

Research



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Taking the beat of the Arctic: are lemming population cycles changing due to winter climate?

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Reports of fading vole and lemming population cycles and persisting low populations in some parts of the Arctic have raised concerns about the spread of these fundamental changes to tundra food web dynamics. By compiling 24 unique time series of lemming population fluctuations across the circumpolar region, we show that virtually all populations displayed alternating periods of cyclic/non-cyclic fluctuations over the past four decades. Cyclic patterns were detected 55% of the time ($n = 649$ years pooled across sites) with a median periodicity of 3.7 years, and non-cyclic periods were not more frequent in recent years. Overall, there was an indication for a negative effect of warm spells occurring during the snow onset

period of the preceding year on lemming abundance. However, winter duration or early winter climatic conditions did not differ on average between cyclic and non-cyclic periods. Analysis of the time series shows that there is presently no Arctic-wide collapse of lemming cycles, even though cycles have been sporadic at most sites during the last decades. Although non-stationary dynamics appears a common feature of lemming populations also in the past, continued warming in early winter may decrease the frequency of periodic irruptions with negative consequences for tundra ecosystems.

1. Introduction

Small mammals play a key role in terrestrial ecosystems through numerous linkages with their forage plants and predators [1–3]. In species-poor systems, such as boreal, Arctic and alpine ecosystems, fluctuations in small mammal populations can regulate trophic dynamics of a significant part of the ecosystem and are crucial to maintain biodiversity of the predator guild and of plant communities [3–6]. Warming climate at high latitudes has a strong potential to disrupt these trophic dynamics especially through changes in snow conditions [7,8]. For instance, changing snow depth can alter predation rate of snowshoe hares (*Lepus americanus*) and disrupt the cyclic dynamics of this food web [9].

Lemmings (*Lemmus* spp. and *Dicrostonyx* spp.) are the most common small rodents of the Arctic tundra and are well known for their large population fluctuations, typically with 3- to 5-year periodicities [10,11]. Their population fluctuations have become classic textbook examples of animal population cycles, the causes of which having generated intense debates (see e.g. [11,12]), although an emerging consensus points toward delayed density dependence governed by trophic interactions [13,14]. Cyclicity of lemming populations, however, appears more variable than generally believed as some populations have been found to be non-cyclic or with irregular fluctuations [5,15,16]. In recent decades, major changes in the dynamics of small mammal populations have been reported in northern Europe [1,17], and lemming populations that were previously described as being cyclic have dampened to no or very weak cycles in Greenland and Fennoscandia [18,19], a phenomenon coinciding with climate warming. Despite limited empirical evidence at large spatial scale, fading lemming cycles due to warmer winters, with dramatic consequences for charismatic predators and the functioning of the food web, have been used as a prime example of climate change impacts on the Arctic wildlife [20].

Lemmings are adapted to the harsh Arctic climate and can breed during the long winters under the snow [21]. Most periodic lemming irruptions depend on high breeding activity in winter [22], and there is evidence that changing snow conditions may be linked to the collapse of lemming and vole populations at certain sites [18,19,23]. During winter, lemmings live in the soft depth hoar that typically forms at the base of the snowpack under a layer of dense, wind-compacted snow [24]. A hardened basal snow layer due to melt-freeze cycles or rain-on-snow events in early winter reduces thermal insulation, may increase the cost of locomotion and limits access to subnivean food plants throughout the snow season for lemmings [25]. The period of snow onset in early winter is especially

critical as it may largely determine the thickness, density and hardness of the depth hoar layer for the rest of the winter [8,26]. Reduced duration of snow cover could also be detrimental to lemmings by shortening how long snow offers protection from predators [19,27]. Rapidly increasing temperatures in the Arctic [28,29] can profoundly change physical properties and duration of the snowpack, thereby negatively affecting lemming populations [8,30].

We present the largest circumpolar analysis of lemming populations ever conducted based on 24 time series from 20 high-latitude sites (figure 1; electronic supplementary material, table S1) where we examine recent changes in their population dynamics. Lemming time series were carefully selected from Ehrich *et al.* [32] to retain only high-quality datasets among those available across the Arctic region and the Fennoscandian orarctic mountain areas (see electronic supplementary material, Material and methods). We first determined the prevalence of lemming population cycles across the circumarctic, their dominant periodicity and the temporal stability of cyclic fluctuations. We further examined whether climatic conditions during winter could be important environmental drivers of change in lemming population dynamics across the circumarctic region, as documented at the local scale [18,19]. We tested two specific hypotheses related to winter climatic conditions. First, warm temperature during the period of snow onset and shortly after should promote melt-freeze and rain-on-snow events, which will lead to a hard basal layer in the snowpack [33,34]. We hypothesized that a hardened snowpack caused by these early winter events should reduce access to subnivean food and impede lemming reproduction, thereby limiting population growth and reducing their abundance (early winter climate hypothesis [8]). Second, shorter winters should limit population growth and densities the following summer by reducing the duration of subnivean reproduction and the period that snow cover protects lemmings from several predators (winter duration hypothesis [19]).

2. Material and methods

(a) Lemming data

The lemming data used in this study were a subset of the population time series assembled from 49 sites across the circumarctic by Ehrich *et al.* [32]. We extracted from this dataset the 24 time series (from 20 sites; some sites had data for two different lemming species) that met the following criteria: (i) they were at least 20 years in length, (ii) data were collected each year during the period 2001–2019, (iii) they had a continuous annual record without any gap (in two cases data were missing for 1 year: Aulavik in 2017 and Åmotsdalen in 2018) and (iv) they used a consistent sampling method with adequate sampling effort throughout the study period. We excluded one series from southern Sweden (Vålådalen/Ljungdalen) where the lemming index was always very low except for 1 year (2011). The criteria applied to select the 24 lemming time series ensured that we had the datasets of highest quality for our analyses among those compiled by Ehrich *et al.* [32] and available for this key group of species across the circumpolar tundra areas. The time series that we retained used different methods to estimate lemming abundance (electronic supplementary material, table S1) but all of these methods were shown to be adequate to monitor lemming population fluctuations [35]. Another line of evidence for that is provided by the abundance of specialized lemming predators, which are known to track local lemming abundance very well. At all sites ($n=9$) where lemming and predator abundance were

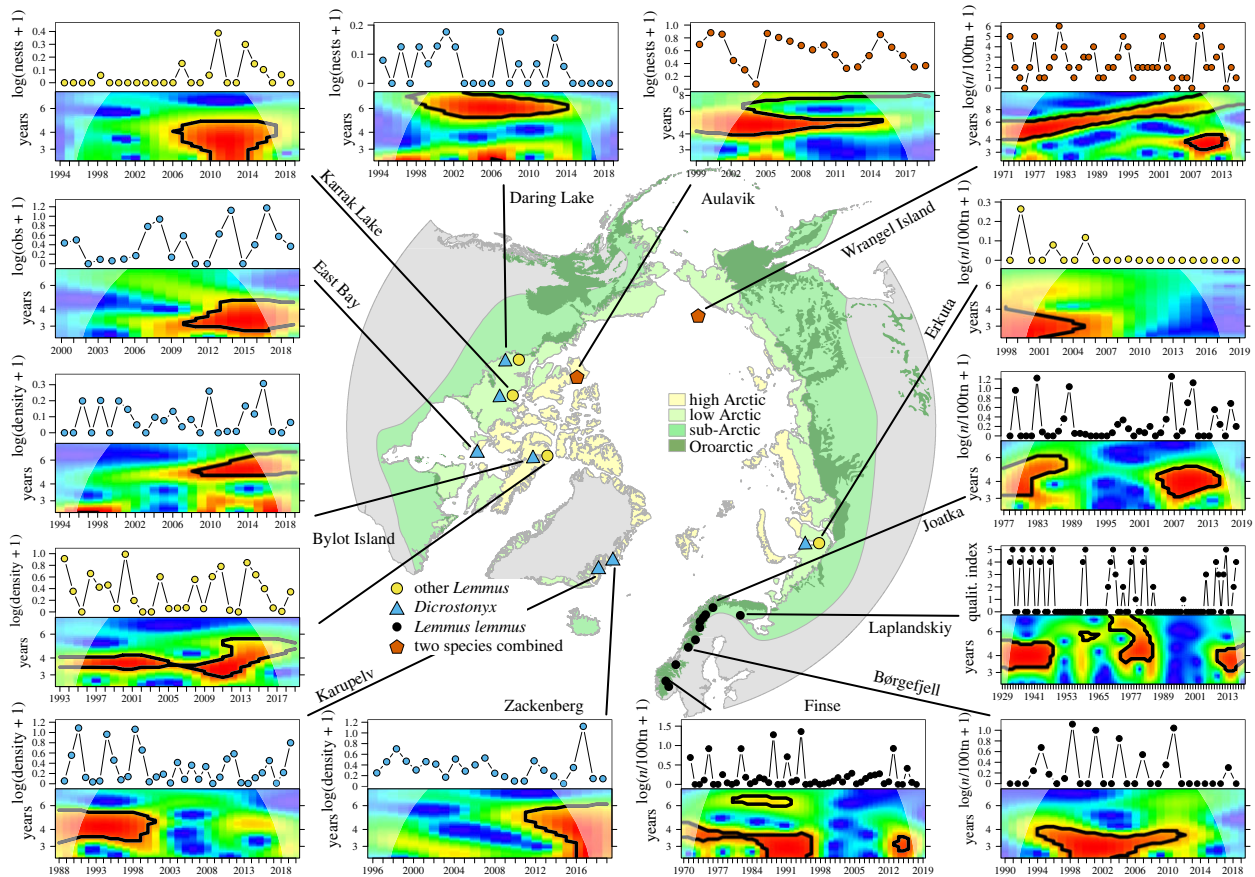


Figure 1. Lemming time series and map of the sites where they were collected. The colours on the map show the bioclimatic subzones of the Arctic [31] and the Oroarctic. For 14 representative time series, the log transformed abundance indices/estimates are shown (colour codes on the time series refer to the species) with results from the wavelet analysis underneath. The colour palette indicates the wavelet power levels from blue to red; red areas with black contour lines show periods with evidence for cyclic dynamics, with the estimated periodicity shown on the y-axis. The pale colours at either end of each wavelet plot are outside the cone of influence, an area where results are subject to edge effects. See electronic supplementary material, figure S3 for additional time series.

both monitored, a remarkable concordance between the two was found [4,5,36–41]. See electronic supplementary material, Material and methods and table S2 for details on the methods used to sample lemming abundance and sampling effort.

(b) Wavelet analysis and cyclic pattern

To assess the cyclicality of the lemming time series and possible transient dynamics, we carried out wavelet analyses [42]. Time series were transformed to $\log(\text{abundance index} + 1)$ [10], except qualitative indices (see electronic supplementary material, Material and methods for justification), and the wavelet power spectrum was calculated using the function *analyze.wavelet* of the package WaveletComp [43] in R v.4.1.3 [44]. The function *analyze.wavelet* applies the Morlet wavelet. We used the option to detrend the time series and the default value of 0.75 for the parameter *loess.span* that determines the degree of smoothing. The significance of periodicity at each time point was assessed from 10 000 simulations and power spectrums were plotted as heat maps showing the contour of significant periods. We used a 0.1 significance level to confirm the presence of cyclic patterns to minimize the risk of inferring the absence of cyclicality in presence of a weak signal. It is also with this significance level that periods of cyclicality that we detected matched most closely those found in previous site-specific analyses at Bylot Island and Finse [18,45,46]. For each time series, we extracted (i) the time over which cyclicality was identified excluding years that were outside the cone of influence and (ii) the periodicity with the highest wavelet power for each year. Mean periodicity was calculated over all time periods in a series for which periodicity was determined to be significant. See electronic supplementary material, Material and methods for more details on calculations.

(c) Climate data

We used temperature data from the ERA5-Land Reanalysis Dataset [47]. This dataset provides hourly temperature data at 2 m above the ground from 1981 to present at a resolution of 0.1° across the globe (approx. 9 km). We extracted temperature data for each of our 20 sites based on their geographical coordinates at 6 h intervals.

We used MODIS snow products [48] (<http://nsidc.org/>) to assess timing of snow melt and onset of snow at each site for the years 2000–2020 except at Kilpisjärvi where snow data was not available. We aimed to delimit a polygon of *ca* 30 km² centred on trapping sites and in relatively homogeneous habitat at each study area to measure snow cover change but in many cases we had to adjust polygon size based on local topography (e.g. to avoid high elevation area or large lakes) or to cover all lemming monitoring plots at sites with multiple plots. Median size of the polygons was 30 km² (range: 13–166 km²; electronic supplementary material, table S2). See electronic supplementary material, Material and methods for details on how the snow data were extracted and for ground validation of snow variables.

We used the snow cover time series and temperature data, either alone or in combination, to define six variables:

Date of snow melt (Melt50): First day in spring when snow cover was equal or less than 50% of the polygon (see electronic supplementary material, figure S1b for an example). We excluded from the calculations apparent early season melting events during which snow cover fell below 50% but returned to cover 100% of the site surface for 5 consecutive days or more. Similarly, we excluded late spring snow precipitation

events when snow cover returned to 100% for 2 consecutive days or less.

Date of onset of permanent snow cover (Onset80): First day in autumn when snow cover reached or exceeded 80% of the polygon and did not return below 50% at a later date (see electronic supplementary material, figure S2a for an example).

Duration of the snow onset period (Onset_duration): Number of days elapsed between the last day in autumn with a snow cover below 5% of the polygon and the date of onset of permanent snow cover as defined above (Onset80; see electronic supplementary material, figure S2a for an example).

Duration of winter (Winter_length) corresponded to the period with snow and was defined as the number of days elapsed between Onset80 and subsequent Melt50.

Warm spell during snow onset (Warm_onset): Cumulative number of degrees above -2°C (absolute value) per period of 6 h during the period of snow onset as defined above, i.e. Onset_duration (see electronic supplementary material, figure S2b for an example). For instance, a temperature of 2°C for two 6 h period would yield a Warm_onset value of 8.

Warm spell after snow onset (Warm_postonset): Cumulative number of degrees above -2°C (absolute value) per period of 6 h during 30 days after the date of permanent snow onset as defined above (see electronic supplementary material, figure S2b for an example).

Warm spells, as defined above, should promote melt–freeze or rain-on-snow events, conditions known to be detrimental to lemmings (see Introduction). We focused on the period of snow onset and the first 30 days following snow onset because it is when the depth hoar of the basal snow layer, where lemmings live throughout the winter, gets established. Melt–freeze or rain-on-snow events during this period should have the greatest potential to disturb and harden the basal snow layer [34,49]. We chose a threshold of -2°C rather than 0°C because snow temperature below the snow surface during daytime is often greater than air temperature due to the absorption of solar radiation. Based on equations derived by Colbeck [50], we evaluated that snowmelt can take place under sunny conditions when the air temperature is at -2°C or above even at high latitudes in early winter. Since this radiative warming can propagate to depths of at least 10 cm [50], the whole, thin early winter snowpack can be affected by such melt–freeze events. However, our conclusions are not strongly affected by this threshold because repeating the analyses with a threshold value of 0°C rather than -2°C to calculate cumulative number of degrees yielded similar results qualitatively but with smaller effects and wider credible intervals (CIs) (results not shown).

(d) Analyses relating lemming abundance and cyclicity parameters to climate data

First, we investigated the relationships between lemming abundance indices and climate during the previous winter over the period 2000–2020 using a state space model that allowed us to take into account the stochastic sampling variability in each time series. Different observation models were used depending on the observation method used at each site. Snap trapping data, consisting of number of individuals trapped during a certain number of trap nights, were modelled as a Poisson process. Variations in the number of traps used over the years were taken into account as a multiplicative factor. A similar observation model was used for winter nest counts and incidental observations, where variation in the area over which nests were counted or the total number of observation hours were taken into account as a multiplicative factor. For time series resulting from statistical analyses and integrating several sources of data (Bylot Island, Karupelv Valley), sampling variability was modelled with a normal distribution

around the mean. Sampling variability of qualitative time series was also modelled as a Poisson process. The process model consisted of a log-linear autoregressive model of order two, a model structure that has been used in numerous studies of cyclic small rodent populations (e.g. [10,51]), and included additional terms representing the possible influence of winter climate on annual population growth as follows:

$$X_{i,t} = a0_i + a1_i \cdot X_{i,t-1} + a2_i \cdot X_{i,t-2} + b \cdot \text{win}_{i,t} + e,$$

where $X_{i,t}$ is the log of lemming abundance in site i at time t , $a0_i$ is a constant specific to the site, $a1_i$ and $a2_i$ are the first and second order autoregressive coefficients (also site specific), b represents coefficients for the effect of variables (win) describing site-specific conditions in the winter preceding summer of year t (win varied between different versions of the model) and e is a normally distributed error term. The coefficients of the autoregressive part of the model (a coefficients) were modelled as site-specific random effects with a global mean. The state space model was implemented in a Bayesian framework (see electronic supplementary material, Material and methods for details and the model script).

We built three variants of the model with different combinations of winter variables corresponding to our two hypotheses: an early winter climate model with variables Warm_onset and Warm_postonset, a winter duration model with variable Winter_length, and an early winter climate + winter duration model (all three variables). These three climatic variables were not strongly correlated (Pearson $r < |0.31|$; electronic supplementary material, table S3). Because of the clear differences in winter climate between the distribution area of *Lemmus lemmus* and that of other lemming species (see electronic supplementary material, Material and methods for details) and some differences in average winter climate among other regions, analyses were carried out using both relative climate data and absolute climate data, both scaled to 0 mean and s.d. of 1 to make effects comparable. Relative values were calculated by subtracting the mean at each site from annual values.

Second, we investigated whether the early winter climate and winter duration differed between periods when the lemming populations were cyclic and when they were not according to the wavelet analysis. We tested for mean differences using linear mixed effect models for each climatic variable (response variable) with cyclicity (cyclic versus non-cyclic) and region (Fennoscandia versus the rest of the Arctic) as fixed effects and times series ID as random effect in the package glmmTMB. For each variable, fixed effects were modelled as additive or as interactive effects. The preferred model was selected with AICc and models that differed by less than 2 in AICc values were considered competitive [52]. Possible temporal autocorrelation of climatic variables was assessed by plotting autocorrelation functions for each site, but no significant pattern was detected (data not shown).

It is also possible that high variability of early winter climate and winter duration, rather than mean suboptimal conditions, leads to periods without lemming cycles. To address this hypothesis, we calculated the standard deviation of each climatic variable for cyclic and non-cyclic periods in each time series. As above, we tested for significant differences in standard deviations for each response variable using linear mixed models.

3. Results

(a) Cyclicity patterns in lemming populations

The 20 sites with time series of lemming population fluctuations covered the circumarctic region with 8 time series located in Canada (5 sites), 2 in Greenland (2 sites), 4 in Russia (3 sites) and 10 in Fennoscandia (10 sites; electronic supplementary material, tables S1 and S2). Individual time

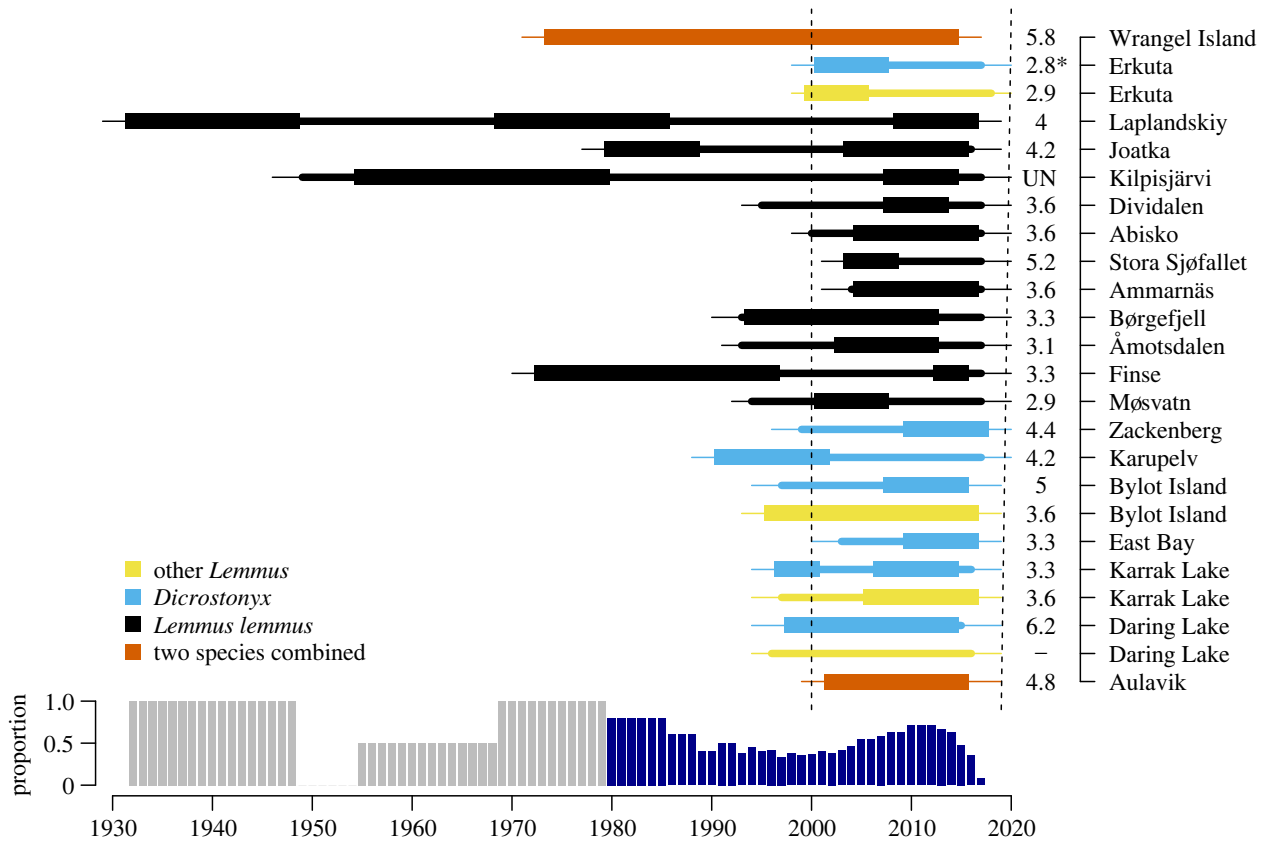


Figure 2. Temporal variation in cyclicity in 24 lemming time series. Thick lines show periods when the time series were characterized as cyclic based on the wavelet analysis whereas thinner lines indicate non-cyclic periods. The very thin lines at both ends of the series represent years outside the cone of influence. The dotted vertical lines indicate the range of years for which climate data were available. The mean periodicity in years is shown for each time series that exhibited cycles. * For *Dicrostonyx* in Erkuta, the periodicity with higher power is reported but there was also a periodicity at 4.3 years; 'UN' for Kilpisjärvi, the periodicity could not be determined. The bar plot at the bottom shows the proportion of time series with cyclic dynamics each year and blue bars represent years with five or more time series. Only time series within the cone of influence were used.

series ranged from 19 to 91 years (median length: 26 years) and included several lemming species: Norwegian lemmings (*L. lemmus*) in Fennoscandia as well as *Dicrostonyx* spp. and other *Lemmus* species at the other sites. Wavelet analysis revealed that all 24 lemming time series except one (*Lemmus* at Daring Lake) showed statistically supported cyclicity in population fluctuations, though in a few cases the cyclic period was short and the pattern rather unclear (e.g. Zackenberg, Stora Sjøfallet; figure 1; electronic supplementary material, figure S3). However, a cyclic pattern was found to be present throughout the study period at only three sites, Wrangel Island, Aulavik (*Lemmus* and *Dicrostonyx* combined at these two sites) and Bylot Island (*Lemmus* only), whereas cyclic patterns disappeared for significant length of time in all other time series (figure 2; electronic supplementary material, table S4).

When considering only years within the cone of influence of the wavelet analyses, 356 study years (all sites pooled) out of 649 (55%) were assigned to cyclic periods (median periodicity: 3.7 years). Disappearance of cycles occurred at different times across sites and there was no evidence that such disappearance was more common in recent years (figure 2; electronic supplementary material, figure S4). Periods with absence of cycles occurred across all lemming taxa (*L. lemmus*, other *Lemmus*, *Dicrostonyx* spp.). At five sites (Joatka, Kilpisjärvi, Laplandskiy and Finse for *L. lemmus*; Karrak Lake for *Dicrostonyx*), cycles were discontinuous as they disappeared for some time and reappeared

later (figures 1 and 2). There was as much variability in patterns of population fluctuations within as between lemming taxa and geographical regions (Fennoscandia, Russia and North America; figure 1; electronic supplementary material, figure S3).

(b) Climatic influence on lemming population fluctuations

Our analysis of lemming abundance indices in response to climatic variables suggested an influence of early winter climate when using relative climatic variables, in agreement with our early winter climate hypothesis, but not of winter duration (figure 3). The results from the three models were congruent and indicated a negative effect of Warm_onset (-0.183 and -0.174 for the early winter climate model and the early winter climate + winter duration model, respectively) on lemming abundance indices. However, given the high degree of stochasticity inherent to this type of data, posterior CIs were wide and 95% CI included 0 ($-0.402, 0.034$ for the early winter climate model and $-0.397, 0.049$ for the early winter climate + winter duration model; figure 3). The mean posterior estimates for Warm_postonset were also negative but indicated a smaller influence (-0.142 and -0.159 , respectively) and the 95% CI also overlapped 0 (figure 3). The analyses suggested no influence of winter duration with 50% CI largely overlapping 0. As expected due to clear regional differences in average climate, the effects were less clear when using absolute

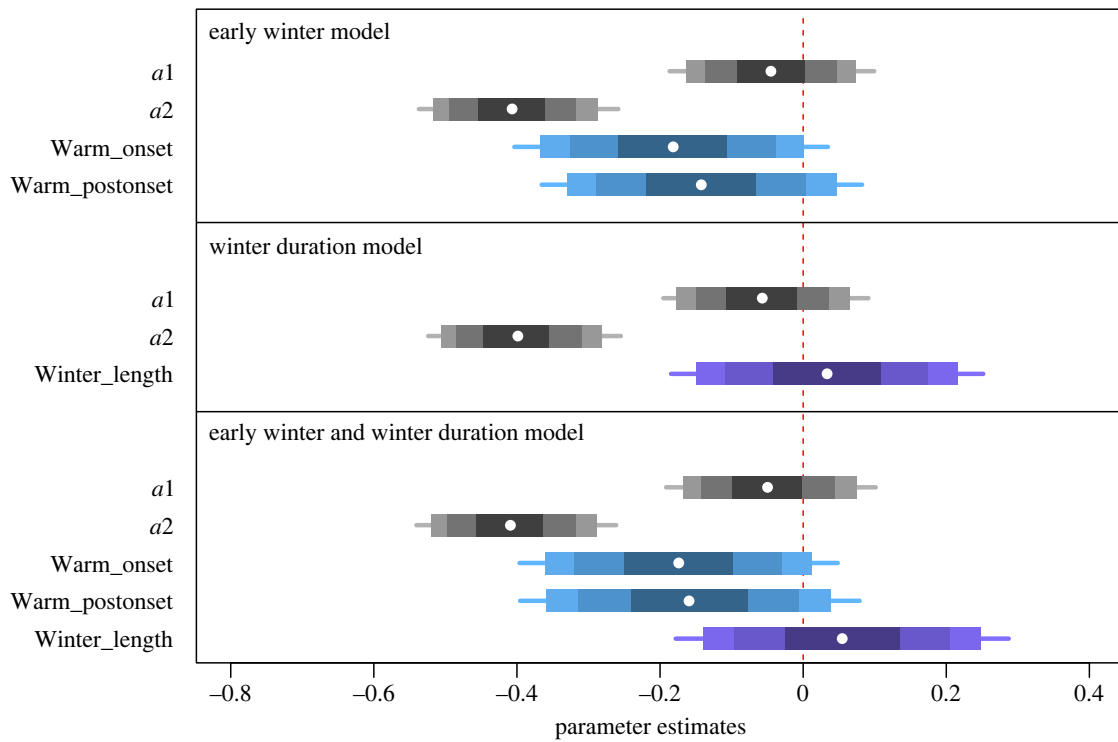


Figure 3. Effect of winter climate on lemming abundance. Parameter estimates for the influence of warm weather in early winter (sum of temperatures above -2°C over periods of six hours) during the period when the snow cover is established (from 5% snow cover to snow cover greater than 80% and not getting reduced to below 50% anymore; Warm_onset) and during the first 30 days after establishment of a permanent snow cover (Warm_postonset), as well as the influence of winter duration (Winter_length) obtained from Bayesian state space models assuming a log-linear autoregressive process of order 2. Climatic variables were scaled to mean 0 and s.d. = 1 prior to analysis making the magnitude of their effects comparable. Autoregressive parameters are shown (a_1 = direct density dependence +1 (see [10]), a_2 = delayed density dependence). Results of the three different models correspond to our three hypotheses with climatic variables expressed as relative to the mean at each site. Dots represent the mean of the posterior distribution, boxes the 50%, 80% and 90% credible intervals and lines the 95% credible interval. Red dotted line illustrates 0.

climatic variables, but showed the same overall tendencies (electronic supplementary material, figure S5). All models also revealed congruent direct and delayed density dependence responses. The mean estimate for the autoregressive parameter for direct density dependence (i.e. direct density dependence parameter in a population model +1) was between -0.055 and -0.047 (lower 95% CI: -0.194 to -0.189 , higher 95% CI: 0.090 to 0.101) and the estimate for delayed density dependence was between -0.408 and -0.395 (lower and higher 95% CI: -0.543 to -0.522 and -0.262 to -0.247 , respectively).

We examined whether early winter climate and winter duration differed on average between cyclic and non-cyclic periods in the lemming time series. However, we found no significant difference in climatic variables between periods with and without lemming cycles as identified by wavelet analysis, both for relative and absolute climatic variables and for the two main biogeographic groups of lemmings (figure 4; electronic supplementary material, figure S6). We also examined annual variability in climatic variable between cyclic and non-cyclic periods. Standard deviations of warm weather following the onset of snow (Warm_postonset) were on average higher ($\beta = 12.3$, 95% CI = 1.9, 22.6) during periods with absence of lemming cycles than during cyclic periods (figure 4; electronic supplementary material, figure S6).

4. Discussion

Our large-scale analysis of lemming dynamics revealed the generality of their cyclic population fluctuations, with a

periodicity of 3–4 years most frequently detected despite variation among sites (electronic supplementary material, table S4). More importantly, however, non-cyclic periods were observed in almost all time series, strongly suggesting that cyclicity is a dynamic process in lemmings and that alternating periods of cyclic and non-cyclic fluctuations is common throughout their range. This was also the case for the longest time series ranging from 45 to 91 years originating from subarctic Fennoscandia. Moreover, these non-cyclic periods did not occur synchronously and were not more prevalent in recent years. Therefore, our data do not provide evidence that the fading or collapse of lemming cycles recently reported at some sites [5,18,19] is at present a general phenomenon across the whole Arctic tundra despite repeated suggestions to that effect [53–56]. We recognize, however, the temporal limitation of our dataset, with relatively few series preceding the 1990s.

Angerbjörn *et al.* [16] suggested that episodes of interrupted cyclicity could in fact be low amplitude fluctuations that are not detected by population monitoring (for instance, see Karupelv Valley in recent years; figure 1). This may be especially the case with snap trapping data series or when lemmings are trapped in suboptimal habitats where they may be present only in high density years, as sometimes is the case in Fennoscandia. It is also possible that the large variation in monitoring methods may have reduced the precision of our analysis. However, we note that non-cyclic periods were detected across all the monitoring methods used in this study. Moreover, the key role of lemmings in the tundra food web, either as a driver of predator reproductive success or in impacting tundra vegetation,

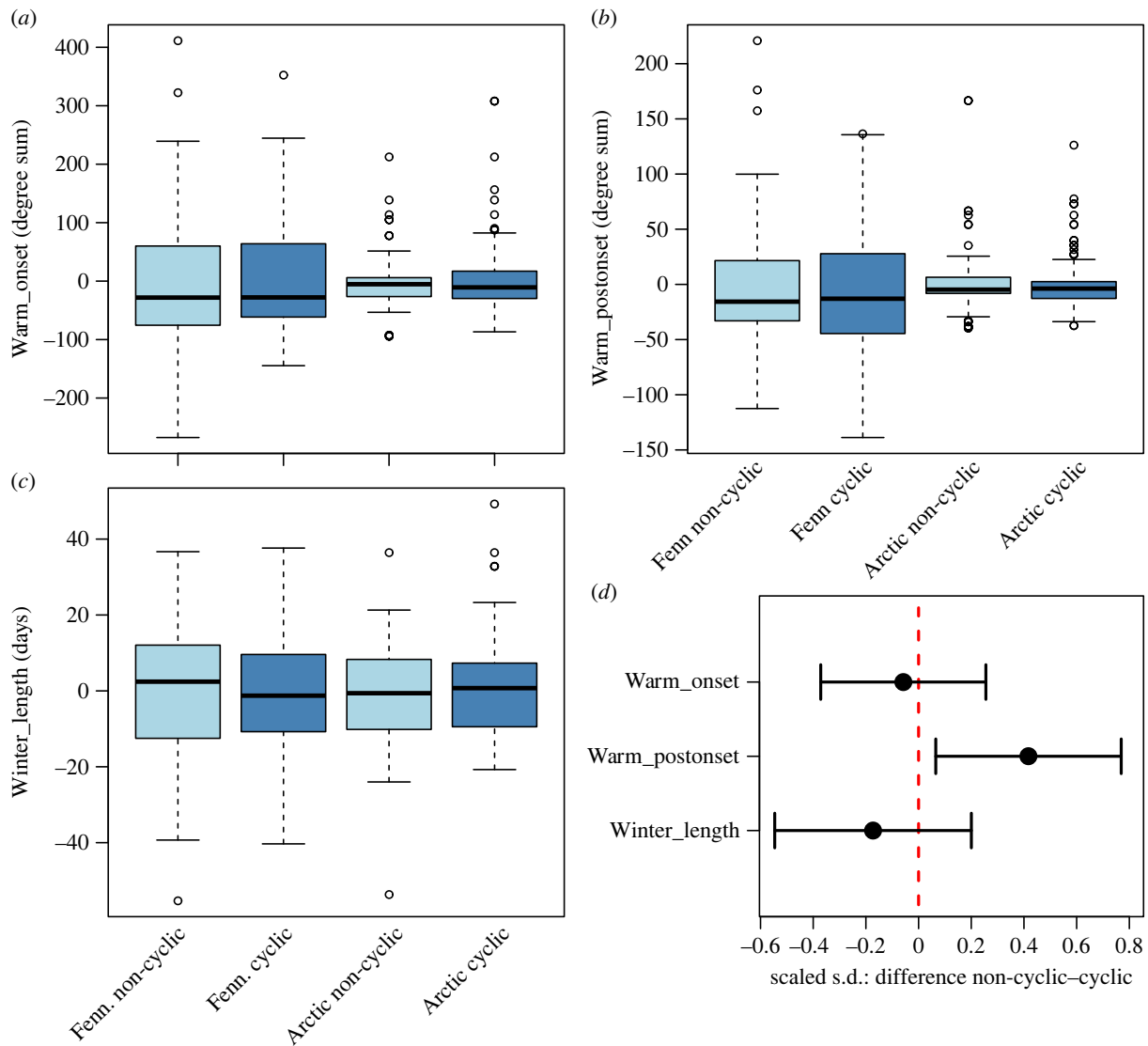


Figure 4. Effect of winter climate on cyclicality of lemming populations. Boxplots of three climatic variables, expressed as relative to the mean at each site, characterizing winter conditions during periods when lemming populations were classified as cyclic or non-cyclic by the wavelet analysis for sites in Fennoscandia (Fenn.) and in the rest of the Arctic (Arctic). The three climatic variables differed between sites with *Lemmus lemmus* in Fennoscandia and sites with other species in the rest of the Arctic (warmer climate and shorter winter in Fennoscandia; electronic supplementary material, figure S7). (a) Warm spells during snow onset; (b) warm spells during the first 30 days after snow onset and (c) winter length. Boxes represent the interquartile distance and horizontal lines show the median. Whiskers show 1.5 times the interquartile range and dots represent values outside this range. (d) Differences in standard deviations for each of the three climatic variables (relative values) between non-cyclic and cyclic periods. Standard deviations (s.d.) were scaled to be displayed on the same plot. A positive difference indicates larger climatic variability during non-cyclic periods. Red dotted line illustrates 0.

depends on their populations reaching high absolute densities periodically. Low amplitude fluctuations, such as those observed in several datasets during non-cyclic periods (figure 1; electronic supplementary material, figure S3), cannot fulfil this role [3,36,57].

It remains unclear if the transient dynamics of lemming population fluctuations that we document results from external forcing. Winter climate has been invoked to explain the disappearance of lemming population cycles at some sites. In Greenland, Gilg *et al.* [19] showed that a reduction in the duration of the snow cover due to climate warming could dampen population fluctuations by reducing breeding performance and increasing the period of exposure of lemmings to predators. However, our results do not support this as a general hypothesis as we found no evidence that the duration of the snow cover affects lemming abundance during the following summer at the circumarctic scale. A possible explanation may be that the predator community or the relative

importance of predators versus other factors in driving lemming population fluctuations vary across sites [23].

In Fennoscandia, some studies have linked the disappearance of lemming cycles to changing snow conditions in early winter or to warm spells in winter leading to melt-freeze or rain-on-snow events [18,22]. We found support for this hypothesis at the circumarctic scale since the abundance of lemmings was reduced in years following a high occurrence of warm spells with alternating periods of melt and freeze in early winter (i.e. our early winter climate hypothesis). Presence of melting and/or rain-on-snow events during this period should hamper the formation of a soft basal depth hoar in the snowpack, which is detrimental to lemmings [8,34,58]. Presence of such conditions could prevent lemmings from reaching peak densities and potentially lead to highly variable dynamics with irregular peaks. However, the occurrence of warm spells in early winter did not differ on average between periods of cyclic and non-cyclic lemming

fluctuations in Fennoscandia, where winter climate is the warmest (electronic supplementary material, figure S7), as well as in other regions of the Arctic.

A climate-induced transition from cyclic to non-cyclic dynamics may not be a one-time event but rather may take place over a transient period during which populations alternate between these two regimes in response to climate variability [59]. For periodic population peaks to occur, weather during the pre-peak increase winter appears crucial. A stochastic occurrence of good and bad winters may thus potentially create alternating periods with cyclic and non-cyclic dynamics. Considering that most of our time series started in the 1990s and covered a period when global warming was already impacting the Arctic [28,29,60], the existing time series provide little information to fully investigate this hypothesis. Our observation that increased interannual variability in the occurrence of warm spells following the snow onset was characteristic of periods when cycles disappeared lends support to this hypothesis. However, we note that the transient nature of lemming cycles had been documented based on qualitative data or fur returns of predators for more than a century in Fennoscandia [16,61], before the beginning of global warming. For other parts of the Arctic, previous analyses using the sparse data available suggested varying patterns [55] except for the classic 65-year series of regular cycles based on fox returns in Canada [62].

Environmental stochasticity modulated by the prevailing climatic regime rather than climate warming per se has been suggested to explain the temporary disappearance of vole population cycles in Finland [63,64]. Other environmental changes leading to increased predation or altered food availability have also been suggested for voles in boreal Sweden [65]. Interestingly, Blasius *et al.* [66] reported the occurrence of transient dynamics in a simple planktonic predator–prey system maintained in a stable microcosm as long periods of cyclic oscillations were interspersed by shorter periods characterized by irregular population fluctuations. In this case, the temporary disappearance of cycles was solely due to internal stochastic processes. There is also evidence from modelling work in small mammals that cycles can change or even disappear and reappear solely due to the internal dynamics of the system, even if the environment remains constant [67].

Although our comprehensive analysis of climate impact on lemming population dynamics is the most geographically extensive study so far, we recognize that it is still spatially restricted with respect to the vast circumpolar range of lemmings. In particular, we lacked good quality time series for a large portion of Russia and, to a lesser extent, North America, potentially limiting the generality of our conclusions. Second, even though our analytical method accounted for heterogeneity in observation error, we had to fit the same model structure to all datasets. However, considering that data came from a mix of field methods, species with potentially different ecology, and different ecosystem contexts, it is likely that our model did not fit all time series equally well. For *L. lemmus*, for instance, it has been suggested that a phase-specific density dependent model could be more adequate [10]. Our parameter estimates, aiming at a general picture, thus represent a rather bold averaging of complex ecological processes, but they still provide indications of climatic effects on lemming populations. Finally, we had to use crude proxies of snow conditions based on remote sensing and Reanalysis Datasets at a relatively large spatial scale (approx. 30 km²) due to the lack of ground

measurements at most sites. This limited the precision of our snow data, and potentially our ability to uncover relationships between lemming abundance and snow measurements, but it was the best we could do given data availability. Future studies should aim to collect *in situ* snow measurements (e.g. snow density or hardness, see [68]) or develop snow models capable of predicting specific Arctic snow properties at a relevant spatio-temporal scale [69] to determine more precisely how snow conditions can explain temporal variations in lemming population dynamics as suggested by our analysis.

5. Conclusion

Climate warming is already impacting tundra food webs in several ways [60]. Even though this appears to have led to large-scale dampening of small mammal population fluctuations in boreal regions [1], we found no clear evidence yet that this is affecting the cyclic dynamics of cold-adapted lemmings globally across the circumpolar tundra. Nonetheless, our study adds to the growing evidence that winter climate and especially snow conditions strongly affect population fluctuations of small mammals at high latitudes [8,18,23,64]. Therefore, future climate warming has the potential to destabilize some populations, such as those found in the warmest climate, although the magnitude of these effects could depend on biotic mechanisms driving local population dynamics [23]. However, the transient nature of lemming population cycles documented here makes it difficult to reach definitive conclusions regarding climatic effects on cyclic dynamics. Indeed, ecological systems characterized by cyclic dynamics are prone to prolonged transient behaviour [59] and determining whether non-stationary dynamics is due to internal processes or external forcing such as climate warming is inherently difficult. A comparative approach based on continued long-term monitoring of lemming populations at sites with contrasting climatic regime is essential to resolve these issues in the future but may not be sufficient. Well planned studies examining the links between winter climate and lemming demographic parameters (reproduction, mortality) based on testable predictions and year-round observational data of snow and lemmings are also needed to fully unravel the mechanisms involved. Regardless, despite ongoing climate warming, so far lemming population cycles remain and thereby still play their key ecological functions in the circumpolar tundra.

Ethics. All animal data used in this paper comes from datasets that had already been published elsewhere (see details in electronic supplementary material, tables S1 and S2). No new field data were collected during the preparation of the paper.

Data accessibility. Data used in the study are provided as electronic supplementary material, files (Gauthier_etal_lemmings_cyclicality.txt and Gauthier_etal_lemmings_climate.txt). The content of each file is described in section 'Description of data files' in the electronic supplementary material [70].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. G.G.: conceptualization, data curation, funding acquisition, project administration, writing—original draft; D.E.: conceptualization, data curation, formal analysis, funding acquisition, writing—original draft; M.B.-B.: formal analysis, writing—original draft; F.D.: conceptualization, writing—review and editing; R.A.: data curation, writing—review and editing; K.C.: data curation, writing—review and editing; F.E.: data curation, writing—review and editing; N.E.E.: data curation, writing—review and editing; E.F.:

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Supplementary Material for

Taking the beat of the Arctic: are lemming population cycles changing due to winter climate?

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This PDF file includes:

Supplementary Materials and Methods

Description of data files

Figs. S1 to S8

Tables S1 to S6

Supplementary Material and Methods

Lemming data

Methods used to sample lemming abundance across sites included: live trapping (2 series), snap trapping (16 series), winter nest counts (3 series), standardized incidental observations (1 series) and qualitative indices (2 series). Density estimates based on capture-mark-recapture methods applied to live-trapping data, which accounts for imperfect detection [1], are considered the most accurate methods to estimate small mammal abundance. Snap trapping, standardized incidental observations and winter nest counts have also been shown to provide reliable estimates of lemming density when adequate sampling scheme and effort are used even if they do not formally account for imperfect detection [2]. At all study sites, sampling effort met the minimum criteria recommended by [2], namely 64 traps and 6 trapping occasions for live-trapping, 400 trap-nights for snap-trapping, 200 person-hours for incidental observations and plots covering 10 ha for winter nest counts (table S2). Therefore, we assumed that time series based on these methods provided robust indices of lemming abundance. Although qualitative indices have not been formally validated with independent data (e.g. density estimates derived from live-trapping), they have been shown to be adequate to track the huge population fluctuations of lemmings (Typically >2 order of magnitude between peaks and lows; [3]) across years [4]. Nonetheless, considering the possible uncertainties associated with qualitative indices, analyses relating lemming abundance to climatic variables were conducted both with and without these datasets. Results were qualitatively the same although credible intervals were slightly larger (results not shown).

We summarize below the field protocol of each method used to sample lemmings across our study sites (more details on lemming sampling methods can be found in [5]. All sites applied

field protocols consistently across the study periods although sampling effort increased over time at a few sites (table S2). At Bylot Island, abundance was estimated by snap-trapping in the early days and live-trapping afterward but a period of overlap between the two sampling methods allowed for a proper calibration [2,6]. Only one, or a few in some cases, experienced researchers were responsible for the field sampling at all sites. When field assistants were required, they were properly trained by experienced researchers. Lemming populations were sampled during the summer at all sites except three (Karupelv, Zackenberg and Aulavik), which relied on lemming winter nest counts. However, winter nest counts were shown to provide a reliable index of lemming abundance in the following summer [2,7,8]. For sites with two annual trapping sessions (spring and autumn), data were averaged.

Live trapping

At Bylot Island, individual trapping grids consisted in 144 trapping stations laid out in a cartesian plane (12 x 12) with each station separated by 30 m. A baited Longworth trap was set <15 m of each station, preferably where signs of lemming activity were detected, and its exact position was recorded. Traps were set and locked in the open position several days before trapping occurred. During a trapping session, traps were visited at 12-h intervals during three consecutive days for a total of 6 trapping occasions. All captured individuals were identified, sexed, marked and released. Densities (expressed in N/ha) were obtained using spatially explicit capture–recapture models (SECR; 1). Densities, probabilities of detection, and effective sampling areas were obtained by maximum likelihood simultaneously using a 100-m buffer and a half-normal detection function [9]. When too few lemmings were captured ($n < 5$), the minimum number known to be alive divided by the average effective sampling area estimated over the years for each trapping grid was used.

Snap trapping

In North America, snap-trapping took place along permanent transects. At each trapping site, trapping stations were set at 15-m intervals along one or two parallel transects (250 m each) separated by at least 100 m. One or two *Museum Special* traps were set within a radius of 1.5 m of each station, preferably where signs of lemming activity such as fresh feces or browsing were detected. Traplines were visited daily for three to ten consecutive days depending of the study site. Once trapped, lemmings were identified to species. Lemming abundance was calculated as the number of lemmings captured divided by the sampling effort (expressed as N/100 trap-nights). Sampling effort was reduced by 0.5 every day that a trap misfire was detected.

In Eurasia, several trapping protocols were used. Snap trapping was carried out along permanent transects with 50-120 traps set at regularly spaced trapping stations at Kilpisjärvi (2 traps within a radius of stations placed every 7 m), Dividalen, Børgefjell, Åmotsdalen, Møsvatn (5 traps arranged in a 2-m square with 1 trap in the center and the others in each corner at stations every 25m), and Erkuta before 2007 (1 trap every 5 m). At Joatka, Abisko, and Erkuta since 2007, snap trapping was carried out according to the small quadrat method [10] which consists in placing 3 traps around each corner of a 15x15 m permanently marked quadrat. At Ammarnäs and Stora Sjøfallet, snap trapping was carried out on 1 ha permanently marked plots spaced by 300m along altitudinal transects (6-9 plots per transect). On each plot, 10 trapping stations with 5 traps each were placed at 10 m interval along the diagonal of the plot. At Finse, trapping was carried out on two permanently marked 1 ha grids. On each grid 10x10 stations with two traps each were placed at 10m interval. Traps were checked once per day for two to five consecutive days (table S2). Once trapped, all small rodents were identified to species and

the number of animals trapped for each species was divided by the number of trap nights to result in a trapping index (expressed as N/100 trap-nights).

Winter nest counts

Counts were conducted within permanent plots (1 ha or more) randomly distributed throughout the study area. Soon after snowmelt, each plot was slowly and thoroughly walked by one or several persons along parallel lines no more than 5-10 m apart. All fresh lemming winter nests was recorded and either removed or destroyed once counted. To express lemming densities, either the total number of nests found was cumulated across all permanent plots and divided by the sum of the area of the permanent plots to provide a lemming abundance index, expressed in nests/ha. At Zackenberg and Karupelv nest densities were converted into spring lemming densities using the equations provided by [8,11] for Greenland.

Standardized incidental observations

During various field activities related to wildlife studies, workers recorded observations of all vertebrates made on the study area while in the field. At East Bay, the 12 km² study area was divided into 1 km² plots, and 2 to 4 plots were visited by 1 or 2 people daily, with visits rotated systematically between plots throughout the field season. All vertebrates encountered, including lemmings, were identified to species and counted. The number of lemmings observed was compiled daily at the end of the day as well as the number of observer-hours spent in the field by each party. The total number of lemmings observed and number of observer-hours were summed at the end of each field season, and the number of lemmings observed per observer-hour was calculated to provide an index of lemming abundance that year.

Qualitative indices

The qualitative index from Laplandskiy was based on incidental observations carried out during standard field work in the study area in spring, summer and autumn (same number of days each year). The index values correspond to the following numbers of lemmings seen (in total): 0 – no lemmings seen; 1 – 1-5 lemmings seen; 2 – 6-10 lemmings seen; 3 – 11-50 lemmings seen; 4 – 50-100 lemmings seen; 5 – more than 100 lemmings seen. The observations have been carried out by two observers over the whole period (O.I. Semenov Tyan-Shanskiy and G.B. Kataev).

The qualitative index from Wrangel Island is based on an integration of all available lemming data from the Island including counts of winter nests and active burrows, snap trapping, live trapping and a qualitative assessment similar to the one used at Laplandskiy. All the data used to assemble the time series are presented by [4].

Wavelet analysis

Lemming time series used to carry out wavelet analyses [12] were transformed to $\log(\text{abundance index} + 1)$ [13] except for qualitative indices (Laplandskiy, Wrangel Island) because they were assessed on a relative scale that follows a logic similar to a logarithm scale (see above and [4]). For the two series that had a missing value for one year (Aulavik 2017 and Åmotsdalen 2018), this value was replaced by the average of the previous and subsequent year for the wavelet analysis. The range of possible periodicities was fixed between 2.5 and 8 years to cover the known cycle lengths for lemmings (typically, 3 to 5 years) with some margin [3,14], except for Wrangel Island where the upper bound was extended to 12 years because an earlier study had documented unusually long lemming cycles at this site [4]. Areas outside of the cone of influence on wavelet plots were not used for data interpretation or when relating cyclicity parameters to climate data as they are subject to edge effects because the spectral information

lacks accuracy [12]. Time spans for which cyclicity was detected based on a single peak in a time series were considered not to represent true cycles and excluded for further analyses (e.g. *Lemmus trimucronatus* in Daring Lake, 2012-2015; figure S3). Mean periodicity was calculated over all time periods in a series for which periodicity was determined to be significant.

Wavelet analyses are well-suited for detecting the presence of transient dynamics (i.e. transition between cyclic and non-cyclic periods, [12]). Recommended minimum sample size to apply wavelets are 25 to 30 years and periodicities smaller than 25% of the time series length [12]. Considering that median length of our time series was 26 years (range: 20 to 91 years, table S1) and that lemming population cycles are typically 3 to 5 years in length, 17 of our 24 time series met the first criteria whereas all of them met the second criteria. However, restricting the analyses to the 17 time series meeting the first criteria as well yielded the same proportion of study years showing a cyclic dynamics (all sites pooled). In addition, wavelet analysis should yield robust results even in presence of observational noise [12].

Climate data

The snow cover time series were derived from MODIS MOD10A1 snow product collection 6 distributed by the National Snow and Ice Data Center (<http://nsidc.org/>). The MOD10A1 snow product has a spatial resolution of 500 m and a temporal resolution of 1 day. MODIS data were clipped, using Python's *polygon.contains()* function in the shapely package, to include only pixels within polygons defined at each site (figure S1a). The MODIS tiles from which site data was clipped are listed in table S5. Snow cover information at the pixel level is provided by the normalized-difference snow index (NDSI) (for detailed information on NDSI calculations, see the collection 6 User Guide; [15]). We transformed the NDSI into binary classes of snow/no snow in order to calculate the daily snow cover fraction at the site level. We used a NDSI threshold of 0.4

for the binary classification, i.e. pixels with $\text{NDSI} \geq 0.4$ were classified as snow-covered (1) and pixels with $\text{NDSI} < 0.4$ as not snow covered (0). Pixels covered by water or clouds were excluded from the binary classification. A NDSI threshold of 0.4 was first suggested by [16] to distinguish snow from other bright materials like clouds, soils or rocks and has since been widely used as a standard value. Some studies have shown that the NDSI threshold can have high spatiotemporal variability for sites with steep terrains, high vegetation canopy and high spatial resolution, but that the standard value of 0.4 performs well for sites with flat topography, low vegetation and with a resolution ≥ 500 m [17-19]. We decided to use the standard value because the area enclosed in our polygons had a relatively flat topography and low vegetation.

The daily fractional snow cover at the site level was established by counting the number of MODIS pixels classified as snow covered versus the total number of cloud-free MODIS pixels within the polygon. Days with a cloud cover of $\geq 75\%$ were discarded. To obtain an approximate daily snow cover value for cloudy days and days with no valid MODIS data, snow cover was linearly interpolated between days with valid observations. MODIS-derived snow cover time series were used to determine the snow melt over the period February to August and the snow onset over the period August to December (see figure S1b for an example the spring snow cover time series at one site).

Snow cover was linearly interpolated for days without valid MODIS data and this interpolation introduced uncertainty in the determination of dates of snow melt (Melt50) or onset (Onset 80). Therefore, as a measure of precision we used the number of days over which we interpolated between usable MODIS data for the interval during which values of Onset80 and Melt50 fell (i.e. interpolation length). This value was 0 (highest precision) if snow melt or onset dates fell between consecutive days with usable MODIS and increased with the interpolation

length. For `Winter_length`, we calculated the mean interpolation length of `Onset80` and `Melt50` and used that as a measure of precision of this variable. For some years, `Onset80` is missing because the polar night sets in at the northernmost sites before a permanent snow cover had formed or the formation of the permanent snow cover could not be observed due to several consecutive cloudy days. For `Onset_duration` and the `Warm_onset` values that are based on it, the precision was calculated as the mean interpolation length of `Permanent_onset` (the last day in autumn with a snow cover below 5%) and `Onset80`. Values with (mean) interpolation lengths of 15 days or more were excluded.

We could validate the `Melt50` determined by the analysis of MODIS data with ground data at two sites. At Zackenberg, snow cover over the whole study area was determined annually using daily images taken by automatic cameras located on a mountain slope overlooking the central part of valley. At Bylot Island, snow cover over the whole study area was visually estimated every year at 2-d interval from an elevated vantage point located in the center of the valley. At both sites, date of 50% snow cover determined on the MODIS data was strongly related to the date of 50% snow cover determined on the ground (figure S8).

Analyses relating lemming abundance to climate data

The state space model described in the main text was implemented in a Bayesian framework and priors were kept wide and uninformative (see Model script below for details). Posterior distributions for all parameters were obtained using Markov Chain Monte Carlo (MCMC) estimation computed through Jags run with the `runjags` package in R [20]. We ran three parallel MCMC chains. The first 20 000 iterations were discarded as burn-in and 100 000 iterations were used with a thinning of 10 for parameter estimation. Convergence of the chains was assessed by visually inspecting the trace plots and by calculating Gelman-Rubin's R statistic

and the effective sample size [21]. Convergence was good for all models with $R < 1.007$ and effective samples sizes were > 2400 for all estimated parameters. We did not perform a formal selection among models with the three different combinations of variables, but rather compared them and assessed the consistency of estimated effects of winter climate [22]. The fit of the model was assessed through a posterior predictive check using Chi-square as a discrepancy measure between the observed and expected values on the one side and simulated and expected values on the other side [23]. In addition to assessing this check graphically, we calculated a Bayesian p-value to summarize model fit [23]. All Bayesian p-values were between 0.5 and 0.6, indicating a good model fit.

Principal component analysis of climate variables across localities

We investigated differences among localities in winter climatic variables (Melt50, Onset80, Onset_duration, Winter_length, Warm_onset and Warm-postonset) through a principal component analysis carried out in the package *ade4* in R [24]. Estimates based on interpolations of snow onset or snow melt dates over 15 days or more were excluded. As expected, winter climate in the Fennoscandian mountain range of *Lemmus lemmus* differed from that in the rest of the Arctic by being warmer, having longer duration of the period of snow onset and shorter winters (figure S7). Within the Fennoscandian region, Finse, which is the site situated at highest altitude, differed considerably from the other sites. Thus, in order to investigate possible relationships between lemming dynamics and winter climate, we used both relative climatic variables calculated by subtracting the mean at each site from annual values and absolute climatic variables for all analyses in this section.

Model script

Scripts of the state-space model assessing the effect of climatic variables on annual lemming abundance as specified in jags.

```

model{
  ## OBSERVATION MODEL ## a different one for the different types of data
  for(m in Mn){
    for(t in fromto[m, 1]:fromto[m, 2]){
      y[m,t] ~ dpois(N[m,t] * eff2[m,t])
    }
  }

  for(m in Ma){
    for(t in fromto[m, 1]:fromto[m, 2]){
      y[m,t] ~ dnorm (N[m,t], tau_o)
    }
  }

  for(m in Mq){
    for(t in fromto[m, 1]:fromto[m, 2]){
      y[m,t] ~ dpois(N[m,t])
    }
  }

  ## POPULATION MODEL ##
  for(m in 1:M){
    for(t in (fromto[m, 1] + 2): fromto[m, 2]){
      mu[m, t] <- beta_0[m] + beta_N1[m] * n[m,t-1] + beta_N2[m] * n[m,t-2] +
        beta_F1 * pdp_5_80_m2[m,t] + beta_F2 * pdp_80_30_m2[m,t] + beta_W *
winter_duration[m,t]
      n[m, t] ~ dnorm(mu[m, t], tau_r)
    }
    for(t in fromto[m, 1]: fromto[m, 2]){
      N[m, t] <- exp(n[m, t])
    }
  }

  for(m in 1:M) {
    beta_0[m] ~ dnorm(mu_b0, tau_b0) #random effect
  }

  for(m in 1:M) {
    beta_N1[m] ~ dnorm(mu_b1, tau_b1) #random effect
  }

```

```

for(m in 1:M) {
  beta_N2[m] ~ dnorm(mu_b2, tau_b2) #random effect
}

## MISSING VALUES ##
for(m in 1:M){
  for(t in (fromto[m, 1] + 2): fromto[m, 2]){
    pdp_5_80_m2[m, t] ~ dnorm(mu_5_80, tau_5_80)
  }}

for(m in 1:M){
  for(t in (fromto[m, 1] + 2): fromto[m, 2]){
    pdp_80_30_m2[m, t] ~ dnorm(mu_80_30, tau_80_30)
  }}

for(m in 1:M){
  for(t in (fromto[m, 1] + 2): fromto[m, 2]){
    winter_duration[m, t] ~ dnorm(mu_wdur, tau_wdur)
  }}

## PRIORS ##
for(m in 1:M) {
  n[m, fromto[m, 1]] ~ dunif(-5, 5)
  n[m, (fromto[m, 1]+1)] ~ dunif(-5, 5)
}

beta_F1 ~ dnorm(0,0.01)
beta_F2 ~ dnorm(0,0.01)
beta_W ~ dnorm(0,0.01)
sigma_r ~ dunif(0,10)
sigma_o ~ dunif(0,10)
tau_r <- 1/(sigma_r*sigma_r)
tau_o <- 1/(sigma_o*sigma_o)

mu_b0 ~ dnorm(0,0.01)
sigma_b0 ~ dunif(0,10)
tau_b0 <- 1/(sigma_b0*sigma_b0)

mu_b1 ~ dnorm(0,0.01)
sigma_b1 ~ dunif(0,10)
tau_b1 <- 1/(sigma_b1*sigma_b1)

mu_b2 ~ dnorm(0,0.01)
sigma_b2 ~ dunif(0,10)
tau_b2 <- 1/(sigma_b2*sigma_b2)

```

```
mu_5_80 ~ dnorm(0,0.01)
sigma_5_80 ~ dunif(0,10)
tau_5_80 <- 1/(sigma_5_80*sigma_5_80)
```

```
mu_80_30 ~ dnorm(0,0.01)
sigma_80_30 ~ dunif(0,10)
tau_80_30 <- 1/(sigma_80_30*sigma_80_30)
```

```
mu_wdur ~ dnorm(0,0.01)
sigma_wdur ~ dunif(0,10)
tau_wdur <- 1/(sigma_wdur*sigma_wdur)
```

Description of data files

We provided with this manuscript two files that contained the data used in this paper. We describe here the content of each of these files.

Gauthier_etal_lemmings_cyclicality.txt

This file contains the abundance indices for each year for the full time series, as well as the yearly classification of the series in cyclic or non-cyclic based on the wavelet analysis. The columns in the file are:

locality (site name)

year

species (lemlem – *Lemmus lemmus*; both – the local species of *Dicrostonyx* and the local species of *Lemmus* observed together; dicgro – *Dicrostonyx groenlandicus*; dictor – *D. torquatus*; lemtri – *L. trimucronatus*; lemsim – *L. sibiricus*),

abundance index (see tables S1 and S2 for details on method used at each site)

cone_influence (whether the given year was within the cone of influence – 1, or not – 0, on the wavelet plot), and cyclic (whether the time series was cyclic – 1, or not – 0, in the given year based on the wavelet analysis).

Gauthier_etal_lemmings_climate.txt

This file contains the numbers of lemmings observed as well as the trapping effort for each year in each time series, as well as the winter climate variables used in the analysis (see Material and Methods and Supplementary Material and Methods for details on their definitions and calculations). The columns in the file are:

locality (site name)

year

species (as above)

effort (monitoring effort, see table S2 for details)

number (number of lemmings recorded)

abundance (abundance index of lemmings)

onset5 (the last day in autumn with a snow cover below 5%)

onset5_days_of_interp (the number of days over which onset5 was interpolated – a measure of precision)

onset80

onset80_days_of_interp (the number of days over which onset80 was interpolated)

onset_duration

melt50

melt50_days_of_interp (the number of days over which melt80 was interpolated)

winter_length

warm_onset_0 (warm_onset calculated for periods above 0°C)

warm_postonset_0 (warm_postonset calculated for periods above 0°C)

warm_onset_2 (warm_onset calculated for periods above -2°C)

warm_postonset_2 (warm_postonset calculated for periods above -2°C)

Supplementary Figures and Tables

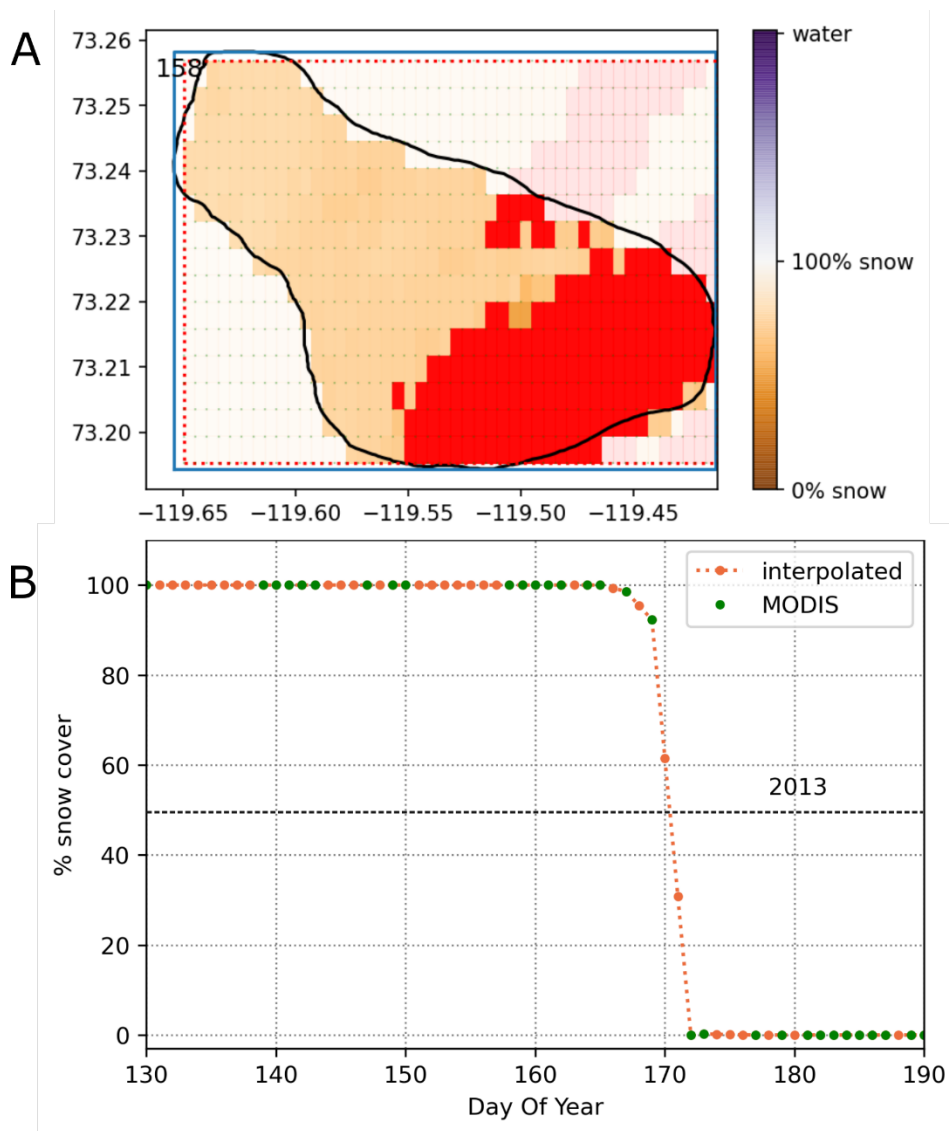


Figure S1. A: Clipped MODIS data for study site Aulavik, Canada, for Day of Year 84 in 2013 (MODIS tile h14v01). Red pixels indicate either clouds or invalid MODIS pixels, blue pixels water, white and light brown pixels ground with different fractional cover of snow and dark brown pixels ground without snow. B: Example of MODIS-derived snow cover time series for the melting period in 2013 for Aulavik. Green dots are values extracted from MODIS and orange dots are linear interpolation on days when MODIS images were unavailable. In this example, interpolation value for the date of 50% snow cover (horizontal dashed line), a measure of precision, is 2 days (see methods).

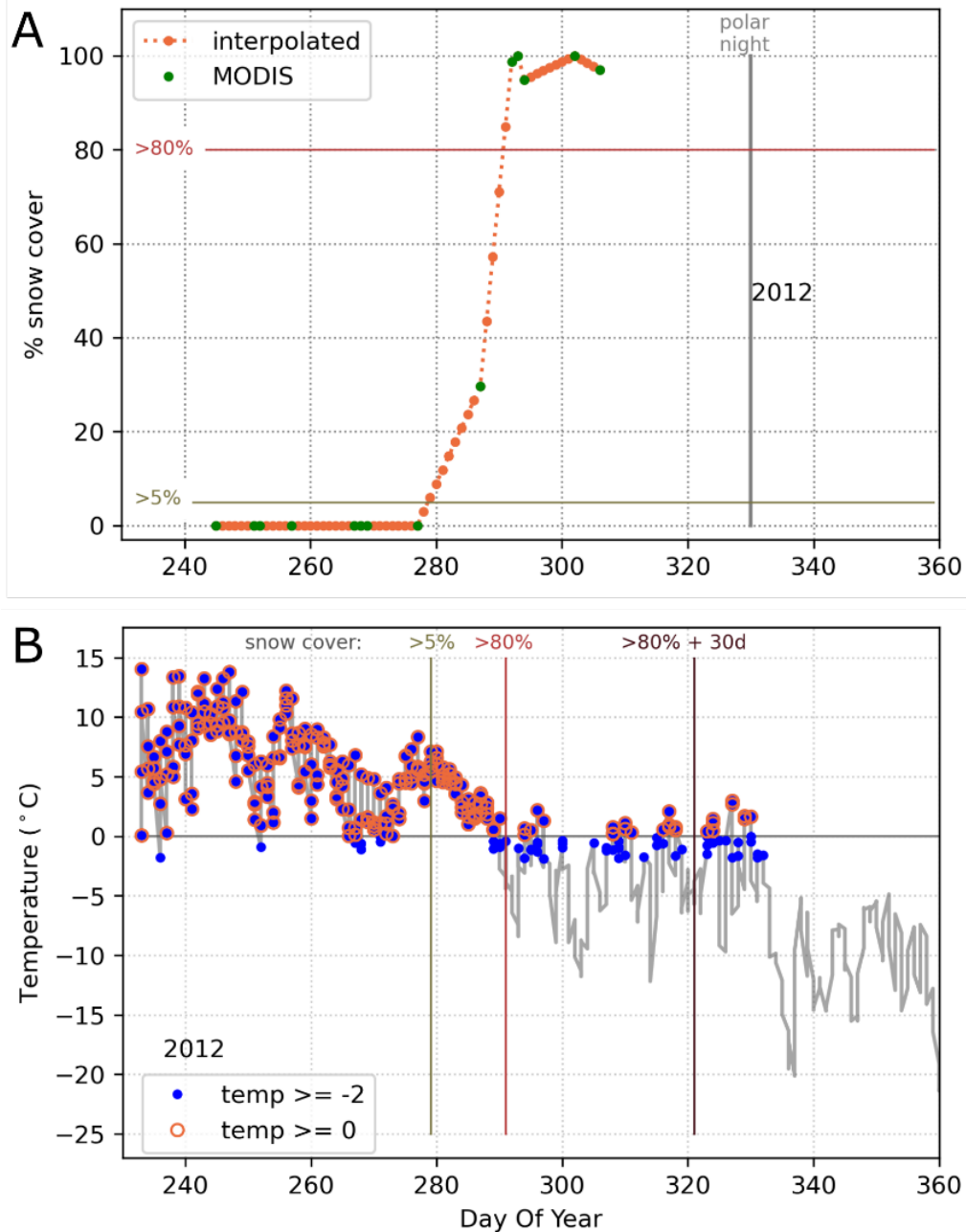


Figure S2. Temporal change in (A) snow cover (daily values) and (B) temperature (every 6 h) at Joatka, Norway, during autumn and early winter 2012. (A) Green dots are values extracted from MODIS and orange dots are linear interpolation on days when MODIS data was unavailable. In this example, interpolation value for the 5% and 80% snow cover dates, a measure of precision, are 9 and 4 days, respectively (see methods). MODIS data became unavailable ~14 d before the

polar night. (B) Vertical lines define the periods of snow onset (between 5% and 80% snow cover; derived from the top graph) and the 30-day period following permanent snow onset. The blue dots are temperature ≥ -2 C and the blue/orange dots ≥ 0 C.

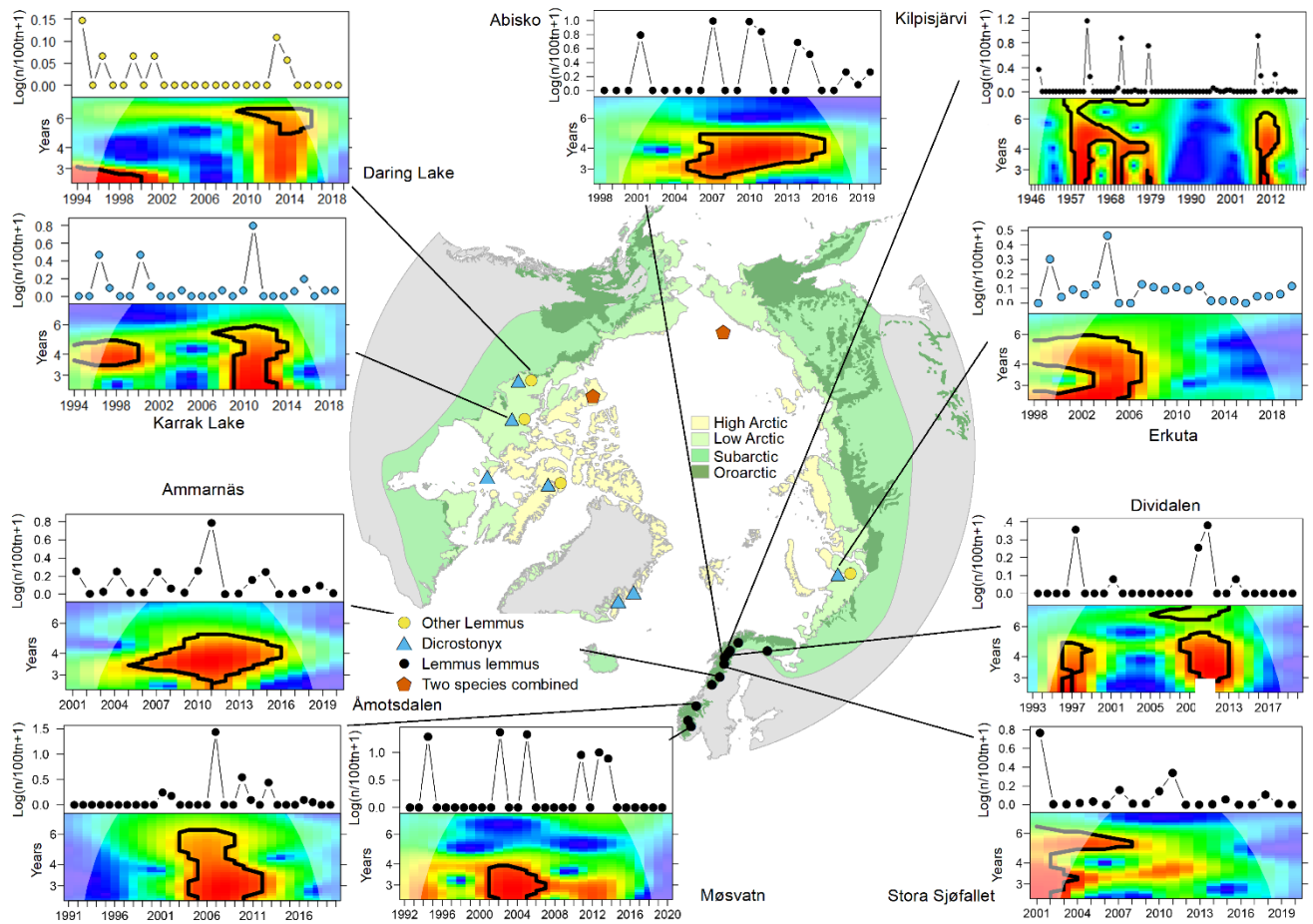


Figure S3. Additional lemming time series and map of the sites where they were collected. The colors on the map show the bioclimatic subzones of the Arctic [25] and the Oroarctic. Log transformed abundance indices/estimates (color codes on the time series refer to the species) with results from the wavelet analysis underneath are shown for the 10 time series that are not presented in figure 1. The color palette indicates the wavelet power levels from blue to red; red areas with black contour lines show periods with evidence for cyclic dynamics, with the estimated periodicity shown on the y-axis. The pale colors at either end of each wavelet plot are outside the cone of influence, an area where results are subject to edge effects.

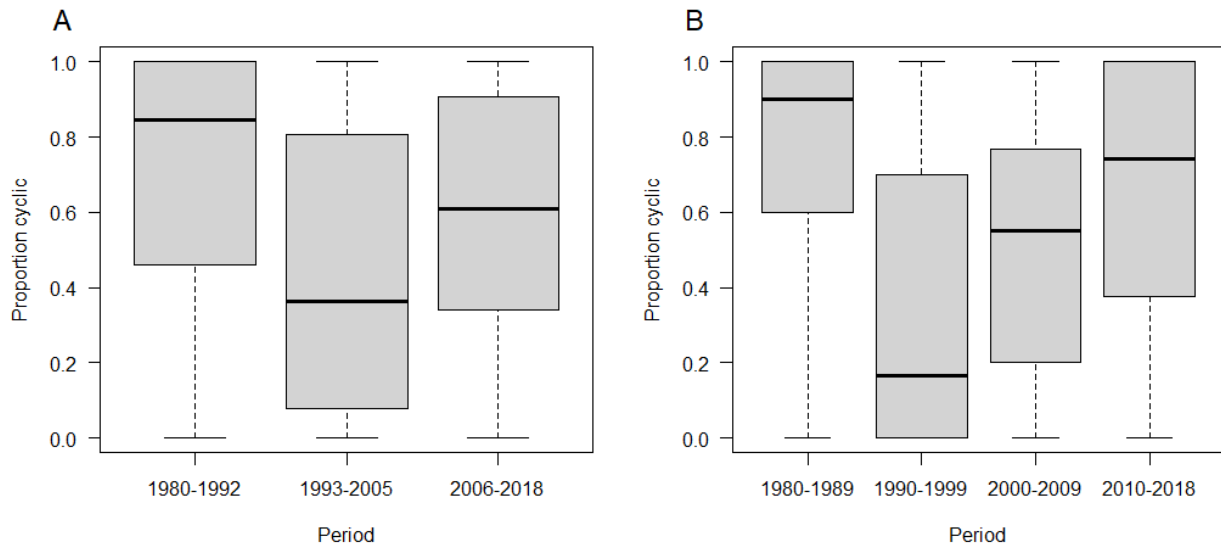


Figure S4. Proportion of cyclic years in each lemming time series calculated over 13-year (A) and 10-year (B) time periods (3 or 4 time periods, respectively). The analysis extends from 1980 to 2018, which are years with 5 or more series available (figure 2). Thick line is median, gray box is the interquartile range and the whiskers show the range of data for each time period. There was no significant difference between time periods (Kruskal Wallis test, A: $p = 0.191$, B: $p = 0.187$).

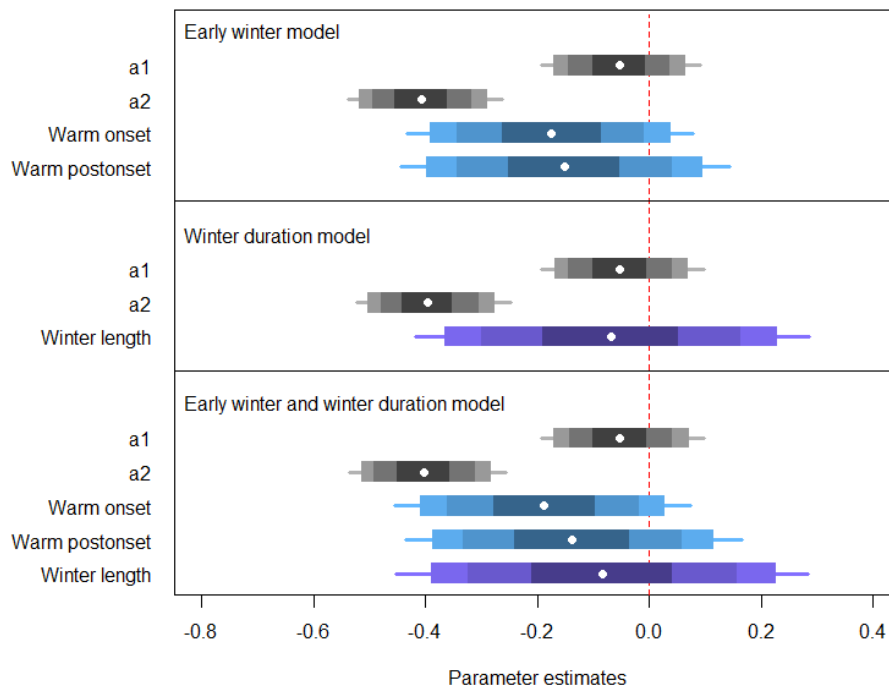


Figure S5. Effect of winter climate on lemming abundance. Parameter estimates for the influence of warm weather in early winter (sum of temperatures above -2°C over periods of six hours) during the period when the snow cover is established (from 5% snow cover to snow cover greater than 80% and not getting reduced to below 50% anymore; Warm onset) and during the first 30 days after establishment of a permanent snow cover (Warm postonset), as well as the effect of winter duration (winter length) obtained from Bayesian state space models assuming a log-linear autoregressive process of order 2. Climatic variables were scaled to mean 0 and SD = 1 prior to analysis making the magnitude of their effects comparable. Autoregressive parameters are shown ($a1$ = direct density dependence + 1 (see [13]), $a2$ = delayed density dependence). Results of the three different models correspond to our three hypotheses and are based on absolute climatic variables. Dots represent the mean of the posterior distribution, boxes the 50%, 80% and 90% credible intervals and lines the 95% credible interval. Red dotted line illustrates 0.

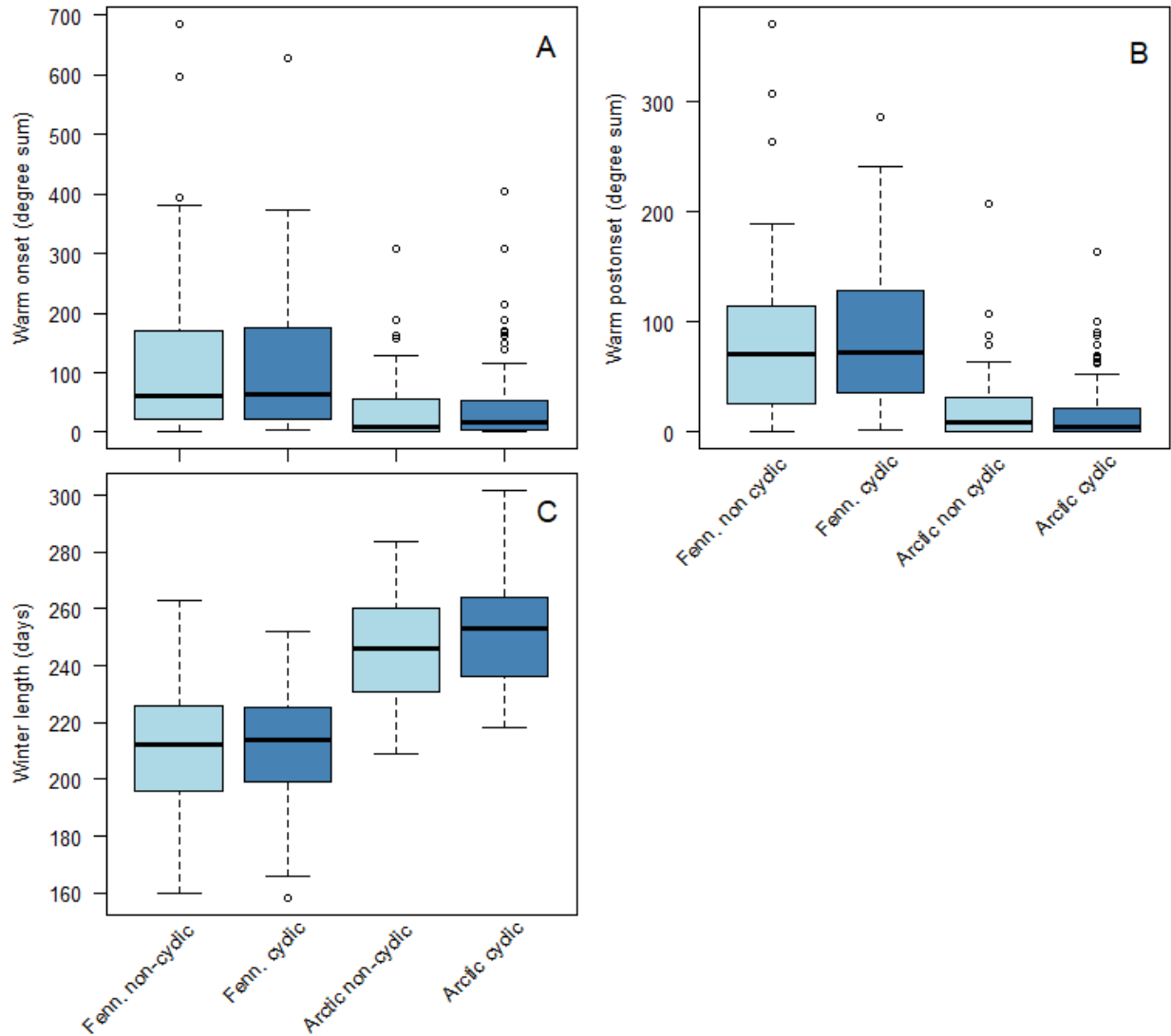


Figure S6. Effect of winter climate on cyclicality of lemming population. Boxplots of three climatic variables (absolute values) characterizing winter conditions during periods when lemming populations were classified as cyclic or non-cyclic by the wavelet analysis for sites in Fennoscandia (Fenn.) and in the rest of the Arctic (Arctic). The three climatic variables differed between sites with *Lemmus lemmus* in Fennoscandia and sites with other species in the rest of the Arctic (warmer climate and shorter winter in Fennoscandia; figure S7). A) Warm spells during snow onset; B) Warm spells during the first 30 days after snow onset; C) Winter length. Boxes

represent the interquartile distance and horizontal lines show the median. Whiskers show 1.5 times the interquartile range and dots represent values outside this range. Differences in deviations based on scaled standard deviations are not presented here because it is the same than with relative values (see figure 4).

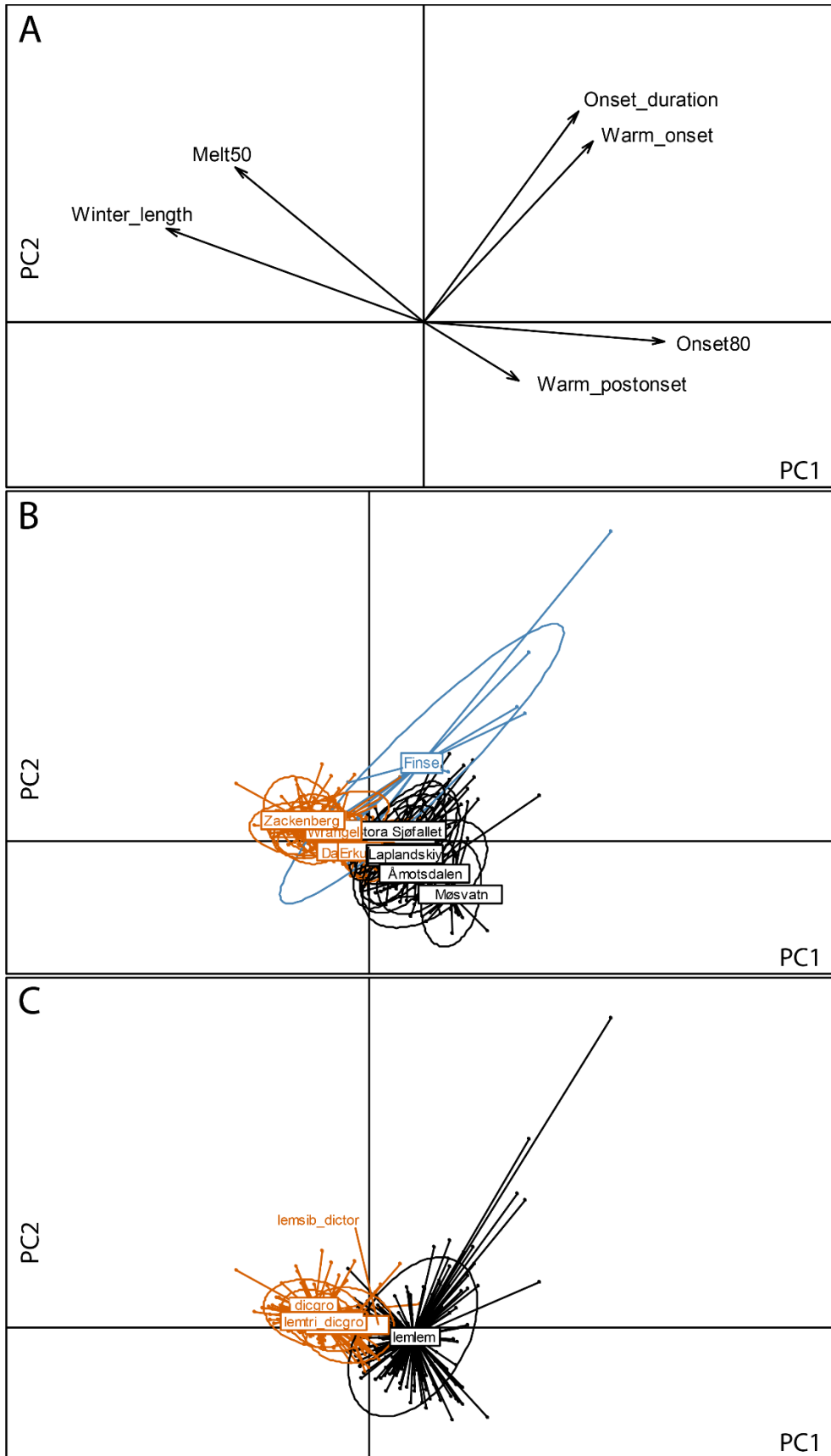


Figure S7. Principal component analysis of the six variables characterizing winter conditions that were determined for each year and site. The first axis (PC1) explained 47% of variation and the second axis (PC2) explained 24%. A) Correlations between the variables, B) Years are grouped by sites where lines link individual years (dots) to the mean for each site. Ellipses show 1.5 standard deviations for each site. Not all site names could be displayed. The Fennoscandian sites are shown in black, the rest of the Arctic in orange and Finse is highlighted in blue. C) Years are grouped by species and displayed as on the previous panel. *Lemmus lemmus* (lemlem) is shown in black and other lemmings in orange (lemtri = *L. trimucronatus*, lemsib = *L. sibiricus*, dicgro = *Dicrostonyx groenlandicus*, dictor = *D. torquatus*).

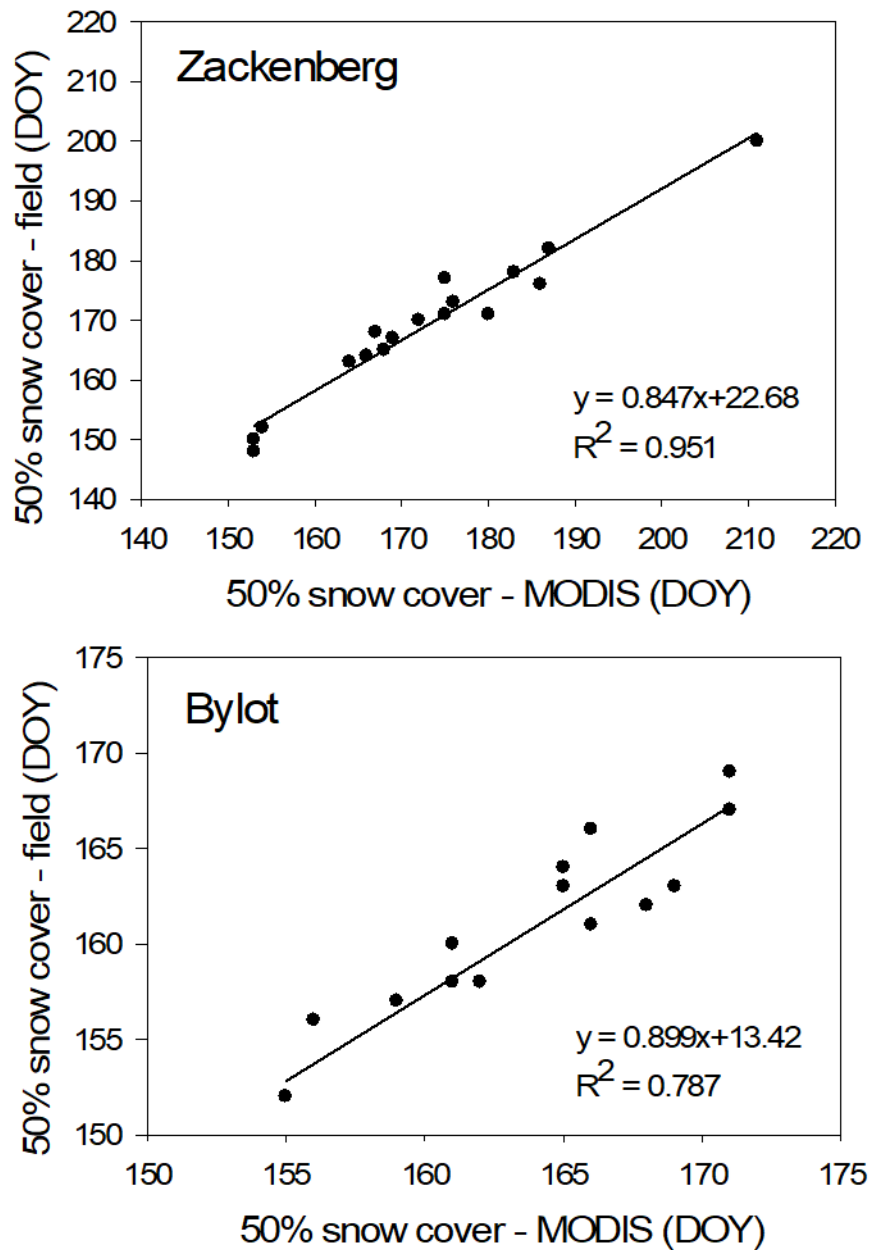


Figure S8. Relationship between local snow melt date (50% snow cover) determined by ground observations and MODIS satellite images at Zackenberg and Bylot Island (DOY = Day of the Year).

Table S1. General information of the time series of annual lemming abundance used for the analyses (updated from [26] where more details can be found). See [27] for the definition of Oroarctic.

| Site name | Region and country | Lead researcher | Coordinates | Climate zone | Time frame | N years | Sampling method ^a | Species |
|----------------------------|--------------------------|---|-----------------------|-------------------------|------------|---------|------------------------------|---|
| Wrangel Island | Chukotka, Russia | I Menyushina | 71.23 N, 179.42W | High Arctic | 1971-2017 | 47 | QI ^b | <i>Dicrostonyx vinogradovi</i> , <i>Lemmus portenkoi</i> |
| Erkuta | Yamal, Russia | N A Sokolova, D Ehrich, & A A Sokolov | 68.25 N, 69.20 E | Low Arctic | 1998-2020 | 23 | ST | <i>Dicrostonyx torquatus</i> , <i>Lemmus sibiricus</i> |
| Laplandskiy Nature Reserve | Murmansk Obl., Russia | G Kataev | 67.650 N, 32.267 E | Subarctic | 1929-2019 | 91 | QI | <i>Lemmus lemmus</i> |
| Joatka | Finmark, Norway | L Oksanen | 69.75 N, 23.98 E | Subarctic/ oroarctic | 1977-2019 | 43 | ST | <i>Lemmus lemmus</i> |
| Kilpisjärvi | Lapland, Finland | H Henttonen | 69.05 N, 20.80 E | Oroarctic | 1946-2020 | 75 | ST | <i>Lemmus lemmus</i> |
| Dividalen | Troms, Norway | E Framstad & N E Eide | 68.71 N, 19.80 E | Oroarctic | 1993-2020 | 28 | ST | <i>Lemmus lemmus</i> |
| Abisko | Norrbottn, Sweden | J Olofsson | 68.3 N, 18.5 E | Oroarctic | 1998-2020 | 23 | ST | <i>Lemmus lemmus</i> |
| Stora Sjöfallet | Norrbottn, Sweden | F Ecke & B Hörnfeldt | 67.60 N, 18.06 E | Oroarctic | 2001-2020 | 20 | ST | <i>Lemmus lemmus</i> |
| Ammarnäs | Västerbotten, Sweden | F Ecke & B Hörnfeldt | 65.96 N, 16.24 E | Oroarctic | 2001-2020 | 20 | ST | <i>Lemmus lemmus</i> |
| Børgefjell | Trøndelag, Norway | E Framstad & N E Eide | 65.06 N, 13.83 E | Oroarctic | 1990-2020 | 31 | ST | <i>Lemmus lemmus</i> |

| Site name | Region and country | Lead researcher | Coordinates | Climate zone | Time frame | N years | Sampling method ^a | Species |
|-----------------------|-------------------------------------|-----------------------|---------------------|--------------|------------|---------|------------------------------|---|
| Åmotsdalen | Trøndelag, Norway | E Framstad & N E Eide | 62.46 N, 9.42 E | Oroarctic | 1991-2020 | 30 | ST | <i>Lemmus lemmus</i> |
| Finse | Hordaland, Norway | E Framstad & N E Eide | 60.59 N, 7.53 E | Oroarctic | 1970-2020 | 51 | ST | <i>Lemmus lemmus</i> |
| Møsvatn | Telemark, Norway | E Framstad & N E Eide | 59.86 N, 8.30 E | Oroarctic | 1992-2020 | 29 | ST | <i>Lemmus lemmus</i> |
| Zackenbergl | Greenland | N M Schmidt | 74.468 N, 20.568 W | High Arctic | 1996-2020 | 25 | WN | <i>Dicrostonyx groenlandicus</i> |
| Karupelv Valley | Greenland | B Sittler | 72.506 N, 23.999 W | High Arctic | 1988-2020 | 33 | WN | <i>Dicrostonyx groenlandicus</i> |
| Bylot Island | Nunavut, Canada | G Gauthier | 73.156 N, 79.972 W | High Arctic | 1993-2019 | 27 | LT, ST | <i>Lemmus trimucronatus</i> , <i>Dicrostonyx groenlandicus</i> |
| East Bay | Southampton Island, Nunavut, Canada | P A Smith | 63.983 N, 81.667 W | High Arctic | 2000-2019 | 20 | IO | <i>Dicrostonyx groenlandicus</i> |
| Karrak Lake | Nunavut mainland, Canada | R T Alisauskas | 67.233 N, 100.250 W | Low Arctic | 1994-2019 | 26 | ST | <i>Lemmus trimucronatus</i> , <i>Dicrostonyx groenlandicus</i> |
| Daring Lake | Northwest Territory, Canada | K Clark | 64.867 N, 111.533 W | Low Arctic | 1994-2019 | 26 | ST | <i>Lemmus trimucronatus</i> , <i>Dicrostonyx groenlandicus</i> |
| Aulavik National Park | Banks Island, Nunavut, Canada | J Frandsen | 73.226 N, 119.591 W | High Arctic | 1999-2019 | 21 | WN ^b | <i>Lemmus trimucronatus</i> , <i>Dicrostonyx groenlandicus</i> |

^a Sampling method: LT = live-trapping, IO = standardized incidental observations, QI = qualitative indices, ST = snap-trapping, WN = winter nest counts.

^b Abundance of both species combined.

Table S2. Sampling effort for each lemming time series used in the analyses and references where more methodological details can be found. Area refers to the polygon used to determine snow cover and which encompasses all lemming monitoring plots at each site (see methods for details).

| Site name | Area covered by sampling (km ²) | Number of sampling periods per year | Period of the year | Number of plots (pl) or transects (tr) | Size of plots or length of transects | Number of traps per plot or transect | Number of trapping occasions | Total number of trap-days | References |
|----------------------------|---|-------------------------------------|----------------------------|--|--------------------------------------|--------------------------------------|------------------------------|---------------------------|------------|
| Wrangel Island | 27 | 1 | Summer | N/A | N/A | N/A | N/A | N/A | [4] |
| Erkuta | | | | | | | | | |
| 1999-2006 | 22 | 1-2 | June-July | 2-4 tr | 250-500 m | 50-100 | 2-3 | 200-2410 | [28] |
| 2007-2011 | 61 | 2 | Late June, Early August | 36 pl | 0.023 ha | 12 | 2 | 1728 | |
| 2012-2019 | 61 | 2 | Late June, Early August | 54 pl | 0.023 ha | 18 | 2 | 2592 | |
| Laplandskiy Nature Reserve | 14 | 1 | Spring-Autumn | N/A | N/A | N/A | N/A | N/A | [29] |
| Joatka | | | | | | | | | |
| 1977-1985 | 28 | 2 | June-early July, September | 15-25 pl | 0.023 ha | 12 | 2 | 720-1200 | [30] |
| 1986-2019 | 28 | 2 | June-early July, September | 25 pl | 0.023 ha | 12 | 2 | 1200 | |
| Kilpisjärvi | | | | | | | | | |
| 1946-1979 | 9 | 2 | Mid-June, September | 1-4 pl | 400 m | ca 120 | 2 | 400-4000 | [31] |
| 1980-2020 | 9 | 2 | September | 4 pl | 400 m | ca 120 | 2 | 1900 | |

| Site name | Area covered by sampling (km ²) | Number of sampling periods per year | Period of the year | Number of plots (pl) or transects (tr) | Size of plots or length of transects | Number of traps per plot or transect | Number of trapping occasions | Total number of trap-days | References |
|-----------------|---|-------------------------------------|-----------------------------------|--|--------------------------------------|--------------------------------------|------------------------------|---------------------------|------------|
| Dividalen | 61 | 1 | September | 5 tr | 475 m | 100 | 3 | 1500 | [32] |
| Abisko | 29 | 2 | Late June, early September | 10 pl | 0.023 ha | 12 | 2 | 480 | [33] |
| Stora Sjöfallet | 166 | 2 | Late June, August-early September | 32-41pl | 1 ha | 50 | 3 | 9600-12300 | [34] |
| Ammarnäs | 145 | 2 | Late June, August-early September | 35-46 pl | 1 ha | 50 | 3 | 10500-13800 | [34] |
| Børgefjell | 30 | 1 | September | 4 tr | 225 m | 50 | 2 | 400 | [32] |
| Åmotsdalen | 1991-1992 | 1 | September | 4-5 tr | 475 m | 100 | 3 | 1200-1500 | [32] |
| | 1993-2020 | 1 | September | 4 tr | 225 m | 50 | 2 | 400 | |
| Finse | 22 | 2 | Late June, early September | 2 pl | 1 ha | 200 | 2-6 | 700-4800 | [35] |
| Møsvatn | 24 | 1 | September | 4 tr | 225 m | 50 | 2 | 400 | [32] |
| Zackenbergl | 27 | 1 | July-August | 1 pl | 106 ha | N/A | N/A | N/A | [36] |
| Karupelv Valley | 30 | 1 | July-August | 1 pl | 1500 ha | N/A | N/A | N/A | [8] |

| Site name | Area covered by sampling (km ²) | Number of sampling periods per year | Period of the year | Number of plots (pl) or transects (tr) | Size of plots or length of transects | Number of traps per plot or transect | Number of trapping occasions | Total number of trap-days | References |
|---------------------------|---|-------------------------------------|------------------------|--|--------------------------------------|--------------------------------------|------------------------------|---------------------------|------------|
| Bylot Island 1993-2003 | 33 | 1 | Late July | 4 tr | 250 m | 25 | 10 | 1000 | [2,9,37] |
| 2004-2019 | 33 | 1 | Late July | 2 pl | 11 ha | 144 | 6 | 1728 | |
| East Bay | 30 | 1 | June-July | N/A | N/A | N/A | N/A | 1000 ^a | [38] |
| Karrak Lake | 60 | 1 | June-July | 3 tr | 250 m | 25 | 10 | 750 | [39] |
| Daring Lake | 38 | 1 | Late July-early August | 2 tr | 250 m | 50 | 6 | 600 | [40] |
| Aulavik National Park | 31 | 1 | Mid-summer | 5-9 pl | 1 ha | N/A | N/A | N/A | |

^a Number of observer-hour in this case

TableS3. Correlations between climatic variables (Pearson correlation coefficients). Only data based on less than 15 days of interpolation for snow onset or snow melt dates were used.

Variables used in the final analyses and correlations among them are highlighted in bold.

| | Melt50 | Onset80 | Onset_duration | Warm_onset | Warm_postonset |
|----------------------|--------|---------|----------------|-------------------|-----------------------|
| Winter_length | 0.75 | -0.87 | -0.30 | -0.30 | -0.19 |
| Melt50 | | -0.32 | -0.01 | -0.09 | -0.10 |
| Onset80 | | | 0.43 | 0.36 | 0.20 |
| Onset_duration | | | | 0.71 | -0.05 |
| Warm_onset | | | | | 0.24 |

TableS4. Summary table of cyclic fluctuations of lemming time series. Number of years that lemming (*Lemmus* and *Dicrostonyx* species) population fluctuations were considered cyclic or non-cyclic within the cone of influence of the wavelet analysis and dominant periodicity during periods of cyclicity across sites (we considered periodicity of <2.5 years as non-cyclic, see methods; median periodicity was 3.7 years). Sites and species in bold are those where cyclicity was present throughout the study period.

| Site | Species | Length of time series (yrs) | Number of years | | Dominant periodicity (yrs) |
|-----------------|---|-----------------------------|-----------------|------------|----------------------------|
| | | | Cyclic | Non-cyclic | |
| Wrangel | <i>Lemmus</i> & <i>Dicrostonyx</i> | 47 | 41 | 0 | 5.9 |
| Erkuta | <i>Dicrostonyx</i> | 23 | 7 | 10 | 2.8 ^b |
| | <i>Lemmus</i> | 23 | 6 | 13 | 2.9 |
| Laplandskiy | <i>L. lemmus</i> | 91 | 42 ^a | 43 | 4.0 |
| Joatka | <i>L. lemmus</i> | 43 | 21 ^a | 16 | 4.3 |
| Kilpisjärvi | <i>L. lemmus</i> | 75 | 32 | 37 | - ^c |
| Dividalen | <i>L. lemmus</i> | 28 | 6 | 17 | 3.6 |
| Abisko | <i>L. lemmus</i> | 23 | 12 | 6 | 3.6 |
| Stora Sjöfallet | <i>L. lemmus</i> | 20 | 5 | 9 | 5.2 |
| Ammarnäs | <i>L. lemmus</i> | 20 | 12 | 2 | 3.7 |
| Børgefjell | <i>L. lemmus</i> | 31 | 19 | 6 | 3.3 |
| Åmotdalen | <i>L. lemmus</i> | 30 | 10 | 15 | 3.1 |
| Finse | <i>L. lemmus</i> | 51 | 27 ^a | 18 | 3.3 |
| Møsvatn | <i>L. lemmus</i> | 29 | 7 | 17 | 2.9 |
| Zackenbergl | <i>Dicrostonyx</i> | 25 | 8 | 11 | 4.3 |
| Karupelv | <i>Dicrostonyx</i> | 33 | 11 | 16 | 4.2 |
| Bylot | <i>Dicrostonyx</i> | 26 | 8 | 11 | 5.0 |
| | <i>Lemmus</i> | 27 | 21 | 0 | 3.7 |

| Site | Species | Length of time series (yrs) | Number of years | | Dominant periodicity (yrs) |
|----------------|--|-----------------------------|-----------------|------------|----------------------------|
| | | | Cyclic | Non-cyclic | |
| Daring | <i>Dicrostonyx</i> | 26 | 17 | 1 | 6.2 |
| | <i>Lemmus</i> | 26 | 0 | 21 | NA |
| Eastbay | <i>Dicrostonyx</i> | 20 | 7 | 7 | 3.3 |
| Karrak | <i>Dicrostonyx</i> | 26 | 12 ^a | 8 | 3.2 |
| | <i>Lemmus</i> | 26 | 11 | 9 | 3.7 |
| Aulavik | <i>Lemmus & Dicrostonyx</i> | 21 | 14 | 0 | 4.8 |

^a Period of cyclicity was discontinuous throughout these time series.

^b The periodicity with higher power is reported but there was also a periodicity at 4.3 years

^c Periodicity could not be determined (see wavelet plot on figure S1).

Table S5. List of tiles of MOD10A1 daily snow cover products used for each site (MODIS/Terra Snow Cover Daily L3 Global 500 m SIN GRID V006).

| Site | Tile number |
|-----------------|-------------|
| Abisko | h18v02 |
| Ammarnäs | h18v02 |
| Åmotsdalen | h18v02 |
| Aulavik | h14v01 |
| Børgefjell | h18v02 |
| Bylot Island | h15v01 |
| Daring Lake | h13v02 |
| Dividalen | h18v02 |
| East Bay | h14v02 |
| Erkuta | h20v02 |
| Finse | h18v02 |
| Joatka | h18v02 |
| Karrak Lake | h14v02 |
| Laplandskiy | h19v02 |
| Møsvatn | h18v03 |
| Stora Sjöfallet | h18v02 |
| Karupelv Valley | h17v01 |
| Wrangel Island | h12v01 |
| Zackenbergl | h17v01 |

Table S6. Site-specific acknowledgements.

| Site | Acknowledgements |
|--|---|
| Erkuta | The research was funded by the State contract of the Institute of Plant and Animal Ecology, UB RAS “Terrestrial ecosystems of North-Western Siberia: assessment of the modern transformation of the communities” (No 122021000089-9), the Research Council of Norway and FRAM – High North Research Centre for Climate and the Environment. Valuable logistical support was provided by “Gazpromtrans” Ltd. |
| Joatka | The Research has been mainly funded by the Swedish Research Council and Academy of Finland. We also acknowledge the direct support from Finnmark University College (today Campus Alta of The Arctic University of Tromsø). Since 2017, Eva Soininen is now responsible of the trapping at this site. |
| Stora Sjöfallet, Ammarnäs | The monitoring of small mammals has been funded by several sources, the most important one being the Swedish Environmental Protection Agency via the National Environmental Monitoring Program. |
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| Zackenbergl | We thank the Greenland Ecosystem Monitoring for access to ecosystem data from Zackenberg. |
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| Site | Acknowledgements |
|----------|---|
| | Knowledge Canada, Canadian Foundation for Innovation, Environment Canada, Indigenous and Northern Affairs Canada, Parks Canada and the Polar Continental Shelf Program (Natural Resources Canada). |
| Daring | Research on small mammals has been supported by the Department of Environment and Natural Resources, Government of the Northwest Territories and is often conducted by students participating in the Tundra Science and Culture Camp hosted every summer at the Research Station. |
| East Bay | The work was supported by Environment and Climate Change Canada, the Polar Continental Shelf Program and the Natural Sciences and Engineering Research Council of Canada. |
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