité des cycles de population de lemming dans le haut Arctique. Les abondances estivales de lemming brun étaient plus élevées suivant les hivers ayant un couvert de neige épais et une couche de neige près du sol de faible densité, mais elles n'étaient pas affectées par la date d'établissement ou de fonte et la durée du couvert nival. Deux variables montraient une tendance temporelle : l'épaisseur de neige moyenne tendait à augmenter et la date d'établissement de l'épaisseur de neige critique tendait à être devancée dans le temps. Ces tendances temporelles, qui seraient favorables aux lemmings, pourraient expliquer pourquoi des cycles de population sains se sont apparemment maintenus à notre site d'étude comparativement à d'autres sites de l'Arctique.

Abstract

Rising temperatures and changes in the precipitation regime will have a strong impact on the quality of the snow cover in the Arctic. A snow cover of good quality protecting lemmings from cold temperatures and predators is thought to be an important factor for maintaining the cyclic dynamic of their populations in the tundra. We examined if the characteristics of annual fluctuations (amplitude and shape of phases) in brown lemming (*Lemmus trimucronatus*) density could be determined by snow depth, snow density, sub-nivean temperature and persistence of snow. Using an 18-year time series of brown lemming abundance on Bylot Island in the Canadian Arctic, we tested if snow variables could explain the residual variation between the observed lemming density and the one predicted by models where cyclicity had been accounted for. Our analysis provides support for the hypothesis that snow cover can affect the amplitude and possibly also the periodicity of lemming population cycles in the High Arctic. Summer abundance of brown lemmings was higher following winters with a deep snow cover and a low-density snow pack near the ground but was unaffected by the date of establishment or melting and duration of the snow cover. Two snow variables showed a temporal trend; mean winter snow depth tended to increase and date of establishment of the hiemal threshold occurred earlier over time. These temporal trends, which should be favourable to lemmings, may explain why healthy population cycles have apparently been maintained at our study site contrary to other Arctic sites.

Introduction

Small mammal population cycles have fascinated ecologists for decades and a large number of studies have tried to explain their high prevalence in northern environments (Stenseth and Ims 1993b, Korpimäki and Krebs 1996, Stenseth 1999, Hanski et al. 2001, Turchin et al. 2000, Oksanen et al. 2001, Gilg et al. 2003, Korpimäki et al. 2005, Pitelka and Batzli 2007, Krebs 2011). In recent years, population cycles in Fennoscandia and some parts of Greenland have faded out and climatic factors, especially snow cover, have been hypothesized to explain this (Hörnfeldt 2004, Hörnfeldt et al. 2005, Ims et al. 2008, Kausrud et al. 2008, Gilg et al. 2009, Ims et al. 2011). During the arctic winter, which can last up to 8 months, these rodents remain active and even reproduce under the snow (MacLean et al. 1974, Sittler 1995, Duchesne et al. 2011b). Variations in characteristics of snow cover can affect quality, and thus selection, of winter habitat (Reid et al. 2012). This in turn can influence survival, especially of young born during winter, and possibly reproduction (Yoccoz and Ims 1999, Aars and Ims 2002). Snow cover can also affect demography by reducing food availability, for instance during episodes of ground icing, or by limiting predator access to small mammals (Ims and Fuglei 2005, Kausrud et al. 2008, Gilg et al. 2009, Duchesne et al. 2011b).

A snow pack of good quality for small mammals should have several characteristics. First, it should favour the formation of a low-density depth hoar and of a sub-nivean space at its base, which facilitate tunnelling and air circulation, and provide room for small mammals to live and feed (McKay and Adam 1981, Marchand 1996, Sanecki et al. 2006). Second, it should insulate small mammals from extreme air temperature variations and protect them from the coldest meteorological events (Pomeroy and Brun 2001, Duchesne et al. 2011b, Reid et al. 2012). The thermal insulation provided by a snow layer is proportional to its depth but inversely proportional to its density (Berry 1981, Marchand 1982). Thermal insulation levels off when snow depth reaches 20-30 cm (depending on snow density), a depth referred to as the "hiemal threshold" (Pruitt 1970). Third, it should prevent ground icing due to rain or melting (Korslund and Steen 2006). This effect is maximized when a deep snowpack forms early in fall (Bergsten et al. 2001, Rixen et al. 2004). Fourth, it should persist long enough for the above effects to occur throughout the cold season.

Snow cover itself is unlikely to cause cyclic fluctuations of small mammal populations, but its high quality is believed to be an essential condition for periodic population outbreaks of arctic rodents like lemmings (MacLean et al. 1974, Ims et al. 2008, Kausrud et al. 2008). Therefore, snow cover could influence several aspects of these fluctuations, such as the stationarity of cycles (i.e. the stability of their period length), the amplitude of peaks, or the shape of individual increase-decrease phases. For instance, food or predator abundance may provide the conditions for a peak to occur, but a snow cover of poor quality may decrease its amplitude or delay its occurrence (Gilg et al. 2009). However, very few studies have tried to relate the different characteristics of the snow cover to those of small mammal fluctuations (Kausrud et al. 2008). We addressed this gap using an 18-year record of fluctuations in brown lemming (*Lemmus trimucronatus*) abundance at a Canadian high Arctic site where population cycles are still occurring (Gruyer et al. 2008). We tested the general hypothesis that a snow cover of high quality and high persistence has a positive effect on the amplitude of lemming cycles. More specifically, we examined if the characteristics of annual fluctuations (amplitude and shape of phases) in lemming density were affected by snow depth, snow pack density, temperature of the sub-nivean space, duration of the snow cover and dates at which it became established and disappeared.

Materials and methods

Study area

The study was conducted on the south plain of Bylot Island, Sirmilik National Park, Nunavut Territory, Canada (73°08'N, 80°00'W). The main study area (70 km^2) consists of tundra polygons, thaw lakes and ponds forming wetlands at the bottom of a valley and is surrounded by drier mesic habitat in the upland areas and nearby slopes and hills. Wet areas are dominated by sedges (*Carex aquatilis*, *Eriophorum sheuchzeri*) and graminoids (*Dupontia fisheri* and *Pleuropogon sabinei*) and mesic areas mainly by forbs (*Saxifraga* spp*., Potentilla* spp*., Ranunculus* spp.), graminoids (*Arctagrostis latifolia, Alopecurus alpinus, Poa* spp*., Luzula* spp.), shrubs (*Salix* spp., *Dryas integrifolia*, *Cassiope tetragona*) and mosses (Duclos 2002, Duchesne et al. 2011b). The Average air temperature from

October to June is -23.4 ± 0.4 °C and the average snow depth at the end of winter is 31.3 cm (Cadieux et al. 2008).

Two species of small mammals live in the study area, the brown and the collared lemming (*Dicrostonyx groenlandicus*). Although both species tend to fluctuate synchronously, only the brown lemming shows clear, large amplitude multiannual population cycles at our study site (Gruyer et al. 2008). Collared lemming populations are low in most years and maximum population size is always an order of magnitude lower than that of the brown lemming. For these reasons, this study focuses only on brown lemmings. In summer, brown lemmings prefer wet habitat but can also be abundant in mesic habitats (Batzli and Jung 1980, Morris et al. 2000, 2011, Ale et al. 2011). During winter, they usually prefer mesic habitat, probably because its topography is, unlike that of flat wetlands, more conducive to the accumulation of a deep snow cover in snow drifts (Batzli et al. 1983, Pitelka and Batzli 1993, Sittler 1995, Duchesne et al. 2011b). Their main predators are the snowy owl (*Bubo scandiaca*), long-tailed jaeger (*Stercorarius longicaudus*), rough-legged hawk (*Buteo lagopus*), glaucous gull (*Larus hyperboreus*), arctic fox (*Vulpes lagopus*) and ermine (*Mustela erminea*). The latter two mammals are the only winter predators.

Lemming densities

We trapped brown and collared lemmings using snap traps from 1994 to 2011 to obtain an index of abundance of each species. Trapping was conducted annually at the end of July on two sites simultaneously, one in wet habitat using four 240-m long parallel transects 100 m apart and the other in mesic habitat (since 1995) using two 500-m long parallel transects. We used Museum special traps baited with oat and peanut butter. Each transect consisted of 17 (wet) to 34 (mesic) stations spaced by 15 m. Until 2006, each station had 1 trap set near burrows or runways (when possible) within a 2-m radius and trapping lasted 10 days (for more details see Gruyer et al. 2008). From 2007 onward, we set three traps per station and trapping lasted 3 or 4 days. Both methods yielded similar results (G. Gauthier unpublished data). The total number of trap-nights varied between 500 (1994-2006) and 720-960 (2007-2011) at each site, depending on year.

From 2004 to 2011, live trapping was also conducted to obtain accurate estimates of brown lemming densities with capture-mark-recapture methods. Live trapping was conducted in mid-July for 3 or 4 consecutive days on two grids, one in the wet and one in the mesic habitat. Trapping grids were 10.9 ha and consisted of 144 traps spaced every 30 m and laid out in a Cartesian plane of 12 rows and columns. Longworth live traps were baited with apple and were checked every 12 h (see Gruyer et al. 2010). Lemming populations during trapping sessions were considered closed for the analysis. The number of individuals trapped annually varied from two to 187, and the recapture rate was relatively high. All density estimates were carried out in DENSITY 4.4 (http://www.otago.ac.nz/density) using Efford's maximum likelihood spatial model (Efford et al. 2004, Borchers and Efford 2008, see also Krebs et al. 2011).

Because snap trapping provides only an index of abundance, we used the more precise density estimate obtained by live trapping. We transformed the abundance index for years prior to 2004 into density estimates using results from the linear relationship between live trapping and snap trapping data from 2004 to 2011, using each trapping grid as a sampling unit ($F_{1,13} = 65.2$, $P < 0.001$, $R^2 = 0.82$).

Snow cover

An automated weather station installed at our field site provided the following hourly, year-round data since 1993: air (2 m above ground) and ground (2 cm below ground) temperatures, air humidity, wind velocity and direction, incoming and reflected radiation, and snow depth (since 2001). To fill in periods when information was missing (primarily snow depth prior to 2001; occasionally other variables due to sensor breakdown), we retrieved data from the Pond Inlet airport weather station situated at 80 km from our site (for snow depth in April and May 1994, we had to use data from the Nanisivik weather station situated 150 km from our site). All climatic data including snow depth were recorded daily at those weather stations. Following Dickey et al. (2008), we used linear models to relate the data from our weather station to those from Pond Inlet (or Nanisivik) during periods of overlap. Strong relationships were found for most variables (e.g. daily snow depth values: $F_{1,464} = 959.2$, $P < 0.001$, $R^2 = 0.67$ for Pond Inlet; $F_{1,719} = 139.5$, $P <$

0.001 $R^2 = 0.14$ for Nanisivik). We used these relationships to predict missing values in our weather data. For winter 2009-2010, no snow depth data were available from any weather station; mean winter snow depth had to be estimated from a relationship between mean snow depth determined at our weather station and that obtained from our snow-melt transects in early spring during years of overlap ($F_{1,7} = 4.04$, $P = 0.084$, $R^2 = 0.37$). Since 1995, snow depth has been measured manually every other day from ca. 1 to 20 June on 50 stations along two 250-m transects located 100 m apart. This information was also used to determine the timing of snow melt (i.e. when snow had completely disappeared).

Prior to snow melt, we dug snow pits at 60 random locations throughout our study site in 2010 (19- 30 May) and 2011 (19- 26 May). At each site, a temperature logger (I-button) had been set at ground level the previous fall to record sub-nivean temperatures at 5-h intervals during winter. We measured snow depth, the number of recognizable layers and their respective thickness, hardness, density, snow grain size and type, following the protocol developed by M. Bernier and Y. Gauthier (personal communication) and the snow classification by Fierz et al. (2009). We also measured the temperature gradient of each snow profile by taking from five to six measurements at varying depth.

We modelled the snow conditions with the SNOWPACK software using our meteorological data as input variables (see Bartelt and Lehning 2002, Lehning et al. 2002a, b for detailed information and methods; Annexe 2). This allowed us to estimate the evolution of the snowpack on a daily basis throughout the winter and especially to estimate snow density at ground level, a key parameter that we could not directly measure during winter. We used the data from our snow profiles made in May 2011 to test SNOWPACK predictions for density of the ground-level snow layer. The weighted-average of snow density of the bottom 5 cm estimated from the snow profiles was 281.2 kg m^{-3} (95% confidence interval: 267.6-294.7 kg m^{-3}). The SNOWPACK estimate for that layer on the same dates (278.8 kg m^{-3}) was very close and well within the confidence interval, which suggests that SNOWPACK performed well.

We could not estimate snow density with SNOWPACK for winter 2009-2010 due to lack of daily snow depth data. As a substitute, we used the average snow density measured at ground level in our snow pits that year (146.8 kg m^{-3}). Density measured before the onset of snowmelt should be representative of the mean winter density because major changes in density usually do not occur prior to that (McKay and Gray 1981).

Statistical analyses

Our premise was that snow cover did not generate the lemming cycle but could modulate some of its parameters. Therefore, we worked in three steps to examine if some descriptive variables of snow cover explained variations in the amplitude and periodicity of annual fluctuations in lemming density: we generated cycles using three different models, we extracted residuals from the relations between these modelled cycles and our observed annual lemming densities, we regressed the obtained residuals with the snow variables that we thought could affect lemming populations. We reasoned that these analytical steps would allow us to assess directly the effects of individual snow cover variables on lemming abundance while removing the potential effects of the other (unknown) variables generating the cycles.

Generation of cycles

We first generated a sinusoidal model with a 4-year periodicity, the average periodicity of brown lemming cycles at our site (Gruyer et al. 2008) using the following equation:

$$(1)\ x_t = 2 \sin(2\ t\ \pi)$$

where x_t stands for the ln (brown lemming summer density + 0.01) in year t.

We then modelled the observed lemming cycle by adjusting first- and second-order autoregressive models (Stenseth et al. 1996, Stenseth 1999) using the following equations:

$$(2)\ x_t = \beta_0 + \beta_1 x_{t-1} + \varepsilon_t$$
$$(3)\ x_t = \beta_0 + \beta_1 x_{t-1} + \beta_2 x_{t-2} + \varepsilon_t,$$

where β_0 is the coefficient of the intercept, β_1 and β_2 represent the first- and second-order autoregressive coefficients and ε_t is the error term.

Extraction of residuals

To obtain residuals, we calculated the differences between the annual densities predicted by the three above models ($\hat{x}_t$) and our annual observed values of lemming densities.

Regression of residuals with snow variables

We used seven variables descriptive of snow cover: mean daily snow depth, mean daily density of the bottom 5 cm of the snow pack, mean daily temperature of the sub-nivean space, date at which the snow cover became established, date at which the hiemal threshold (defined as 20 cm snow depth; Pruitt 1970) was reached, date when snow had completely melted, and duration (in days) of the snow cover. We also added year as a continuous variable in our model to test for any temporal trend in population densities. We tested for multicollinearity among snow variables. Duration of snow cover and time of snow establishment were highly correlated ($r = -0.87$, $t = -7.09$, $df = 16$, $P < 0.001$) and these two variables were thus never used in the same model. Correlations among the remaining independent variables (all, ≤ 0.61) were considered acceptable (Grewal et al. 2004).

To avoid model saturation due to our relatively short time series (17 and 18 years according to habitat), a maximum of three variables were used at the same time in each model. All models were compared using second-order Akaike's information criterion adjusted for small sample size (AICc) and AICc weight (Burnham and Anderson 2002). All analyses were conducted in R 2.11 (R Development Core Team 2010). Mean values are presented with SE throughout.

Results

Lemming cycles

Throughout the study period, brown lemmings showed a fairly regular population cycle (Fig. 1) of high amplitude with peaks occurring every 3-4 years. During peak years, densities reached up to 41.4 lemmings ha^{-1} in the wet grid and 20.4 lemmings ha^{-1} in the

mesic grid. During the low phases, densities were as low as 0.07 lemmings ha^{-1} in both habitats. Based on the mean densities for peak and low years obtained with live trapping, this represents 37-fold and 94-fold variations in the wet and mesic grids, respectively.

Snow variables

Most of the seven snow variables examined showed moderate to large fluctuations over the 18-year period (coefficient of variation ranging from 3.9 to 27.8 %) and only two of them showed a temporal trend (Fig. 2). Mean winter snow depth tended to increase ($F_{1,16} = 4.31$, $P = 0.054$) and date of establishment of the hiemal threshold occurred earlier over time ($F_{1,16} = 8.69$, $P = 0.009$). These trends are consistent with those reported elsewhere in the Arctic (SWIPA 2011).

Modelling of cycles

Whereas the sinusoidal approach always generated a cycle and thus allowed extraction of residuals between the generated cycle and the observed values, the same was not necessarily true with the autoregressive approach. Only the first-order autoregressive model yielded a discernible cyclic pattern of fluctuations in the mesic grid, though the fit was not as good as with the sinusoidal model. None of the autoregressive (i.e. first- and second-order) models yielded a cycle in the wet grid, and thus the effect of snow variables was not tested on those residuals.

Effect of snow variables on lemming abundance

Mesic habitat

Model selection for residuals of brown lemming summer density from the sinusoidal model indicated that some snow variables affected lemming density in the mesic grid (Table 1). One variable appeared most influential, mean winter snow depth (cumulative AICc weight across models = 0.99). Models including ground temperature and mean winter density of the bottom snow layer were close competitors (ΔAICc = 0.61 and 0.94, respectively). However, across models snow density had more weight than ground temperature

(cumulative AICc weight = 0.32 and 0.22, respectively). Snow depth was positively related to lemming densities ($F_{1,15}$ = 6.83, P = 0.020, R^2 = 0.31; β = 28.2 ± 10.8; Fig. 3) whereas snow density was negatively related ($F_{1,15}$ = 4.58, P = 0.049, R^2 = 0.23; β = -0.017 ± 0.008; Fig. 3). There was a positive, though non-significant, trend between lemming density and ground temperature ($F_{1,15}$ = 2.56, P = 0.131, R^2 = 0.15; β = 0.44 ± 0.28). Adding snow depth and density to the sinusoidal model improved its fit with the observed data (Fig. 4). For instance, the model with snow variables predicted well the low lemming density observed in summer 1999 and the increase that started in 2010 and lead to a peak in 2011, 3 years after the previous peak instead of 4 years as in the preceding ones. This suggests that snow characteristics may not only affect the amplitude of lemming fluctuations but possibly also their periodicity. However, the sharp 2005 decline remained unpredicted.

The same analysis based on the residuals from the first-order autoregressive model also suggested that brown lemming density was affected by mean snow depth (cumulative AICc weight = 0.76; Table 2) as it was positively related to it ($F_{1,15}$ = 4.68, P = 0.047, R^2 = 0.24; β = 26.5 ± 12.3). Even though ground temperature and snow density in the bottom layer were not retained in the model selections, lemming density also showed a positive trend with ground temperature ($F_{1,15}$ = 2.43, P = 0.140, R^2 = 0.14; β = 0.47 ± 0.30) and a negative one with snow density ($F_{1,15}$ = 2.45, P = 0.139, R^2 = 0.14; β = -0.014 ± 0.009).

Wet habitat

In the wet grid, model selection for residuals of brown lemming summer density from the sinusoidal model indicated that the null model was preferred (Table 3). Although a model with density of the bottom snow layer was a close competitor (ΔAICc = 0.32), overall the evidence for this effect was moderate (cumulative AICc weight = 0.42). There was a weak trend for a negative relationship between lemming abundance and snow density ($F_{1,16}$ = 2.48, P = 0.135, R^2 = 0.13; β = -0.012 ± 0.008). Adding snow density to the sinusoidal model slightly improved the fit of the model to the observed data as the low abundance in 1995, as well as the high abundance in 2010 were better predicted (Fig. 5).

Discussion

The logic of our approach was to remove analytically the cyclicity in lemming population fluctuations in order to better assess the effect of snow parameters on their abundance. This approach is analogous to detrending a time series before evaluating the effects of covariates (Votier et al. 2009). Autoregressive models were not always successful in generating cyclic oscillations with our data. Nonetheless, it is reassuring to find that, whether we detrended the data with a sinusoidal or an autoregressive model, the effect of snow variables on residual variations in lemming abundance remained qualitatively the same. This suggests that our analysis was not highly sensitive to the model used to control for the cyclic pattern of fluctuations.

Our analysis provides support for the hypothesis that winter snow cover can affect the amplitude and even possibly the periodicity of lemming population cycles in the High Arctic. Based on the relationships presented in Fig. 3, a twofold increase in snow depth could increase summer density of brown lemmings by a factor of 17 in mesic habitat whereas a twofold increase in snow density could decrease their density by a factor of 27. Evidence for an effect of snow cover in the wet habitat was weaker, with only a possible negative effect of snow density on brown lemming abundance. Although brown lemmings tend to prefer wet habitats in summer, when our trapping occurred, they can use both habitats (Morris et al. 2000, Gruyer et al. 2010) and during winter they actually tend to avoid wet habitats where snow accumulation is shallower (Duchesne et al. 2011b). If brown lemmings concentrate in wet habitat during the summer, especially when densities are low, this may distort the amplitude locally, and possibly weaken our ability to detect an effect of snow cover. However, considering that the mesic habitat composes the majority of the landscape of our study area (85 %), patterns observed in this habitat may be more representative of the population at large.

Depth is a key component of the snow cover, influencing most other snow-related parameters (Pomeroy and Brun 2001). For instance, greater snow depth will permit higher sub-nivean temperatures and lower snow layers will be less subject to compaction (by wind for example) and thus have lower densities. Higher sub-nivean temperatures will reduce the

physiological stress that lemmings undergo during winter (Chappell 1980, Casey 1981). As deeper snow will provide a more favourable thermal environment (Duchesne et al. 2011b, Reid et al. 2012) and potentially reduced predation (Duchesne et al. 2011b), survival should be higher. Although we found only weak positive trends of sub-nivean temperature on density, ground temperature was not measured in the areas of deepest snow but at standard weather stations. When snow accumulation is high, this measurement bias could have a disproportional effect in areas conducive to high snow accumulation (i.e. depressions) and thus lead to an improvement in sub-nivean temperature in areas of deepest snow. Lemming winter habitat selection is also greatly influenced by topography, with preferred habitat being under greater snow depth (Sittler 1995, Duchesne et al. 2011b, Reid et al. 2012).

Deeper snow could also improve winter reproduction, a condition believed to be essential for summer outbreaks in lemmings (Ims and Fuglei 2005, Ims et al. 2011). By providing a better thermal environment, it could enhance winter survival of young after weaning. In contrast, Bilodeau et al. (2013d) found no effect of experimentally increased snow on reproductive effort based on proportion of winter nests with reproduction. However, they could not measure other parameters such as litter size or early survival of weaned young.

Snow density is a difficult parameter to monitor in the field throughout the winter and this is why we had to resort to a modelling approach (SNOWPACK) based on weather data collected at the study site. SNOWPACK has been validated in multiple studies (Lundy et al. 2001, Hirashima et al. 2004, Nishimura et al. 2005, Rasmus et al. 2007) and improved over the years (Schweizer et al. 2006) although it has been mostly used in alpine environments to forecast avalanche risks. In the one year where we could validate the predictions of the model with field density measurements, predicted and observed values were in good agreement, but more validations of this model under arctic conditions are desirable.

Snow density at the base of the snowpack is important for lemmings because this is where they live during the winter. A dense, hard snow pack may be less conducive to the formation of a sub-nivean space and less suitable for digging and tunnelling (Sanecki et al.

2006). Lemmings may need to expend more energy to dig in dense snow or, in the worst case, dense snow could prevent them from moving to new or better feeding sites, thereby reducing food availability. Both situations could lead to increased winter mortality, and thus it was not surprising to find that dense snow had a negative effect on lemming abundance.

Contrary to what Gilg et al. (2009) found in Greenland, temporal variations in the establishment, duration or melting of the snow cover did not seem to play any major role in modulating lemming abundance even though we found a significant temporal trend in the hiemal threshold date, which is now reached earlier in fall than in the past. Because our study site is located in the High Arctic where the winter is very long (~ 8 months), inter-annual variability in winter length is perhaps too low to have significant effects. To modulate peaks, reproduction and survival of young under the snow may be more important than adult survival (Aars and Ims 2002). Therefore, what happens in fall (i.e. faster establishment of the hiemal threshold) could be less important, especially if reproduction occurs mostly in late winter or early spring. Unfortunately, we have no information on timing of reproduction under the snow.

At our study site, temperature has increased, mostly in fall and somewhat in summer, but not in winter (Gauthier et al. 2011), which remains very cold. At other sites where annual temperature is warmer and where small mammal cycles have collapsed, such as East Greenland and Fennoscandia, researchers have linked the latter phenomenon with climatic changes that occurred mostly in winter, such as freeze-thaw cycles, freezing rain and ground-icing events (Hörnfeldt 2004, Hörnfeldt et al. 2005, Kausrud et al. 2008). Winter ground-icing events in the Canadian High Arctic are relatively rare and no ice was found at the bottom of the snow profiles that we dug. Furthermore, as the SNOWPACK model provides estimates of the density of every snow layer, it can help in detecting the occurrence of icing events. No such events were detected based on the long-term climatic record at our study site.

The temporal trend towards greater snow depth that we detected, which should have a positive effect on lemming population growth based on our results, and the faster establishment of the hiemal threshold, may both result from the recent increase in fall air temperature (Gauthier et al. 2011, SWIPA 2011). Indeed, higher temperatures may have increased air humidity, which in turn may have accentuated precipitation. In this context, it is not surprising that lemming cycles have not collapsed in our region of the Arctic.

Although our analysis provided some insights on the role of snow cover in brown lemming population dynamics, it was somewhat limited by the climatic data available. A first problem is that those data came from standard weather stations, which may not always accurately represent conditions experienced by lemmings in their micro-habitat. A second problem was that some of the variables that we used were not directly measured but had to be indirectly derived (e.g. snow density). A third problem is that several measurements were taken at a single site (e.g. sub-nivean temperature, snow depth) and thus did not take into account spatial variability. More accurate field measurements of snow properties and of its persistence taken during the entire course of the winter and in the different habitats occupied by lemmings would be important to validate and strengthen our findings. However, accessing study sites in winter, particularly in the Canadian Arctic, is logistically difficult and very costly. Improvements in automated recording systems could alleviate some of these problems. For instance, systems recently developed to automatically record snow conductivity and density (Morin et al. 2010) could vastly improve our abilities to monitor changes in the thermal properties of the snow over the winter. Nonetheless, finding the most relevant climatic variables at the scale experienced by small mammals will remain a challenge.

Table 1. Model selection for the effect of snow variables on residuals of summer brown lemming density in the mesic habitat from the sinusoidal model. Dens = mean snow density of the bottom 5-cm of the snow pack over the winter, Depth = mean daily snow depth over the winter, Snowdate = date at which the snow cover became established, Hiemal = date of establishment of the hiemal threshold, Melt = date when snow has completely melted, Snowperiod = length of the snowperiod, Temp = mean daily temperature of the sub-nivean space over the winter, Year = continuous variable (temporal trend), K = number of parameters.

Rank	Model	Δ AICc	AICc Weight	K
1	Depth	0.00	0.22	1
2	Depth + Temp	0.61	0.16	2
3	Depth + Dens	0.94	0.14	2
4	Depth + Snowperiod	1.84	0.09	2
5	Depth + Snowdate	2.12	0.08	2
6	Depth + Dens + Snowperiod	2.21	0.07	3
7	Depth + Dens + Temp	2.60	0.06	3
8	Depth + Dens + Snowdate	2.85	0.05	3
9	Depth + Hiemal	3.45	0.04	2
10	Depth + Melt	3.49	0.04	2
11	Depth + Year	3.49	0.04	2
12	Null	6.27	0.01	0

Table 2. Model selection for the effect of snow variables on residuals of summer brown lemming density in the mesic habitat from the 1st order autoregressive model. See Table 1 for definition of variables.

Rank	Model	Δ AICc	AICc Weight	K
1	Depth	0.00	0.27	1
2	Depth + Temp	1.12	0.15	2
3	Null	2.17	0.09	0
4	Temp	2.60	0.07	1
5	Depth + Snowdate	2.88	0.06	2
6	Depth + Dens	2.92	0.06	2
7	Depth + Snowperiod	3.00	0.06	2
8	Depth + Hiemal	3.02	0.06	2
9	Depth + Melt	3.42	0.05	2
10	Depth + Year	3.48	0.05	2

Table 3. Model selection for the effect of snow variables on residuals of summer brown lemming density in the wet habitat from the sinusoidal model. See Table 1 for definition of variables.

Rank	Model	Δ AICc	AICc Weight	K
1	Null	0.00	0.22	0
2	Dens	0.32	0.19	1
3	Depth	2.02	0.08	1
4	Depth + Hiemal	2.16	0.08	2
5	Dens + Hiemal	2.23	0.07	2
6	Temp	2.67	0.06	1
7	Depth + Dens	2.92	0.05	2
8	Depth + Year	2.96	0.05	2
9	Dens + Temp	3.15	0.05	2
10	Depth + Snowperiod	3.81	0.03	2
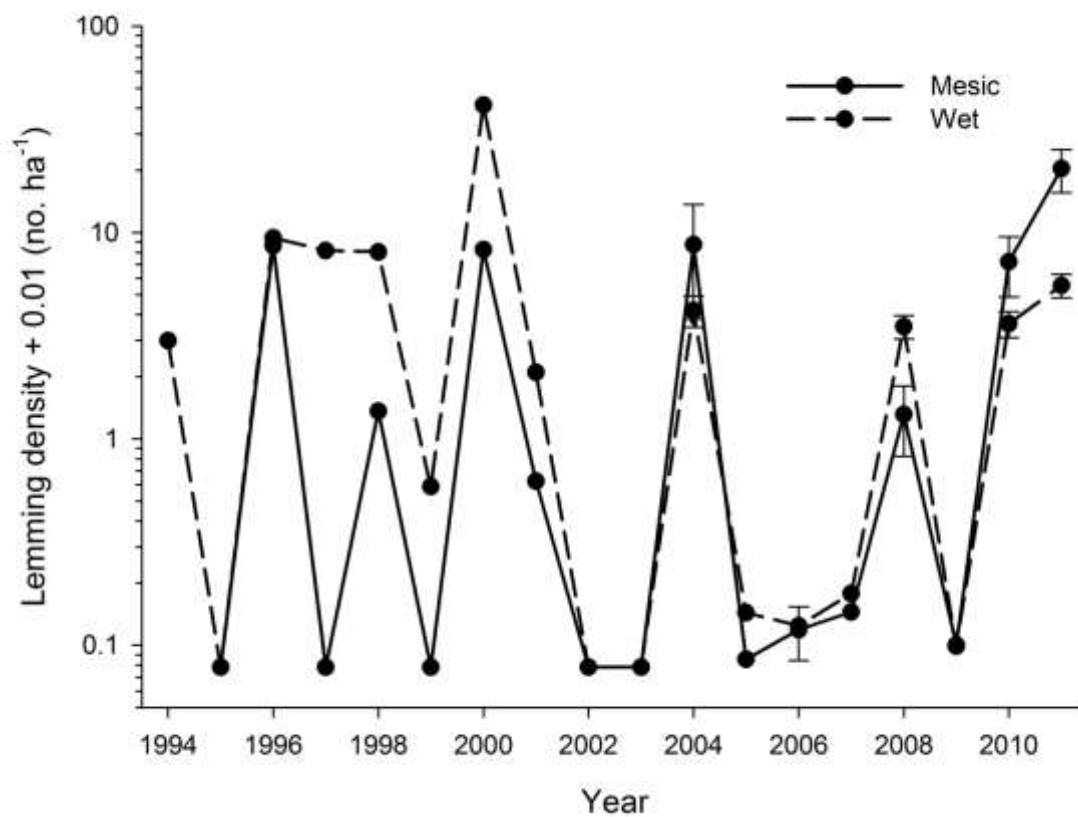
Figure 1. Time series of summer brown lemming densities (no. ha^{-1}) in the mesic and wet grid from 1994 to 2011. Error bars represent SE (only available for the period where data were from live trapping).
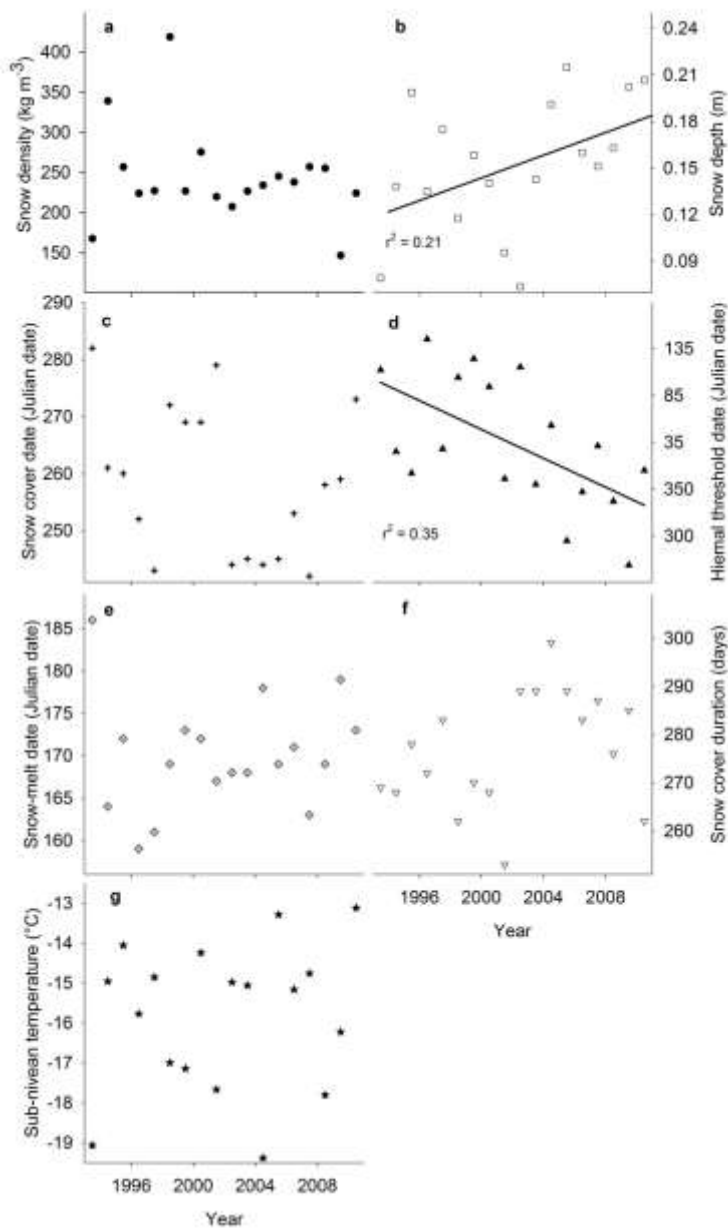
Figure 2. Time series of mean density of the bottom 5 cm of the snow pack over the winter (**a**; *black circles*), mean daily snow depth over the winter (**b**; *white squares*), date at which the snow cover became established (**c**; *black crosses*), date of establishment of the hiemal threshold (**d**; *upward black triangles*), date when snow has completely melted (**e**; *grey diamonds*), duration of the snow cover (**f**; *downward white triangles*), and mean daily temperature of the sub-nivean space over the winter (**g**; *black stars*), from winter 1993-1994 to 2010-2011 on Bylot Island, Nunavut. Solid lines represent temporal trends (P ≤ 0.05).
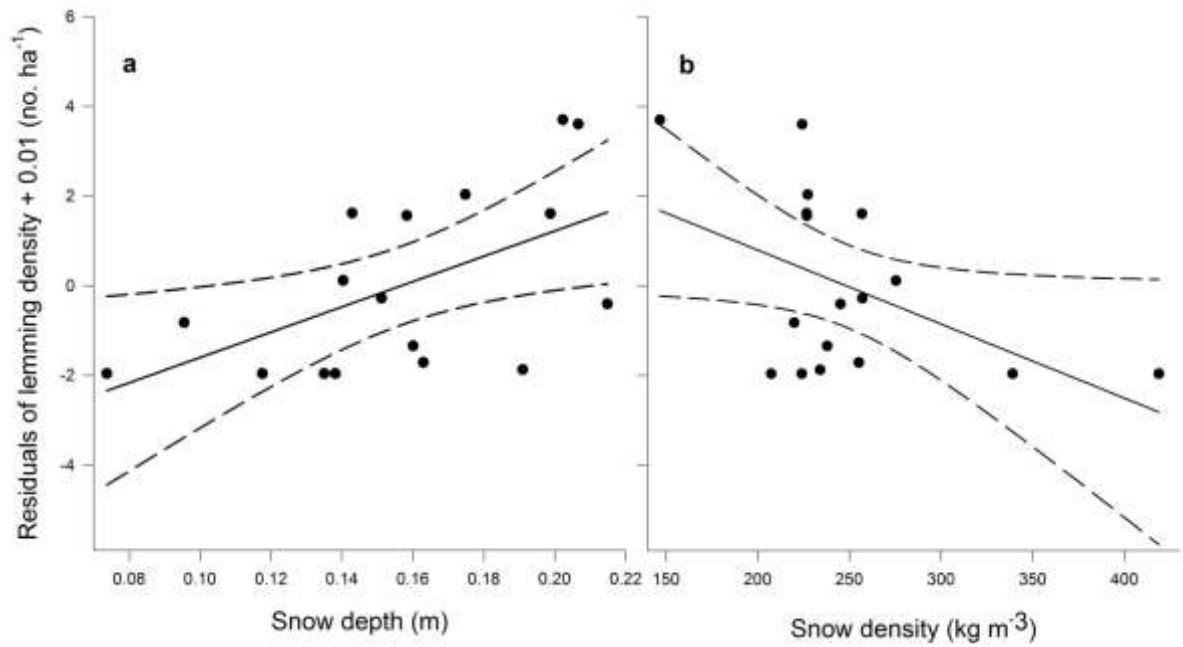
Figure 3. Plot of the residuals of brown lemming summer density [ln(density+0.01)] from the sinusoidal model in relation to the mean daily snow depth (**a**) and the mean density of the bottom 5 cm of the snowpack (**b**) from 1995 to 2011. Solid line is the regression line and dashed lines show 95% confidence interval.
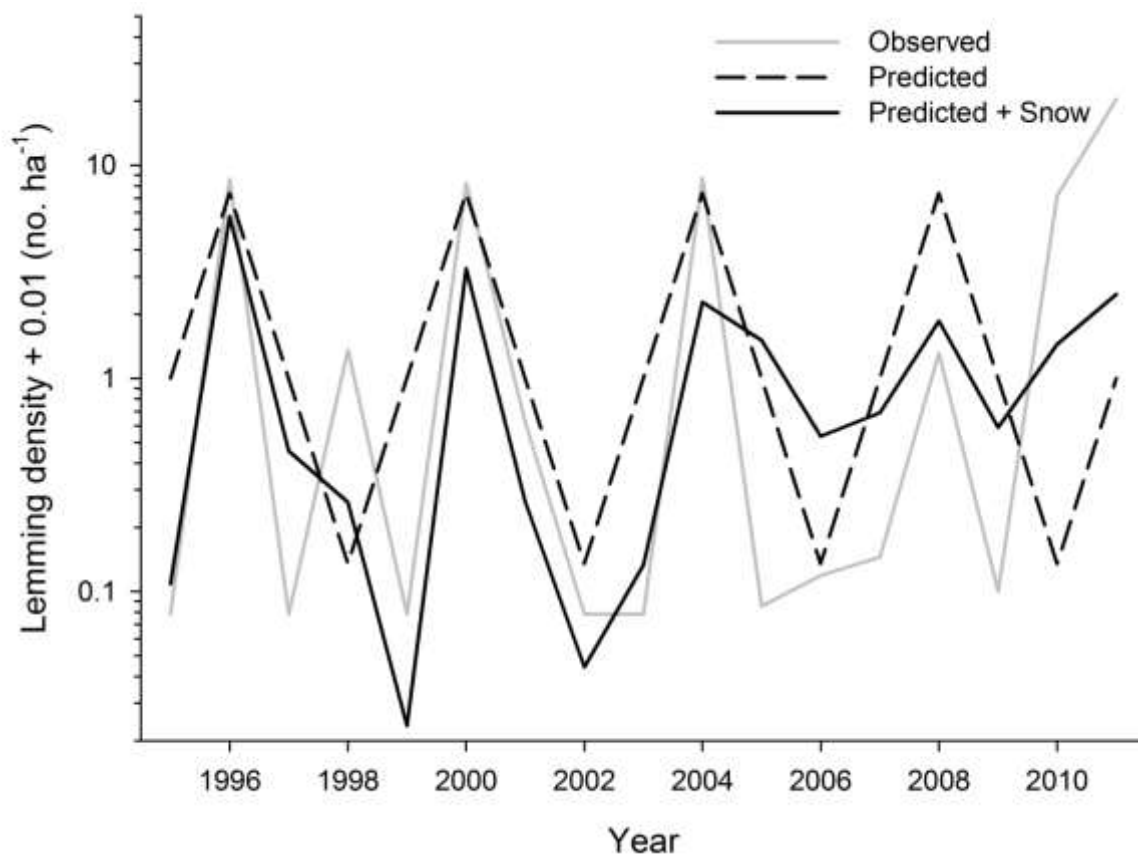
Figure 4. Time series of brown lemming summer densities (no. ha^{-1}) in the mesic grid from 1995 to 2011. Observed values (*Observed*), values predicted from the sinusoidal model (*Predicted*) and values predicted from the sinusoidal model with snow depth and snow density (*Predicted + Snow*) values are shown.
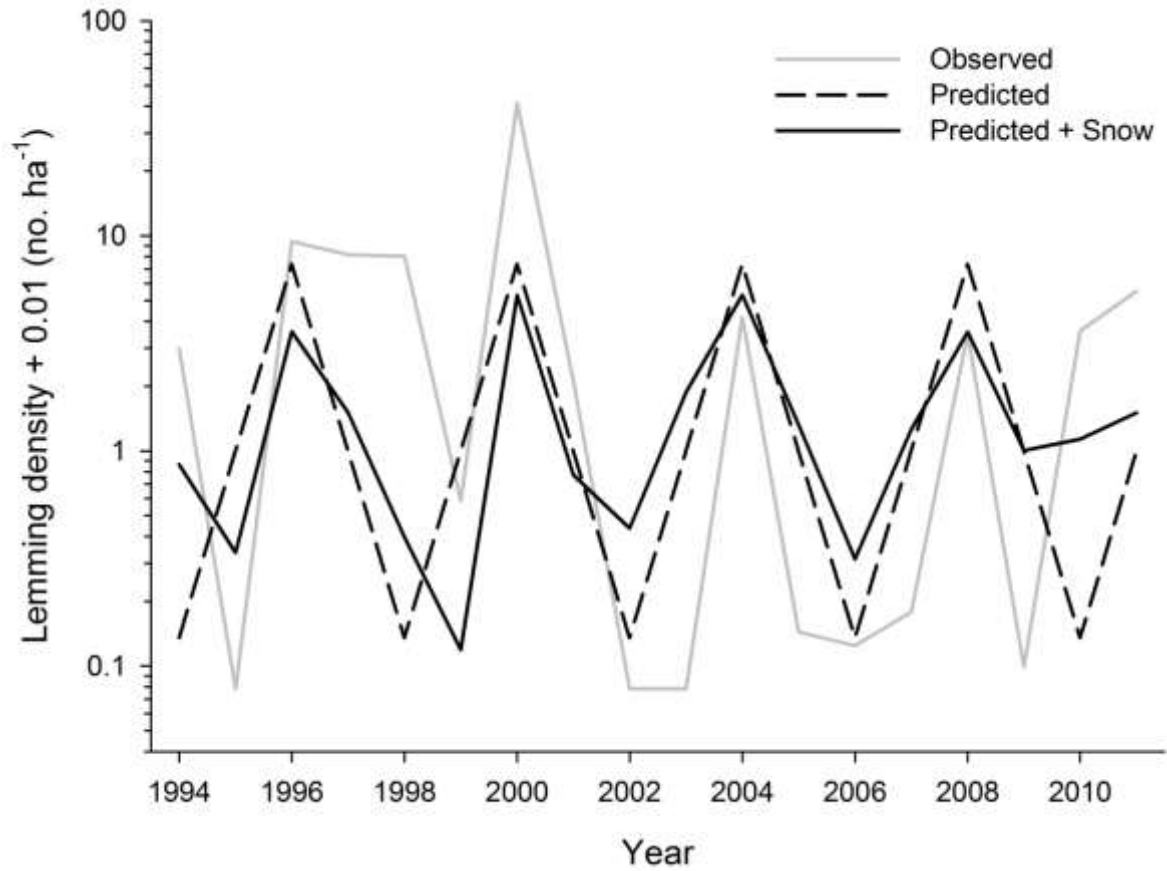
Figure 5. Time series of brown lemming summer densities (no. ha^{-1}) in the wet grid from 1994 to 2011. Observed values (*Observed*), values predicted from the sinusoidal model (*Predicted*) and values predicted from the sinusoidal model with snow density (*Predicted + Snow*) are shown.

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