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Florent Domine, Gilles Gauthier, Vincent Vionnet, Dominique Fauteux, Marie Dumont, et al.. Snow physical properties may be a significant determinant of lemming population dynamics in the high Arctic. *Arctic Science*, 2018, 4 (4), pp.813-826. 10.1139/as-2018-0008 . hal-02393184

HAL Id: hal-02393184

<https://hal.science/hal-02393184>

Submitted on 4 Dec 2019

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Snow physical properties may be a significant determinant of lemming population dynamics in the high Arctic

Florent Domine, Gilles Gauthier, Vincent Vionnet, Dominique Fauteux, Marie Dumont, and Mathieu Barrere

Abstract: Cyclic population fluctuations are common in boreal and Arctic species but the causes of these cycles are still debated today. Among these species, lemmings are Arctic rodents that live and reproduce under the snow and whose large cyclical population fluctuations in the high Arctic impact the whole tundra food web. We explore, using lemming population data and snow modeling, whether the hardness of the basal layer of the snowpack, determined by rain-on-snow events (ROS) and wind storms in autumn, can affect brown lemming population dynamics in the Canadian high Arctic. Using a 7-year dataset collected on Bylot Island, Nunavut, Canada over the period 2003–2014, we demonstrate that liquid water input to snow is strongly inversely related with winter population growth ($R^2 \geq 0.62$) and to a lesser extent to lemming summer densities and winter nest densities ($R^2 = 0.29$ – 0.39). ROS in autumn can therefore influence the amplitude of brown lemming population fluctuations. Increase in ROS events with climate warming should strongly impact the populations of lemmings and consequently those of the many predators that depend upon them. Snow conditions may be a key factor influencing the cyclic dynamics of Arctic animal populations.

Key words: lemming, population dynamics, snow, high Arctic, climate.

Résumé : Des fluctuations cycliques de population sont fréquentes chez des espèces boréales et arctiques mais les causes de ces cycles sont encore débattues. Parmi ces espèces, les lemmings sont des rongeurs arctiques qui vivent et se reproduisent sous la neige et dont les grandes variations de population cycliques dans le haut-arctique impactent tout le réseau trophique toundrique. Au moyen de données sur les populations de lemming et de modélisation de la neige, nous examinons la possibilité que la dureté de la couche de neige basale, déterminée par des événements de pluie sur neige (PSN) et

Received 26 April 2018. Accepted 27 August 2018.

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des épisodes venteux en automne, puisse affecter la dynamique de population des lemmings bruns dans le haut arctique canadien. En utilisant 7 années de données collectées à l'île Bylot, Nunavut, Canada, sur la période 2003–2014, nous démontrons que l'apport d'eau liquide dans la neige est inversement relié à la croissance hivernale de la population ($R^2 \geq 0,62$) et dans une moindre mesure aux densités estivales de lemming et aux densités de nids d'hiver ($R^2 = 0,29-0,39$). L'augmentation des fréquences de PSN avec le réchauffement climatique devrait fortement impacter les populations de lemming et par conséquent celles des nombreux prédateurs qui en dépendent. Les conditions de neige pourraient être un facteur clé influençant la dynamique des cycles des populations animales arctiques. [Traduit par la Rédaction]

Mots-clés : lemming, dynamique des populations, neige, haut arctique, climat.

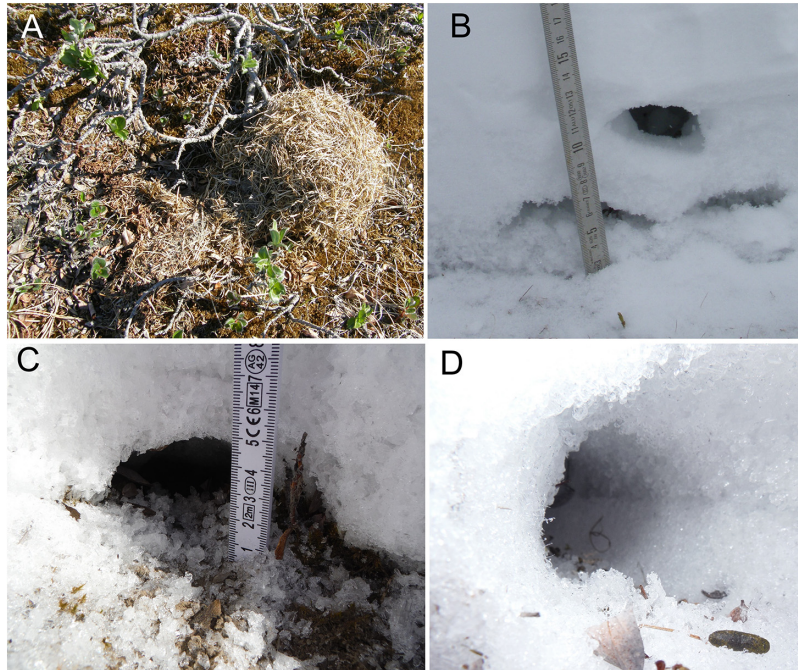
Introduction

Large amplitude cyclic population fluctuations have been documented in several vertebrate species for a long time (Elton 1924; Krebs 2013) and are especially prevalent in boreal and Arctic species (Stenseth 1999; Krebs 2011). These cycles have intrigued scientists for decades and their causes are still debated (Turchin et al. 2000; Gauthier et al. 2009; Oksanen et al. 2009; Krebs 2013). Although specialized trophic interactions have often been invoked as potential drivers of cycles, the possible role of climatic factors in these cyclic dynamics has recently received considerable attention (Kausrud et al. 2008; Gilg et al. 2009; Cornulier et al. 2013), especially in the context of a warming Arctic climate (Serreze and Barry 2011; Cohen et al. 2014).

Small mammals of the Arctic tundra such as lemmings and voles provide food for a whole suite of avian and mammalian predators such as snowy owls (*Bubo scandiacus*), ermines (*Mustela erminea*), long-tailed jaegers (*Stercorarius longicaudus*), rough-legged hawks (*Buteo lagopus*), and Arctic foxes (*Vulpes lagopus*) (Gauthier et al. 2013). They therefore constitute a central link in the terrestrial food web (Gilg et al. 2003; Krebs 2011). Their populations typically show high amplitude cycles with periods of 3–5 year (Stenseth 1999; Gauthier et al. 2013). Many theories have been proposed to explain them, the leading ones involving food supply and predators (Gilg et al. 2003; Pitelka and Batzli 2007; Fauteux et al. 2015). However, snow conditions may also play a role in the cyclic dynamics of small mammals because they live, feed, and can reproduce under the snow for most of the year (Ims et al. 2008; Fauteux et al. 2015; Berteaux et al. 2017).

Lemmings build nests and dig networks of burrows in the basal snow layer to access food (Fig. 1). We postulate that the effort and energy expense required to move around depends on snow hardness, and that soft snow facilitates access to food and favors reproduction under the snow, leading to a large population at snow melt, thereby creating favorable conditions for a population irruption (Fauteux et al. 2015). On the contrary, hard basal snow is expected to limit access to food, hinder reproduction, resulting in low spring and summer populations. Investigations in Fennoscandia, where precipitation is much more abundant and the climate much warmer than in the high Arctic, tend to support this hypothesis. At Finse, Norway (average yearly temperature = +2.6 °C), recent warming increased the frequency of formation of ice layers at the base of the snowpack (Kausrud et al. 2008), which may explain the recent dampening of lemming cycles observed there and of lemming and vole cycles observed elsewhere (Hornfeldt et al. 2005; Ims et al. 2008; Schmidt et al. 2012; Cornulier et al. 2013).

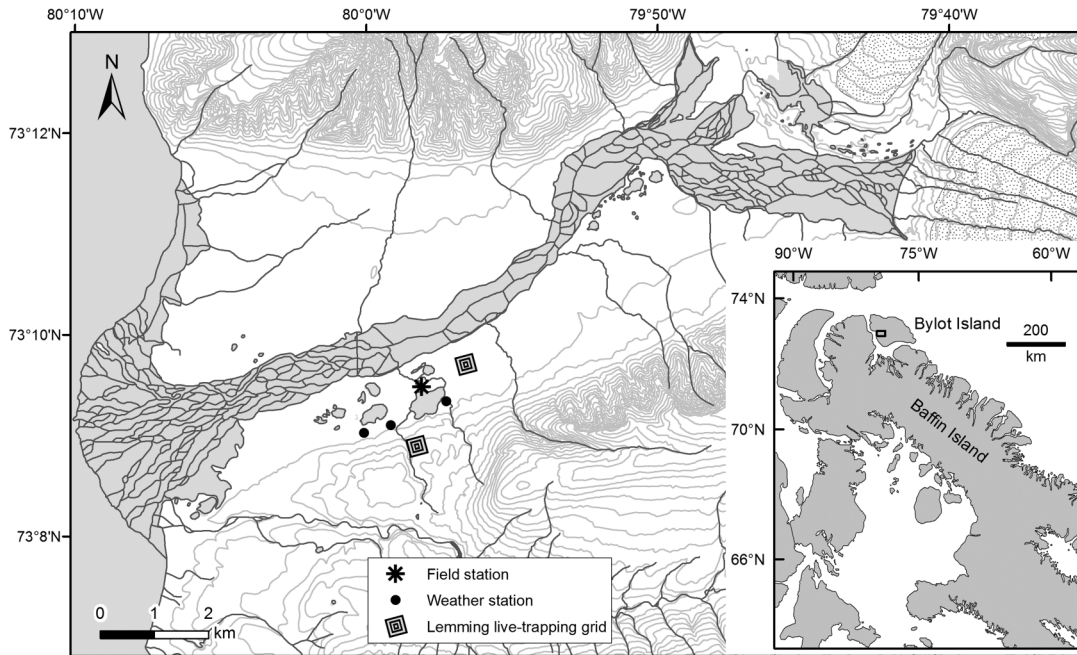
Fig. 1. Lemming winter nest and burrows on Bylot Island. (A) Winter nest in willow shrubs. Burrows in a thick snow drift (B), under willow shrubs (C), and in hummock terrain (D).



In the high Arctic, a region characterized by open, low-stature vegetation (Walker et al. 2005), snow-lemming interactions are expected to be somewhat different because ice layers at the base of the snowpack are rare and field observations (Domine et al. 2012, 2016b) indicate that snow hardness is mostly determined by wind. In autumn, snow that deposits calmly and is not raised by wind transforms into soft depth hoar at the base of the snowpack, whereas wind-drifted snow forms hard, wind-packed slabs that may transform into hard depth hoar during the winter (Domine et al. 2016b). Since lemmings live at the base of the snowpack, our interest is in the bottom 5 cm layer which forms in autumn. Because of low precipitation and low temperatures in the high Arctic, the formation of thick layers of ice or hard refrozen snow at the bottom of the snowpack is much less likely than in low Arctic regions like Fennoscandia. However, moderate melting or rain can still happen in autumn when the snowpack is thin and the temperature fluctuates around 0 °C. This may form melt–freeze layers which, even though they do not resemble ice layers found in wetter climates, might still impede lemming movement and access to food. The occurrence of these events in autumn therefore needs to be considered together with wind effects to evaluate the hardness of the basal snow layer.

We evaluated the hypothesis that the hardness of the basal snow layer is a determinant of lemming population dynamic in the High Arctic. We predicted that a hard bottom snow layer due to rain-on-snow events and/or wind storms in autumn negatively affect the winter demography of lemmings. This was examined in a population of brown lemmings (*Lemmus trimucronatus*) studied at Bylot Island (73°N, 80°W; Fig. 2) since 1993, a cold Canadian high Arctic site (average yearly temperature: −14.5 °C).

Fig. 2. Location of Bylot Island in the Canadian High Arctic and details of our study sites in Qarlikturvik valley. Contour line interval: 20m. Map credit: Marie-Christine Cadieux.



Methods

Study site

Our study site is located on Bylot Island, Nunavut, Canada (73°08'N, 80°00'W) in the Qarlikturvik valley (Fig. 2). The average winter (December–January–February) temperature is -31°C (1995–2008 data) and the area has experienced a warming trend in all seasons except winter with a 37% increase in the number of thawing degree-days during 1989–2011 (Gauthier et al. 2013). Snow usually covers the ground from late September to mid-June. The average (1995–2008) snow depth on 1st June based on measurements at 50 stakes is 31 cm (range: 8–53 cm) but can reach up to a meter or more in snow drifts. Brown lemming and collared lemming (*Dicrostonyx groenlandicus*) are the only rodent species present on the island. Both species are cyclic but we focus on brown lemmings because they are far more abundant than collared at our study site, especially in years of peak population (Gauthier et al. 2013; Fauteux et al. 2015).

Snowpack onset date

Since a major objective here is to model the properties of the basal snow layer, determining when the snowpack started forming in the autumn is critical, as an error on the onset date would lead to erroneous simulations of snowpack properties. We used a combination of data from automated snow gauges, satellite images, and time-lapse photographs to determine the snowpack onset date from autumn 1993 to 2014. One snow gauge was installed in summer 2001, another one in 2004, and a third one in 2013. Time-lapse photographs are also available in autumn 2014, with a Reconyx[®] camera taking three pictures a day of mesic habitat. Given these data sources, the number of independent snow start dates that could be obtained ranged from 1 (in 1993) to 6 (in 2014).

Table 1. Snowpack onset dates and dates when snow reached a height of 5 cm.

Year (autumn)	Reliability index	Onset date	Date 5 cm
2003	80%	6 October	15 October
2006	90%	30 September	1 October
2009	80%	26 September	16 October
2010	90%	3 October	15 October
2011	90%	15 September	16 September
2012	100%	27 September	3 October
2013	100%	12 October	13 October
2014	100%	12 September	19 September

Note: Only years where reliable lemming matching data and where the snowpack onset date could be determined with a reliability index $\geq 80\%$ are reported.

Regarding satellite images, we used data from MODIS, Globsnow-2, and Landsat. Satellite images give more representative data but cloud cover is often a problem especially in the Arctic. We used MODIS rapidfire satellite photographs of autumn 2009, 2010, and 2014 and MODIS snow cover product (MOD10A1, collection 5; Hall et al. 2002) for 2003, 2007, 2009, 2012, and 2013, which provide information on the surface snow cover fraction at 500 m spatial resolution on a daily basis. These data were collected from the National Snow and Ice Data Center website. In addition, we use the daily Globsnow-2 Snow Extent products, available at <http://www.globsnow.info/index.php?page=Data>, derived from the Advanced Along-Track Scanning Radiometer (A-ATSR) and ATSR-2 sensor at 0.01° spatial resolution for years 1997 and 1998 (Metsamaki et al. 2015). This dataset was complemented by 30 m spatial resolution true color images from Landsat satellites (5, 7, and 8) for years 1993–2014. Landsat data were collected from the USGS web site (<https://earthexplorer.usgs.gov/>).

Despite these multiple data sources, the snow start date was sometimes far from certain and we attributed a reliability index for the snowpack onset date of each year based on the coincidence between dates given by satellites, snow gauges, and time-lapse photographs. This index was 100% when at least four dates were identical and there was no conflicting date. The index was 90% when three dates were identical and a fourth date was most likely the same, and there was no conflicting data. This happened for example when a signal for a snow gauge was low, or when a satellite image indicated significant but incomplete snow cover. The index was 80% when three dates were identical with no conflicting dates (typically some methods yielded no date because of persistent cloud cover in satellite data). An index lower than 80% indicated either fewer than three reliable dates or conflicting dates. For example, in 2005 Landsat and MODIS both indicate partial snow cover in Qarllikturvik valley on 21 September, with no snow east of our research station and some snow west of it. One snow gauge indicated snow starting on 27 September and the other no snow on that date. Cloud cover then persisted until 6 October, at which date the snow cover was complete. We therefore could not determine the snow onset date reliably in 2005. On the contrary, in 2014, MODIS, Landsat, three snow gauges, and time-lapse photographs all indicate a snow onset date on 12 September, and we therefore consider this date 100% certain. Snowpack onset dates as well as the dates when snow height reached 5 cm as determined by Crocus are reported in Table 1.

Snow hardness

In the absence of field measurements in autumn, we evaluated the hardness of the basal snow layer using a snow physics model. Detailed snowpack models initially developed for avalanche hazard forecasting such as Crocus (Vionnet et al. 2012) are appealing as they have

a strong focus on snow mechanical properties. Our approach was to quantify the main processes contributing to snow hardness, wind drift and the amount of liquid water in snow, and to use both these variables as proxies for snow hardness. We used Crocus to quantify drifting snow as implemented by Vionnet et al. (2012). Essentially, the procedure calculates a unitless driftability index D_i that depends on wind speed and type of snow at the surface of the snowpack. If $D_i > 0$, then snow is wind-drifted and Crocus simulates fragmentation and compaction of surface snow by wind-induced snow transport. The higher the value of D_i , the more the snow is drifted and consequently the denser and harder the snow formed in drifts will be (Kotlyakov 1961; Domine et al. 2011). Regarding the impact of melting, our approach was to quantify the amount of liquid water, W_i , in kg m^{-2} (equivalent to mm of column water) formed in the snowpack, either by melting of deposited snow because of warm air temperature or strong radiation, or brought by rain (Vionnet et al. 2012). Since liquid water is preferentially found at junctions between snow grains (Colbeck 1973), the more liquid water is present, the stronger the bonds between grains will be when the water refreezes and therefore the harder the snow will be.

Crocus driving data was obtained from local stations (wind speed at 10 m height and temperature at 2 m height) or from reanalysis data [ERA-Interim, as described by Domine et al. (2016a)] for the other atmospheric forcings (incoming radiation, precipitation, and specific humidity). When wind speed and air temperature were not available, they were taken from ERA-Interim and adjusted for local conditions as detailed in Domine et al. (2016a). The phase (rain or snow) of precipitation events happening before the observed snowpack onset date was set to rain to reproduce the correct snowpack onset date. After the snowpack onset date, the partitioning of precipitation relied on a fixed threshold on air temperature (1°C). Additional simulations revealed that the choice of this threshold value did not affect simulated snow hardness. Crocus simulations were carried out from 1 August 1993 to 31 March 2015. They were initialized from output of a simulation covering the period 1980–1993 driven by ERA-Interim adjusted for local conditions. This aims to initialize near-surface soil temperatures consistent with the local climate conditions at Bylot Island.

Crocus output was used to calculate D_i and W_i for each 3 h time step between the onset of snow on the ground and the time when snow height reached 5 cm. We then summed up the positive values of D_i over this period to calculate a total snow drift index, SD_i . We also determined the maximum liquid water content W_i in the snowpack resulting from each melting or rain-on-snow events (ROS) events over this period. These maximum values have then been summed up over all events to define a snow liquid water index, SW_i , representative of the water storage in the snowpack during this period. The values of SD_i and SW_i were then studied to investigate the effect of both snow hardening processes on lemming population variables.

Lemming population data

We estimated brown lemming summer densities using a capture-mark-recapture approach from 2004 to 2015. Lemmings were live-trapped in two 11 ha permanent grids with 144 traps laid out in a Cartesian plane (12×12) at 30 m intervals (Fig. 2). Trapping grids were separated by >500 m. One grid was located in the wet tundra habitat and the other in the mesic/gully habitat (referred to as mesic grid hereafter). There is no interest in counting lemmings separately in gullies because after snow-melt this mesic habitat is no longer preferred by lemmings. Traps were activated during three primary trapping sessions: mid-June (as early as possible after snow-melt), mid-July and mid-August (four sessions from 2004 to 2007 as two sessions were conducted in July in those years). Traps were visited twice a day for three consecutive days (4 days from 2004 to 2007) at each primary session. Each lemming captured was identified to species and individually marked. Lemming densities

(in $N\ ha^{-1}$) were calculated for each primary session with spatially explicit capture–recapture models [more details on trapping methods and data analysis can be found in Fauteux et al. (2015)]. The number of lemmings captured per primary sessions, X , ranged from 0 to 103 where $X > 10$ in most cases. In early summer 2007, we trapped very few lemmings, which was inconsistent with their avian predators snowy owls and long-tailed jaegers that nested on or near our study area that year. These species track rather well lemming abundance in early summer and only nest in years when lemmings are sufficiently numerous (Therrien et al. 2014). The 2007 lemming population data indeed appear as outliers in Fig. 2 of Therrien et al. (2014), which is based on data collected at our study site. This suggests that for some unknown reason our early summer estimate of lemming abundance was biased low in 2007. Because of that, we discarded lemming population estimate for that year.

The population growth rate over the winter was obtained by dividing the June lemming density of year $t + 1$ by the August density of year t on the natural log scale (due to some zero values, we added 0.05 to the denominator, as 0.05 roughly corresponds to half the lowest density that could be estimated on our grids). In June 2010, lemming density was likely underestimated due to a persistent snow cover on our live-trapping grid. To correct for that, we used the average of the June/July density estimates for our calculations. In summer 2003, there was no live-trapping of lemmings but an index of abundance was obtained by snap-trapping in late July (Gruyer et al. 2008). We converted this value to densities using an equation modified from Gauthier et al. (2013) and used it to calculate the growth rate over the 2003–2004 winter.

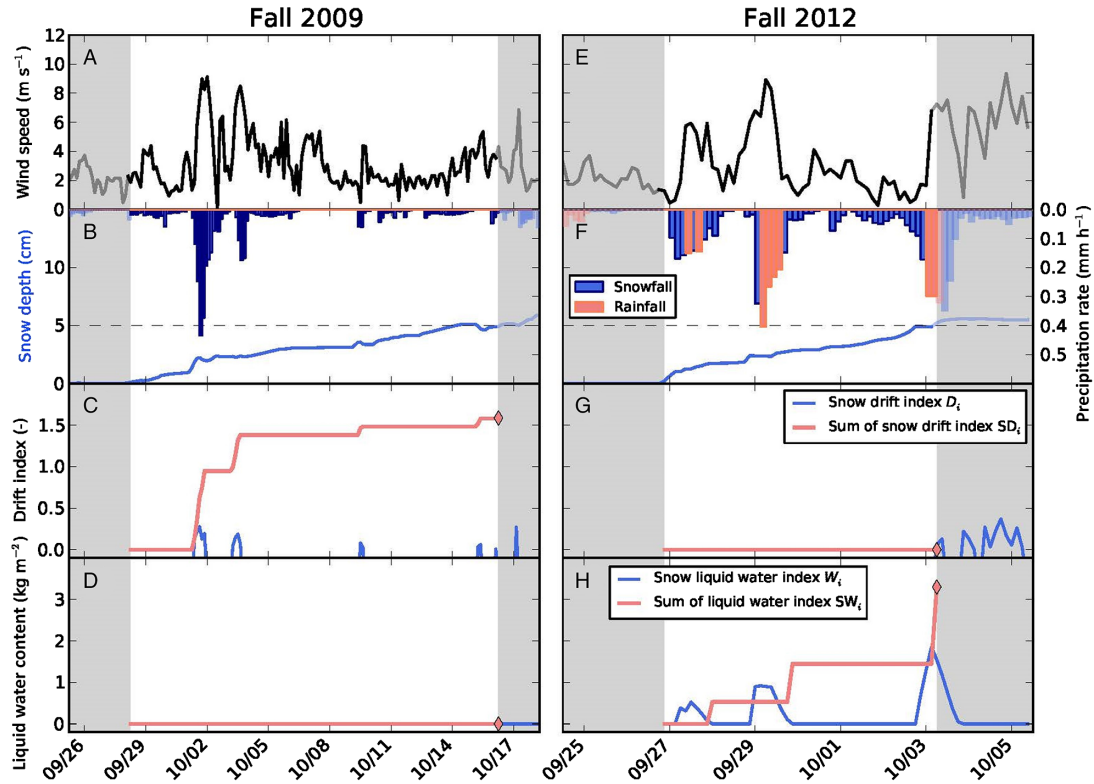
Starting in 2007, lemming winter nests were sampled soon after melt. In 2007, we randomly laid out across the study area seventy-five 500-m-long transects equally split among the three winter habitats, i.e., wet, mesic, and gullies and sampled all of them. In 2008, only 30 transects were sampled (10 per habitat) and from 2009 onward, 60 were sampled annually (20 per habitat). We walked along each transect and recorded all winter nests encountered along the way and the perpendicular distance between individual nests and the transect line. The species that used a winter nest was determined based on feces characteristics (Duchesne et al. 2011). To consider imperfect detection of winter nests along transects, we fitted distance sampling models to estimate nest densities ($N\ ha^{-1}$) with the package “Distance” (<http://CRAN.R-project.org/package=Distance>, 2016). Nest density provides an index of lemming abundance during the winter (Krebs et al. 2012). Nest densities in the wet habitat were not used for our analyses because they were always present at low density, likely due to the thin snow cover in that habitat (Duchesne et al. 2011). Lemming population data are archived in the Nordicana D repository (Gauthier 2018).

Results

Examples of values of the indices D_i , SD_i , (unitless), W_i , and SW_i (in $kg\ m^{-2}$, equivalent to mm of column water) are shown in Fig. 3 for two very different years to illustrate our approach. In early autumn 2009, wind drifting was significant but there was no liquid water in the snowpack. On the contrary in early autumn 2012, no drifting took place but snowpack wetting by rain was extensive. Interestingly, model runs revealed that all contributions to SW_i in autumn were from ROS events. No melting took place in the absence of rain.

Table 2 shows the values of snow hardness indices SD_i and SW_i and lemming population data for years where both data types were judged sufficiently reliable. The quality of the snow data increased over the years because of the increase in sources of data to determine the snow onset date, so that the analysis includes mostly recent years starting in 2004. Likewise, lemming population monitoring methods improved over time. In particular, live-trapping data are the most reliable (Fauteux et al. 2015) and these data were obtained

Fig. 3. Example time series of the drift indices D_i and SD_i (panels C and G) and of the liquid water indices W_i and SW_i (panels D and H) affecting the snowpack in early autumn, with relevant meteorological data: wind speed (A and E), precipitation and snow depth (B and F). Areas of actual interest are white- and grey-shaded areas are shown to widen the context. In autumn 2009, several windstorms (A) led to snow drifting on 1, 2, 9, and 14 October so that the drift index D_i (blue curve on C) then had positive values. Summing up these values between the snowpack onset date on 26 September and when it reached 5 cm depth on 18 October (B) led to $SD_i = 1.59$ (red curve on C). In autumn 2012, extensive rainfall (F) led to positive values of W_i (blue curve on H) on 27 and 29 September and on 3 October. Summing up liquid water occurrences in the snowpack (0–5 cm depth) leads to $SW_i = 3.30$ (red curve on H).



starting in 2004. We therefore concentrated on lemming data obtained over the period 2004–2015 for our analysis even though this reduced sample size.

Table 3 reports the relationships between the lemming population variables and the snow variables SD_i and SW_i . Selected plots concerning SD_i are reported in Fig. 4, whereas all plots concerning SW_i are shown in Fig. 5. Regarding the snow drift index SD_i , Fig. 4 shows that spring population sizes and winter nest densities increase as SD_i increases, which is contrary to our initial prediction, whereas winter population growth rates show no relationship with SD_i . R^2 values range from 0.00 to 0.55 and the lowest p value is 0.08, indicating poor significance of the relationships.

Regarding the sum liquid water index SW_i , all relationships (Fig. 5) show that lemming population variables decrease as SW_i increases, as predicted from our hypothesis. R^2 values range from 0.29 to 0.64 and two relationships were nearly statistically significant ($p < 0.07$). These results indicate that winter and spring lemming densities as well as winter population growth all decrease when the hardness of snow induced by liquid water increases.

Table 2. Data on snow variables that determine hardness in autumn, and on brown lemming population the following spring, for years where both snow and lemming data are reliable (see methods).

Year (autumn)	SD _i	SW _i (kg m ⁻²)	Year (spring)	Lemming density (N ha ⁻¹)		Winter growth rate		Winter nest density (N ha ⁻¹)	
				Wet	Mesic	Wet	Mesic	Mesic + gullies	Gullies
2003	3.38	0.00	2004	1.89 ± 0.40	3.67 ± 0.94	3.63	4.30		
2006	0.00	0.00	2007					2.41 ± 0.72	3.21 ± 1.62
2009	1.59	0.00	2010	1.99 ± 0.29 ^a	1.83 ± 0.24 ^a	1.60	4.29	13.56 ± 1.93	15.47 ± 4.1
2010	3.82	0.00	2011	8.09 ± 1.87	6.47 ± 1.02	1.35	0.57	14.10 ± 1.61	12.29 ± 1.71
2011	2.28	0.88	2012	0	0.52 ^c	-4.76	-1.87	1.15 ± 0.22	1.20 ± 0.67
2012	0.00	3.30	2013	0	0	NA ^b	NA ^b	0.73 ± 0.27	1.67 ± 0.77
2013	0.09	0.00	2014	3.34 ± 0.71	1.46 ± 0.34	4.90	4.07	8.37 ± 0.94	11.15 ± 2.24
2014	0.00	1.25	2015	1.92 ± 0.42	2.54 ± 0.58	-1.29	-0.65	2.76 ± 0.26	3.80 ± 0.73

Note: Values of the snow drift index SD_i and snow liquid water index SW_i of the basal snow layer (5 cm) are given. Lemming variables are population density in June (at snow-melt), population growth rate over winter (August year *t* – June year *t* + 1) in two summer habitats (wet and mesic), and total nest density sampled at snow-melt in two wintering habitats (mesic and gullies). Standard errors are indicated for lemming and nest counts.

^aBased on mean density June to July.

^bNo lemming was trapped in August 2012 and again in June 2013.

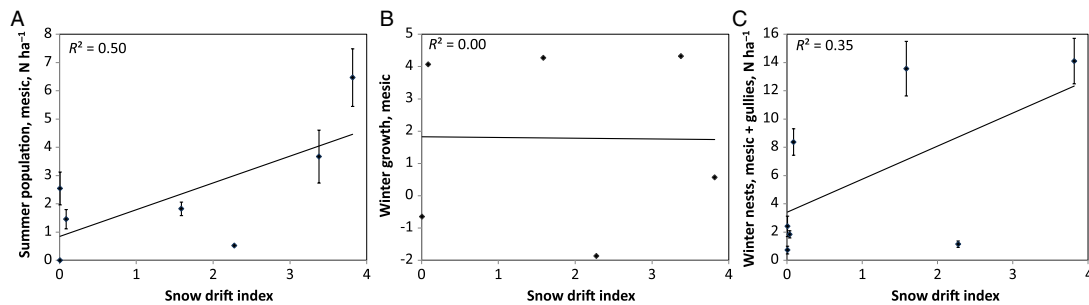
^cThis is a minimum number of live lemmings, with no associated error.

Table 3. Statistical relationships between the six brown lemming population variables of Table 2 and snow variables SD_i (wind drift) and SW_i (liquid water formation) that promote the formation of hard snow in the basal layer.

Hardness variable	Parameters	Lemming density		Winter growth rate		Winter nest density	
		Wet	Mesic	Wet	Mesic	Mesic + gullies	Gullies
SD_i	Slope	0.83	0.94	-0.04	-0.02	2.34	1.54
	95% CI	(-0.85, 2.52)	(-0.15, 2.04)	(-3.05, 2.97)	(-2.41, 2.37)	(-1.28, 5.95)	(-2.53, 5.61)
	R^2	0.24	0.50	0.00	0.00	0.35	0.16
	p	0.26	0.08	0.97	0.98	0.16	0.38
SW_i	Slope	-1.22	-1.01	-4.8	-3.94	-2.99	-2.94
	95% CI	(-3.38, 0.95)	(-2.70, 0.67)	(-10.18, 0.45)	(-8.04, 0.16)	(-7.34, 1.35)	(-7.23, 1.34)
	R^2	0.29	0.32	0.62	0.64	0.39	0.38
	p	0.21	0.18	0.064	0.055	0.14	0.14

Note: We present the slope, its 95% confidence interval, the R^2 and the p values. p values that are significant or nearly so, $p \leq 0.07$, are in bold.

Fig. 4. Plots of the relationships between the snow drift index SD_i in autumn of year t and selected brown lemming population variables in late spring of year $t+1$ (for panels A and C) or from late summer of year t to late spring of year $t+1$ (panel B). Negative population growth indicates a decline over winter. Error bars for lemming and nests counts are shown. To avoid error bar overlap and improve legibility, some values where $x=0$ have been slightly shifted.



Discussion

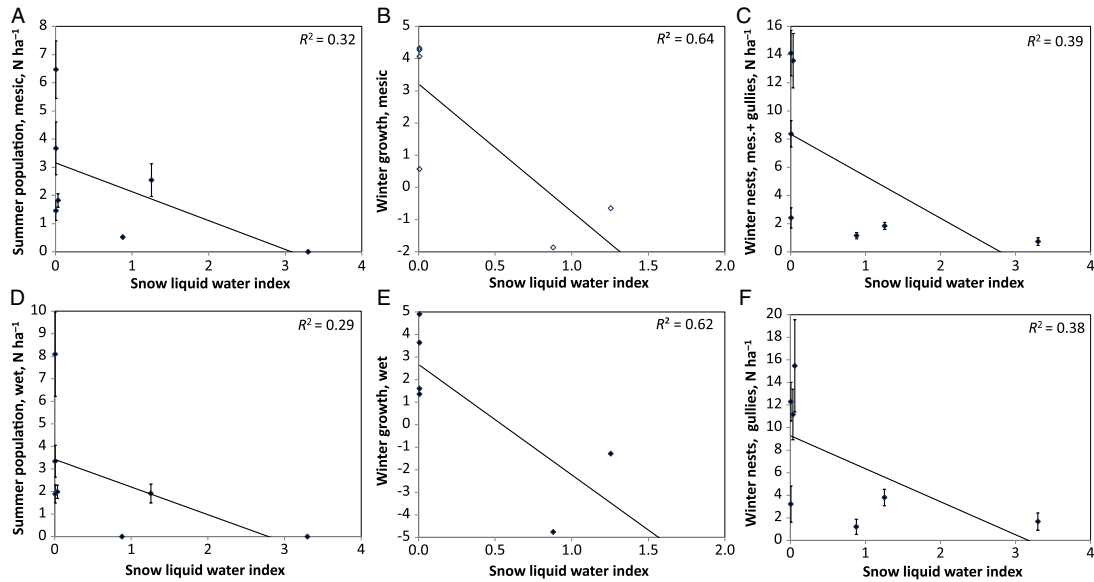
Effect of rain and wind on snow

Our results generally support our hypothesis that the hardness of the basal snow layer, as predicted by the amount of liquid water brought by ROS events in the autumn, negatively affects brown lemming demographic parameters. On the contrary, snow hardness derived from wind drift effects shows either no trend or weak trends opposite to those predicted in our hypothesis. We hypothesize that the impact of wind effects on lemming abundance is difficult to detect at Bylot Island because wind effects are difficult to evaluate independently from ROS.

Snow driftability depends on the properties of surface snow. When the snow is wet or refrozen, its resistance to drifting increases (Vionnet et al. 2012) so ROS happening simultaneously to strong winds prevent drifting. This happened on 27–28 September 2012, when a ROS event depositing 3.3 mm of water on the snow (Table 1) was accompanied by winds reaching 10 m s^{-1} which did not produce the expected vigorous drifting and the resulting snow hardening (Fig. 3). It is noteworthy that this intense ROS event resulted in the lowest lemming populations recorded (2013 data in Table 2) even though the wind contributions appear as zero (2012 SD_i data in Table 2, and Fig. 3).

We therefore propose that it is not possible to evaluate the effect of wind independently from that of ROS, since both sometimes happen at the same time and ROS masks wind

Fig. 5. Plots of the relationships between the snow liquid water index SW_t in autumn of year t and selected brown lemming population variables in late spring of year $t + 1$ (for panels A, C, D, and F) or from late summer of year t to late spring of year $t + 1$ (panels B and E). Negative population growth indicates a decline over winter. Error bars for lemming and nests counts are shown. To avoid error bar overlap and improve legibility, some values where $x = 0$ have been slightly shifted.



effects, while the reverse is not true. The presence of liquid water thus appears to be the dominant factor leading to snow hardening in autumn at our study site. Melting due to warm air or strong radiation could lead to more complex considerations but here all liquid water occurrences were caused by ROS events. Based on these considerations, we now explore the relationship between the occurrence of liquid water in the snowpack in autumn and brown lemming demographic variables.

The winter population growth rate is probably the variable we expect to be the most sensitive to snow conditions because it takes into account population sizes in both autumn and spring. This attenuates the confounding effect of factors such as summer predation (Therrien et al. 2014), and this variable should therefore not be very sensitive to the phase of the population cycle. A key observation is that in both mesic and wet environments, lemming populations always declined during the two winters when the basal snow layer was hardened by ROS events, whereas population grew during the four winters without such events, when the basal snow was presumably soft (Fig. 5). Obviously, factors other than snow conditions may contribute to variability in the winter population growth rate. For instance, high ermine populations in winter (Duchesne et al. 2011) may be sufficient to prevent lemming population growth even in years when snow conditions are favorable for lemmings. The density of winter nests is also considered a good indicator of winter population (Krebs et al. 2012). As expected, nest density was high when no ROS event took place in autumn (Figs. 5C and 5F). The weakest relationships with liquid water were found for lemming early summer population sizes (Figs. 5A and 5D). This is expected because this variable alone does not take into account the population at the start of the winter.

Space and time considerations

These considerations raise two general questions: (i) do snow conditions have a strong impact on brown lemming populations across the Arctic in general? and (ii) how might

climate warming affects lemming populations in the high Arctic? In addition, studies of lemmings and snow characteristics at several sites with different climatology and in particular with stronger winds may provide valuable responses to question (i). Barrow, Alaska, where lemming populations have been studied (Pitelka and Batzli 2007) would be a good site to test whether ROS events remain the most important factor under more windy climates. Nonetheless, we believe that our conclusions are likely to be valid for other circumpolar high Arctic regions and especially in moderately windy areas. We have concentrated our ideas on the autumn formation of the basal snow layer in contrast to what might happen in mid-winter, because the snow where lemmings live forms in early autumn and the basal snow layer is not affected by subsequent meteorological events and in particular ROS events are unlikely in the middle of winter in the high Arctic. Extreme ROS events in the middle of the winter have been reported in western Svalbard, a high Arctic site characterized by a strong maritime influence that can lead to extended mid-winter warm spells with intense precipitation, with dramatic negative effects on small mammals (Stien et al. 2012). Weaker mid-winter ROS events have also been reported elsewhere in the Arctic (e.g., Russia; Forbes et al. 2016; Sokolov et al. 2016) but are not widespread yet even though their frequency may increase in the future with climate warming.

Regarding (ii), the occurrence of ROS in autumn depends on how long temperature hovers around 0 °C at that time. Clearly, the colder the climate, the faster the autumn cooling so that we may surmise that colder climates are less likely to experience ROS events. Nonetheless, warming can be expected to lead to a greater probability of ROS events, including in autumn, as indicated by data analysis and modeling studies (Ye et al. 2008; Cohen et al. 2015). Our results suggest that under such scenarios, a collapse of lemming populations may occur even in the high Arctic, with devastating consequences for the numerous predators that depend upon them for their reproduction and survival (Schmidt et al. 2012). Similar impacts of ROS events have been reported for large Arctic herbivores such as reindeer (*Rangifer tarandus*) (Stien et al. 2012; Berteaux et al. 2017). These climatic-induced effects may have cascading effects on the whole tundra food web. Winter climate has been shown to play a role in the temporal fluctuations and large-scale spatial synchrony of abundance in several animal populations (Grøtan et al. 2005; Hansen et al. 2013). Our study expands these previous results and suggests that for northern small mammals like lemmings, climatic factors, and in particular snow condition during a critical period at the onset of winter, may be a key factor affecting the cyclic dynamics of these Arctic animal populations.

Future studies should aim to examine the relationship between autumn weather conditions, the hardness of the basal snow layer and the winter demography of lemmings at sites with various climate regimes. There is currently no method to automatically monitor snow hardness in the field but thermal conductivity may be an appropriate proxy (Domine et al. 2011) and it is currently monitored at several Arctic sites including Bylot Island (Domine et al. 2016b). Examining the relationship between this snow variable and lemming population data when several years of data become available may shed extra light on snow-lemming interactions. Even though our study spanned several years, we covered only two population cycles and thus longer studies would be desirable considering the cyclic population fluctuations of lemmings. It will also be interesting to examine whether collared lemming, a species potentially better adapted to dig in hard snow (Nowak 1999), is affected by snow properties to the same extent as brown lemmings. Such studies would allow for a more robust test of the generality of our conclusion that ROS in autumn has a strong negative effect on winter population growth of arctic lemmings and could contribute to a dampening of their cycle under a warming climate.

Conflict of interest

The authors have no conflicts of interest to report.

Acknowledgments

This research was funded by NSERC through Discovery and Frontiers to Discovery grants to FD and GG, the ArcticNet network, and by the French Polar Institute (IPEV). The Polar Continental Shelf Program efficiently provided logistical support for the research at Bylot Island. We are grateful to Denis Sarrazin for his precious technical support on the weather stations. Bylot Island is located within Sirmilik National Park, and we thank Parks Canada and the Pond Inlet community (Mittimatalik) for permission to work there (permits SIR-2013-14174 and SIR-2015-22238 to FD and SNP-2004-01, SIR-2007-1091, SIR-2009-3433, SIR-2011-8213, SIR-2013-13953, and SIR-2015-18820 to GG). Constructive comments by Charles J. Krebs, Nigel G. Yoccoz, and Samuel Morin are gratefully acknowledged. The map of Fig. 2 was kindly drafted by Marie-Christine Cadieux. CNRM/CEN is part of LabEx OSUG@2020.

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