Documenting lemming population change in the Arctic: Are we keeping the pace?

Running head: Circumarctic lemming populations

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Abstract

Lemmings are a key component of tundra food webs and changes in their dynamics can have large affects on the whole ecosystem. We present a comprehensive overview of lemming monitoring activities and assess recent trends in lemming abundance across the circumpolar Arctic. Since 2000, lemmings have been monitored at 49 sites of which 38 sites are still active and the distribution of monitoring sites was not evenly distribution with especially Russia being underrepresented. Abundance was monitored at all sites but with a variety of methods, which do not have the same levels of precision. Other important CBMP components such as health and genetic diversity, as well as potential drivers of population change, were generally not monitored. We did not find evidence that lemming populations were decreasing in general, although a negative trend was detected for arctic populations sympatric with voles. However, low precision of the data limits the reliability of these conclusions. This study also illustrates the importance of maintaining long-time monitoring programs and we recommend to improving spatial coverage and harmonizing the methods used.

Keywords

Dicrostonyx, *Lemmus*, population monitoring, temporal trends, arctic, small rodent

Kommentoinut [GG1]: Limited to 150 words.

Kommentoinut [GSa2]: Spell out abreviations on first use (personally I prefer not to use abbreviations at all as it is generally helpful only for the writer – not the reader).

Kommentoinut [GSa3]: I assume it is population change but not clear (so good to clarify what type of change we mean).

Kommentoinut [GSa4]: All sites are artic, right? If so we do not need to say arctic here I think.

Kommentoinut [GSa5]: DETAIL but good to clarify what type of monitoring we mean.

INTRODUCTION

Lemmings are key herbivores in arctic tundra ecosystems where they play a major role both for the flow of energy and the dynamics of the systems ((Ims and Fuglei 2005, Legagneux et al. 2012). For example, lemmings can consume more plant material than large herbivores (Batzli et al. 1980) and during population peaks their impact on the vegetation can, in some areas, be seen even from space (Olofsson et al. 2012). As prey, they constitute the main resource for many terrestrial arctic predators that depend on them for survival and reproduction (Krebs 2011; Schmidt et al. 2012). Lemmings are well known for their regular population outbreaks, the lemming cycles (Stenseth and Ims 1993). These cycles create boom and bust dynamics which influence the whole ecosystem (Ims and Fuglei 2005). The annual fluctuations of furbearers such as arctic foxes resulting from these resource pulses have been known by arctic hunters and trappers for centuries (Elton 1924). In addition to plants and predators (Samelius and Alisauskas 2017) which interact with lemmings directly, many birds, such as geese and waders, are indirectly affected by the lemming cycles as alternative prey for predators (Bêty et al. 2002; Lamarre et al. 2017).

Arctic lemmings belong to two genera, collared lemmings (*Dicrostonyx* ssp.) and brown lemmings (*Lemmus* ssp.), which are represented by six and four geographic species in the Arctic, respectively (Reid et al. 2013). The Norwegian lemming (*Lemmus lemmus*), the only mammal endemic to Fennoscandia, were the object of the first scientific interest for the lemming cycles nearly a century ago (Elton 1924). It may be the most conspicuous species due to their aggressive behaviour at high densities. Lemmings are present in Norwegian culture notably with the saying “to become angry as a lemming”.

The two genera of lemmings appear to have evolved together with the tundra in the beginning of the Pleistocene (Oksanen et al. 2008). With long winters, they have developed convergent adaptations to life under the snow (*Dicrostonyx*, and to a certain extent Norwegian lemmings, grow large claws in winter for digging) and to coarse food plants of low nutritive value (robust teeth and strong jaws; (Oksanen et al. 2008)). These adaptations to harsh arctic conditions may have occurred at the cost of agility to escape predators, making lemmings particularly vulnerable to predation (Oksanen et al. 2008). In the high Arctic, lemmings are the only naturally occurring small rodent species, whereas in the low Arctic and sub-arctic mountain areas (oroarctic; (Virtanen et al. 2016)) they usually occur together with one or several species of voles (genus *Microtus* and or *Myodes*). The dynamics of sympatric species are often synchronous, and indirect interactions mediated by shared predators have been hypothesized to limit lemming outbreaks (Oksanen 1993; Hanski and Henttonen 1996).

Kommentoinut [DE6]: The whole text with references should in the end not exceed 6000 words – I will shorten it after you comments.

Kommentoinut [RA7]: I suggest this, only because it is a direct demonstration using mark recapture of how lemming cycles affect the cycling of reproduction in arctic fox, but not fox apparent survival. You may decide not to keep it. I also added the reference in the lit cited, if you do keep it.

Kommentoinut [GSa8]: Interesting but can skip this if short of space (and move the next paragraph up).

Kommentoinut [L9]: but persist primarily at higher altitudes, where vole densities are low (Ekerholm et al. 2001)

As small rodents specialized for life under the snow, lemmings are able to reproduce in winter (Dunaeva 1948; Millar 2001). In high Arctic areas where summer predation is intense, the main population growth occurs in winter and density declines over the summer (Gilg 2002; Fauteux et al. 2015). Because winter reproduction appears to be a prerequisite for lemmings to reach peak densities, they are likely to be more sensitive to changing winter climate than northern voles (Ims et al. 2011). In particular unstable autumn and winter weather with warm spells and rain, leading to icing at the bottom of the snow pack, may reduce subnivean movement by lemmings and access to food plants (Kausrud et al 2008, Berteaux et al. 2016). In recent decades, a fading out of lemming outbreaks leading to generally lower abundance has been reported from several regions, notably from high Arctic Greenland (Gilg et al. 2009) and southern Fennoscandia (Kausrud et al. 2008), and these changes in dynamics have been attributed to changes in winter climate.

In the highly connected Arctic food webs (Legagneux et al. 2012, Schmidt et al. 2017), changes in lemming dynamics are likely to have cascading impacts on many other species. In eastern Greenland the collapse of the lemming cycles to low density populations has had dramatic consequences for specialist predators such as snowy owls (Schmidt et al. 2012). Lemmings are therefore not only a key functional component of the tundra ecosystem, but also a key monitoring target for changes in the arctic tundra biome (Petersen et al. 2004). Detecting and understanding the multifaceted changes arctic ecosystems are experiencing in relation to global change requires well designed biodiversity monitoring systems (Meltofte et al. 2013, (Berteaux et al. 2017). Lemmings and other arctic small rodents have been identified as an important Focal Ecosystem Component (FEC) in the Circumpolar Biodiversity Monitoring Program (CBMP; Christensen et al 2013).

Here we present a comprehensive overview of recent lemming monitoring activities in the Arctic, including oroarctic areas. We assess spatial and temporal coverage of current monitoring efforts and the extent to which they address the core attributes for small mammals defined by the Circumpolar Biodiversity Monitoring Program. We discuss the consequences of gaps in monitoring effort and data availability, and identify ways (and limitations) to harmonize monitoring initiatives and methods, and to coordinate availability of data. The second aim of this study is to assess the status and trends of lemming populations across the circumpolar Arctic. To ensure wide coverage, we also include short (less than X years) and discontinuous series consisting of both quantitative and

Kommentoinut [GSa10]: DETAIL but isn't this known (that leming cycles have large impact on the whole ecosystem)? Might just be a matter of wording but sounds similar to what we have said above (that changes in lemming numbers have lage impact on the whole system).

Kommentoinut [GSa11]: I advise against using abbreviations (makes it more difficut to read and does not save much space).

Kommentoinut [L12]: agree; abbreviations should only be used for those concepts which are discussed recurrently, so that saving of space is substantial. This also keeps the number of abbreviations reasonable, so that they are easy to remember

Kommentoinut [L13]: add :
which are customarily pooled with the arctic tundra in global biome treatises (Olson et al. 2001, Kaplan et al. 2003, Virtanen et al. 2016)

Kommentoinut [GSa14]: Might be good to define what we mean by short.

qualitative data. As far as data allow, we asses geographic patterns in multiannual density fluctuations with respect to abundance and amplitude. Moreover, we examine temporal trends in lemming abundance, and assess whether there is empirical evidence for a circumpolar decrease in lemming populations, which could be related to climate change.

Kommentoinut [GSa15]: How is this different from assessing the status and trends across the Arctic mentioned in a few sentences above? Omit here or in the sentence above?

MATERIALS AND METHODS

Inventory of lemming monitoring initiatives

For our overview of lemming monitoring, we collected information from recent small rodent monitoring activities from throughout the Arctic , as well as monitoring programs from sub-arctic and oroarctic sites where lemmings were important. Temporally, we included all monitoring programs which have been collecting data after 2000 (Table S1). The lead authors contacted relevant scientists from the Small Mammal Expert network of CAFF (https://www.caff.is/terrestrial/terrestrial-expert-networks/small-mammals) and through their collabortive networks. Scientisits were asked to provide information about their monitoring activities and protocols used. We also asked which Focal Ecosystem Component attributes were addressed and which other ecosystem components were monitored (Table S2). All scientists were asked to forward the request to other people having relevant data. For Russia, we also used the rodent abundance overview of The International Breeding Conditions Survey on Arctic Birds (http://www.arcticbirds.net/) to identify ongoing monitoring projects. The information collected was summarized to provide an overview of methods used and to assess how well ongoing small rodent monitoring in the Arctic meets the recommendations of the CBMP.

Kommentoinut [GSa16]: Might avoid saying « all » studies and just say that we collected information from throughout the arctic and then say (as you do) how the data was gathered.

Kommentoinut [GSa17]: DETAIL but should these be spelled with apital letters (if Arctic is spelled with capital letter I mean)?

Assessment of status and trends

All scientists contacted for the monitoring inventory were asked to share time series of small rodent abundances or indices to contribute to this circumpolar assessment. Annual time series for each lemming species at each site were presented graphically to assess population dynamic patterns and the frequency of outbreak years where outbreak years were defined by XXXX following YYYY et al. (YEAR). Where relevant, sympatric voles were included on the plots. The amplitude of multiannual density fluctuations was quantified by the standard deviation of the log-10 transformed annual estimates (s-index; (Henttonen et al. 1985). Values of 0 were replaced with half of the

Kommentoinut [GSa18]: Is this how the data were analysed (graphically) or how it was presented by the different study sites (i.e. how you got the data)? I am guessing that what you mena here is that the data was **analyzed or examined** graphically.

Kommentoinut [GSa19]: Important to define what characterized an outbreak year and idellay refer to a paper that used such definition.

smallest value which could have occurred in the series (i.e., half of one animal trapped or half of one nest found) (Gruyer et al. 2008). As suggested by Henttonen et al. (1985), the s-index was calculated for all series with at least five years of data. Index values above 0.5 indicate high amplitude population fluctuations (Henttonen et al. 1985). In some sites, notably in Fennoscandia, lemmings appeared sporadically and were not registered in all years. Therefore, we also quantified the irregularity of lemming presence in the series as the proportion of years where 0 values were recorded. For sites where both lemmings and voles occurred, community composition was characterized by calculating the mean of the annual proportions of lemmings in the data. Similarly, for sites with two species of lemmings, the mean of the annual proportions of each species was calculated relative to the total abundance of lemmings.

Trends of lemming abundance were estimated as the coefficient of a linear regression of abundance estimates against time. Estimates were scaled to a mean of 0 and a standard deviation of 1. We included also qualitative series with four or more levels into these trend analyses. For comparison of summary statistics between different species and sites we only used time series with observations over at least 10 years. Moreover, we focussed on data from the last 25 years (1993-2017) to compare trends over a specific time period. We tested for differences in linear trends between biogeographic zones, geographical regions, species, and among sites with different community composition using linear models with trends as response variable and the respective categories as explanatory factors. To account for different lengths of the series, length was included as a weighing parameter. Results are presented as predicted means with 95% confidence intervals. For sites where lemmings co-occurred with voles, we also estimated linear trends in the proportion of lemmings and in the proportion of voles [?], where two lemming species were present. All statistical analyses were carried out in R (R Development Core Team 2018).

Kommentoinut [GSa20]: Why not the slope?

Kommentoinut [GSa21]: How were these leves defined and is there a paper we can refer to for explanation?

RESULTS

Inventory of monitoring projects

We obtained information from 49 sites, where lemmings were monitored after the year 2000 (Fig. 1, Table S1). The sites are from all regions of the Arctic: 15 in North America, three in Greenland, 21 in Fennoscandia including the Kola Peninsula and 10 in Russia east of the White Sea (hereafter referred to as Russia). Fennoscandia is thus clearly overrepresented relative to the geographical area it covers, whereas Russia is underrepresented. Considering only ongoing monitoring initiatives (78 %), the skew in the distribution is even stronger with only six ongoing monitoring programs in Russia, 18 in Fennoscandia, three in Greenland and 12 in North America. Regarding biogeographic zones, 15 sites are located in the high Arctic (12 ongoing), 12 sites in the low Arctic (8 ongoing), 19 sites in the oroarctic (16 ongoing) and 2 sites in the subarctic. The biased geographical coverage resulted also in a biased species coverage with an overrepresentation of the Norwegian lemming.

Temporally, the monitoring activities extended over periods ranging between 3 and 87 years (Fig. 2, Table S1) and in several sites, observations were lacking for some years. A majority of the ongoing monitoring activities started in the beginning of the 1990s or later and only one program in each of North America and Greenland, five in Fennoscandia and three in Russia go back to before 1990. There were, however, other monitoring programs taking place in the 20th century, which are not included here as they stopped before 2000 (Kokorev and Kuksov 2002; Krebs et al. 2002; Pitelka and Batzli 2007).

Among the essential FEC attributes of the CBMP monitoring plan, annual measures or indices of lemming abundance are recorded at all sites (Fig. 3). The methodologies, however, vary between sites and included snap-trapping, live-trapping, winter nest counts, systematically recorded incidental observations, and qualitative indices (Fig. 4). Live trapping is mostly used in North America, whereas snap trapping is used a lot in Fennoscandia, and was overall the most used method. Qualitative indices based on a general impression of lemming abundance in the field were used at least partly in half of the Russian series. In some sites, this index also takes into account lemming predator activity (e.g. Meduza Bay). Among these methods, only live trapping allows the estimation of true densities and all other methods provide relative abundance indices. At many sites several census methods were used (Table S2).

The two other essential FEC attributes received limited attention. Health (diseases, parasites) was only monitored systematically at few sites. Phenology was monitored only on Wrangel Island, where dates of first appearances on the snow, migration to summer habitat and observations of first juveniles were recorded (Virhe. Viitteen lähdettä ei löytynyt.~~Figure~~ 3, Table S2). Of the recommended FEC attributes, about half of the sites monitored some aspects of lemming demography and spatial structure regularly. In many trapping protocols, sex, age classes and sometimes reproductive status of trapped animals were recorded, but mortality was rarely determined. As trapping was often carried out in a design of replicated plots in different habitats, the data provided also some information about spatial structure (habitat use). Similar information can be obtained from winter

Kommentoinut [JO22]: I know we should not add new references but it would be good to add a reference for the delimitations of these regions.

Gustaf : I agree. Perhaps this can be added in the methods?

Kommentoinut [JO23]: I do not think the average make a lot of sence

Kommentoinut [GSa24]: Again, better to spell out abbreviations – they don't save much space and makes reading harder as the reader have to go back and see what the abbreviatiosn stand for (abbreviations help only the writer I think).

nest counts. Genetic diversity was surveyed in some sites, but often only once (**Virhe. Viitteen lähdettä ei löytynyt.**~~Figure~~ 3). In addition to these FEC, a few programs examined lemming diets, and tissue sampling, for instance for stable isotope analysis, was carried out occasionally (Table S2). Regarding other ecosystem parameters, the abundance and reproduction of lemming predators, as well as the availability of alternative prey for the predators was monitored at about half of the sites, but plant productivity and phenology received less attention. Finally, less than half of the sites monitored abiotic conditions annually (ESM Table S2). The size of the study areas and the total effort used in monitoring also varied considerably between sites (table S1).

Kommentoinut [RA25]: Best to stick to past tense throughout.

Kommentoinut [GSa26]: Tissue sampling in general or for some specific reason? Good to specify what the tissue sampling was for.

Status of lemming populations

Through our common effort and willingness to share data, we were able to assemble time series from 42 sites (Fig. 1, ESM Fig. S1). Excluding sites where data were collected for <5 years, we had 14 time series for *Dicrostonyx*, 17 series for *Lemmus lemmus* and eight series for other *Lemmus* species. As some methods did not distinguish between species, nine series reflected the combined abundance of collared and brown lemmings. In addition to lemmings, abundance indices for voles were recorded at 26 sites (62% of the sites; table S1). Small rodent communities were composed of both voles and lemmings at all sites south of the high Arctic defined as XXXX, except Walker Bay (Fig. 1). In Fennoscandia, voles were on average more abundant than lemmings in trapping data, whereas in North America several mixed communities occurred where lemmings were dominating.

Kommentoinut [GSa27]: Have we defined what we mean by the high arctic? I don't think so so please add a definition here and preferably a reference for this.

The available data present a very heterogeneous picture of temporal dynamics (Fig. 1, Fig. S1). Considerable multiannual fluctuations in abundance were recorded in all sites and for most species, but patterns of fluctuation differed considerably. Norwegian lemmings exhibited typical outbreak years at intervals of three to six years, but sometimes considerably longer periods occurred without outbreaks or even without lemming records at all (Fig. 1B). Vole peaks in Fennoscandia were often synchronous with lemming peaks, but sometimes vole peaks occurred without lemmings. Outside of Fennoscandia, heterogeneity in dynamic patterns was even larger (Fig. 1A). Rather regular cycles with a period of 3-4 years were observed at some sites such as Bylot Island, but this pattern does not appear to be the general rule. Other study sites exhibited multiannual fluctuations with a period of 4 or 5 years, but patterns were much less apparent because of large differences in abundance indices between different peak years (e.g. Barrow, Aulavik).

Kommentoinut [GSa28]: Thius must be for Fennoscandia (but sounds like vole peaks in general as it was worded) so I suggest to clarify that this is for Fennoscandia.

Kommentoinut [GSa29]: Not clear what you mean by « in the rest of the arctic » b

Amplitude, as estimated by the s-index, ranged from 0.26 to 0.91. The s-index was below the threshold for high amplitude population fluctuations (0.5) at 11 study sites (26%) and in most of these, lemmings occurred only rarely or at very low abundances (Kilpisjärvi, Erkuta, Nenetsky, Daring Lake). On average, amplitude estimates were higher for Norwegian lemmings than for other species (Fig. 5). The observation method seemed to be important as well for recorded amplitude, and the s-index values were considerably lower for series based on winter nests and higher for incidental observations than for observations based on trapping. The proportion of years with zero lemmings trapped had a lower median for *Dicrostonyx* than for the other species, but there were large differences among study sites, and between trapping methods (Fig. 5). Snap trapping data had more zero observations than other methods.

Comparing real abundance of lemmings between the sites is extremely difficult because of differences in methods used. Indeed, genuine density estimates are available only for three high Arctic sites (Fig. 1). Snap trapping indices show large differences in the number of lemmings trapped in peak years with captures of up to 15 (Joatka) and even 30 (Finse) individuals per 100 trap-nights in Fennoscandia, whereas at some other sites captures were always less than 1 capture per 100 trap-nights (e.g. Daring Lake). In addition to differences in densities between areas and species, these differences werere likely related to difference in trapping design among studies (Fauteux et al. 2018) and in the local habitat where the trapping was carried out.

Kommentoinut [GSa30]: Are there any test statistics for this (e.g. p-values or similar)?

Kommentoinut [GSa31]: Important to clarify that less than 1 capture per 100 trap-nights was only for some study areas – not for all other areas outside Fenoscanda!!!

Trends

Linear trends for scaled lemming abundance during the last 25 years (41 series, mean length of the series 19.3 years, standard deviation SD = 4.8) varied between -0.87 (Chaun) and 0.82 (East Bay) standard deviations per decade (Fig. 6). The mean trend was -0.07 (SD = 0.45), indicating that there is no evidence for an overall increasing or decreasing trend for lemming populations over the last 25 years. The linear models showed that there were no consistent differences between species or biogeographical zones, although estimates for the low Arctic were slightly negative (Fig. 6). Concerning geographical regions, there was an indication for a negative trend in Russia. Community composition revealed the clearest differences in trend. Whereas trends were on average 0 for sites where only lemmings are present and for Fennoscandian sites with Norwegian lemmings and voles, they were significantly negative for sites where arctic lemmings and voles co-occured.

Trends in the proportion of lemmings compared to voles and in the proportion of each species among lemmings were mostly weak and not significant (ESM table S3). A change in species composition was, however, recorded at two low Arctic sites. In Churchill, Manitoba, no voles had

Kommentoinut [GSa32]: I assume it is in trend.

Kommentoinut [GSa33]: Any test statistics for this?

Kommentoinut [GSa34]: Test statistics?

been trapped in the 1990's, but when trapping was resumed in 2010, northern red-backed (*Myodes rutilus*) voles were caught. Similarly, no voles had been seen or trapped in South-eastern Taimyr before 2013, but in 2013 and 2014 several *M. middendorffii* individuals were observed (Golovniuk et al. 2017).

DISCUSSION

Monitoring

The present inventory showed that considerable effort to monitor lemming and vole abundance continues in the circumpolar Arctic during the last 25 years. Monitoring initiatives are at present on-going at 38 sites covering most regions of the Arctic, and in many sites data are available for 20 years and more. While in some programs lemmings are the focus of specific research questions (e.g. Bylot, Finse), at other sites small rodent abundance are mostly collected to explain variation in other ecosystem components, such as breeding birds (e.g., south-eastern Taimyr, Karrak Lake). This is likely to influence the choice of methods and resources which can be allocated to this task. Together with the inherent challenges of long-term field work in remote arctic locations, it can explain why methods used to monitor lemming abundance vary so much. Despite an important overall effort, biases in geographic distribution and many rather short time series (less than X years), some of them with gaps, limit the conclusions about the status and long-term trends of lemming populations that can be made with confidence.

The geographical distribution of monitoring sites is not proportional to the extent of different geographical areas (Fig. 1), but rather related to the regional researcher density. Numerous sites in Scandinavia lead to a good coverage for the Norwegian lemming, whereas other more widespread species, such as the Siberian lemming, are not monitored as well. In the Russian Arctic, which encompasses nearly all of the Eurasian arctic tundra, there are only four ongoing monitoring initiatives with more than five years of data. The lack of data from Russia not only regarding lemming but for many components of the arctic ecosystems has been highlighted in previous assessments (e.g, Ims et al. 2013) and hampers a circumpolar understanding of changes in the tundra ecosystems. Continuing effort to include Russian sites and researchers in international initiatives is thus very important. Monitoring in the Canadian Arctic Archipelago is also sparse. Another gap in spatial coverage in monitoring of lemmingsis the subarctic outside of Fennoscandia despite distributions of several species extending into this area (Stenseth and Ims 1993). This limits our ability to detect possible range shifts (Marcot et al. 2015).

Kommentoinut [L35]: or vegetation dynamics (e.g. Joatka, Abisko)

Kommentoinut [GSa36]: Again, good to clarify what we mean by short

Kommentoinut [GSa37]: To me the limitation is largely for the specific study site – not for the arctic as a whole as we have data from 38 sites.

Kommentoinut [L38]: add :
where infrastructure is superb by arctic standards and distances between universities and lemming habitats are short

Kommentoinut [L39]: and oroarctic habitats…

e.g. the Central Siberian plateau south of Tajmyr is a huge oroarctic area, with arctic fauna and flora

Temporally, many of the longer series go back to the beginning of the 1990s, which represents 25 years or more of field work and a substantial field effort. This is also the period during which climate in the Arctic warmed to temperatures above the 1981-2010 mean values (Overland et al. 2015). The data do thus not allow a direct comparisons to the period before the impact of climate change. In this paper, we deliberately considered monitoring ongoing after 2000 and excluded thus data on lemming dynamics from older and completed research programs. Assessments of long-term changes in lemming dynamics for a few specific regions integrating all available information have been published elsewhere (Angerbjörn et al. 2001; Aharon-Rotman et al. 2015).

Seasonally, lemming monitoring is usually carried out during one or two periods in summer. Apart from winter nests found after snowmelt, there are virtually no data on lemming abundance or activity during the long winter period, although it is likely to be critical to understand population dynamics (Krebs 2011) and the impact of climate change (Kausrud et al. 2008) in a group specialized for life under the snow. This asynchrony has been stressed for a while (Stenseth and Ims 1993; Krebs 2011), but the challenges of trapping lemmings under the snow in remote arctic locations are difficult to overcome. However, new technology is about to open new possibilities through the development of camera tunnels which monitor lemmings year round in a non-invasive way and can provide information that will be important for increasing our understanding on lemming dynamics (Soininen et al. 2015).

Population abundance is a crucial parameter in ecology, but is often difficult to estimate reliably (REF). Most methods used to monitor lemmings provide only abundance indices. Real density estimates are obtained only from live trapping and subsequent mark-recapture analyses (Williams et al 2001), which is a labour-intensive method usually carried out with a rather limited spatial extent. However, several sites in North America moved from snap trapping to live trapping during the monitoring period, (e.g. Bylot, Igloolik) improving data quality considerably and providing additional information on vital rates such as survival. A recent study assessing how well different abundance indices are correlated with true density estimates concluded that systematic incidental observations and snap trapping provided equally good proxies for lemmings in the high Arctic (Fauteux et al. 2018). Incidental observations are easy to implement, but they usually do not distinguish between species. Moreover, it is unclear whether it would work as well in the lusher vegetation of the low Arctic, and whether also voles would be detected reliably. Snap trapping is the most commonly used method, but lemmings, at least Norwegian lemmings, are less easily trapped than voles (REF) and sampling design to trap small mammals often does not target lemming habitat

Kommentoinut [GSa40]: I am not following here – the last 25 years is a period when the temperatures raised above the mean temperature for that time period (how can the temperature rise above the mean for the same period). I am probably just reading this wrong but maybe this could be rephrased to explain a bit more clearly what you are saying.

Kommentoinut [GSa41]: Must be some good references for this – like mark-recapture papers by Nichols and CO. Either of the references below should be good as a general reference I think.

Nichols J.D. 1992 Mark-recapture models : using marked animals to study population dynamics. BioScience 42 : 94-102.

Williams B.K., Nichols J.D. and Conroy M.J. 2001. Analysis and management of animal populations. Academic Press, San Diego.

Kommentoinut [L42]: may depend on snap trapping method. the regression between liver trapping and SQM indices had high R^2 values for both voles and lemmings though the best models for lemmings and voles were very different – see Ruffino et al. 2016.

Kommentoinut [GSa43]: Would be good with a reference suporting this statement or motivate why (lemmings larger than voles and large individuals my not always get caught?).

Kommentoinut [L44]: we do not agree. lemmings are hard to live trap, but snap trapping is easy as their runways are visible and lemmings move more than voles. When relating SQM index trapping to live trapping, conducted in the same habitats, Ruffino et al. (2016) found that snap trapping grossly overestimated the share of lemmings in the rodent community, especially in peak years.

specifically, which results in series with many zero values and subsequent analytical challenges (Fig. 1). Moreover, snap trapping is ethically questionable to some.

Differences in methods applied may be a challenge when inferring large scale patterns (Berteaux et al. 2017). Indeed, the large heterogeneity in lemming abundance s between sites as seen on Figure 1 may, in part, be due to differences in methodology. For instance, incidental observation series have considerably less 0 values than snap trapping series, and qualitative index series tend to have more regular cycles than quantitative series. This type of variation in data collection can also be problematic for long time series, as there can be an effect of shifting base line when assessing abundance, making it difficult to infer long-term trends. While all quantitative methods allow comparisons of dynamic patterns and trends, it remains difficult to compare abundance, which may be the most important parameter when studying various aspects of population dynamics such as the response of predators (Henden et al. 2010). Such considerations argue in favour of standardization of monitoring methods across sites. But, adoption of new protocols can also break long data series if data collected cannot be compared directly, speaking rather for harmonization of different protocols such as we do here/where … (see Berteaux et al 2017 for similar suggestion). To maintain long-term series and improve the monitoring method, old and new protocols should be run along each other for some time to establish correction factors between time series. This may be difficult to implement logistically, but can result in well assembled long time series, such as in Bylot or Karupelv (Gilg et al. 2006; Gauthier et al. 2013).

Other FEC attributes recommended by CBMP are less well covered by current monitoring programs, in particular health, genetic diversity and phenology. Parasites and diseases of lemmings have been studied at some sites (Table S2), but are usually not included into regular monitoring protocols. This can be seen as part of a general tendency to study parasites separately from food web oriented ecosystem research (Lafferty et al. 2008), to which most lemming monitoring programs belong. Genetic diversity is also usually addressed in one time studies looking at population structure or phylogeography (Ehrich et al. 2001), but is not surveyed regularly. Phenology, in particular timing of winter reproduction, is an important parameter to understand the impact of winter climate on lemming population dynamics. However, present monitoring methods such as discrete trapping sessions or winter nest count do not provide this information largely due to the logistical challenges of winter work as discussed above.

An ecosystem-based approach to monitoring, structured around explicit models for interactions between components and drivers of change, is recommended by the CBMP (Christensen et al. 2013), and applied in some of the initiatives providing lemming data (e.g, Varanger, Zackenberg;

Kommentoinut [L45]: Please remove. We do see any reason to give water to the mills of animal protection extremists. Besides, they do not accept live trapping, either. We cannot understand what ethical problems there can be with properly done snap trapping – at least as long as hunting is legal. Live trapping is, to our judgment, at least equally problematic as animals can suffer in traps, especially if there are many in the same trap, where they can become aggressive and injure or kill each other.

Moreover, live trapping is now really hard to conduct in the Nordic countries (at least in Norway), because the new law requires traps to be checked at intervals of 3 hrs. We can see the reason but the consequence is that we can forget about CRM in future long term studies, except as a short term effort, used for calibrating indices obtained by other methods

Kommentoinut [GSa46]: «used»?

Kommentoinut [L47]: or periodic simultanous use of labor intensive CRM methods and snap trapping methods, which allow coversion of snap trapping indices to real density estimates (Ruffino et al. 2016).

Kommentoinut [GSa48]: Would be very good to explain what we mean by harmonization of protocls (what we do here or more harmonizing how tha data is collected?)!!

Kommentoinut [GSa49]: I think it would be good to refer to other papers talking about the importance of harmonisation and suggest o cite Berteaux at al (2017) here.

Berteaux D., Thierry A.M., Alisauskas R., Angerbjörn A., Buchel E., Doronina L., Ehrich D., Eide N.E., Erlandsson R., Flagstad Ø., Fuglei E., Gilg O., Goltsman M., Henttonen H., Ims R.A., Killengreen S.T., Kondratyev A., Kruchenkova E., Kruckenberg H., Kulikova O., Landa A., Lang J., Menyushina I., Mikhnevich J., Niemimaa J., Norén K., Ollila T., Ovsyanikov N., Pokrovskaya L., Pokrovsky I., Rodnikova A., Roth J.D., Sabard B., Samelius G., Schmidt N.M., Sittler B., Sokolov A.A., Sokolova N.A. Stickney A., Unnsteinsdóttir E.R. and. White P.A. 2017. Harmonizing circumpolar monitoring of arctic fox: benefits, opportunities, challenges, and recommendations. Polar Research 36: sup 1, 2.

Kommentoinut [GSa50]: I assume that this is not harmonization of data as this can be done also when changing methods. Would be good to clarify a bit more here how harmonization differ from challenges when changing methods (i.e.we say a few sentences ago that changing methods is challengin and that we instead suggest harmonization). Maybe you mean that harmonization is the transition periods when using two methods to get the correction factors between methods?

Kommentoinut [GSa51]: I hate to nag but I really don't like abbreviations (probably because I am a bit slow and keep forgetting them but don't think I am alone and think that abreviations are helpful only for the writer – not the reader).

(Ims et al. 2013; Ims and Yoccoz 2017; Schmidt et al. 2017). Correlating trends in populations with ecological drivers is only possible if likely drivers of change are also measured at a relevant scale. In order to address how abiotic and biotic drivers influence lemming population dynamics and other FEC, monitoring projects should take an ecosystem-based approach and collect data about a selection of important state variables (Lindenmayer and Lichens 2009). Addressing the hypothesized importance of snow conditions for lemmings requires for instance some local data about snow, which is rarely done at current monitoring site.

Status and trends

The large heterogeneity in patterns of lemming dynamics observed here is in accordance with previous work. For example, the amplitude of lemming fluctuations often varies (Reid et al. 2013), and dynamics in some areas can look more like irregular outbreaks than typical population cycles (Ims et al. 2011, Oksanen et al. 2008). In addition, at least for Norwegian lemmings, non-stationary dynamics characterized by periods with regular cycles followed by periods with persistent low densities over a decade or more, have been reported (e.g. Finse, Joatka and ~~or~~ Laplandsky, Fig. 1; (Angerbjörn et al. 2001). Such transitions in dynamics have been related to climate change (Kausrud et al. 2008), but the relationship to a hypothesized climatic driver does not always appear obvious. This natural variability in lemming dynamics makes population trends inherently difficult to detect (McCain et al. 2016), in particular considering the modest length of most time series. The exception are abrupt changes in dynamics such as in NE Greenland (Karupelv and Zackenberg) or rapid declines such as in Erkuta. It is also reflected in the fact that almost none of the linear abundance trends over the last 25 years was statistically significant. This implies that our result of no overall trend in lemming populations across the circumpolar region needs to be considered cautiously (McCain et al. 2016).

Regionally, our results suggest that sub-arctic lemming populations outside Fennoscandia co-occurring with one or several species of voles showed a declining trend. This finding is in agreement with a predicted decline of specialized arctic species at the southern edge of their distribution (Loarie et al. 2009). In fact, voles have recently appeared in two sites (Churchill and Southeastern Taimyr) indicating a northward advance of these boreal species. It has been hypothesized that Norwegian lemmings at low altitudes may be exposed to apparent ~~indirect~~ competition (Holt 1977) from voles mediated by shared predators (Oksanen 1993). It is possible that a similar mechanism, together with an increase of generalist predators from adjacent boreal

Kommentoinut [GSa52]: This is all great but maybe this can be changed in light of the challenge that most studies (or at least a lot of them) monitor lemmings as a covariate to understand other things and understanding leming dynamics thus not the main objective – that in turn results in that the data is not ideal for evaluating how the numbers of lemming vary over time. As it is now I think we are a bit overly critical or unfair as it makes it sound that people that monitor lemmings at these sites are not doing a good job. I know that it is not what you mean but think it would be good to pitch the highlighted section in light of that the data is often not obtained with ambition to evaluate various aspects of lemming dynamics but to understand how variation in lemming abundance affect other biological processes.

Kommentoinut [L53]: O&al. covered many time series so the work is quite illustrative in this context

Kommentoinut [L54]: we had very low lemming catches from 1989 to 2005, even in the « lemming country » at high altitudes (500 – 600 m.a.s.l)

Kommentoinut [GSa55]: What if that is onlt a change from a period with regular cycles to periods with low densities as in Finse and Laplandsky)? Can we for sure say that it is a rapid decline (i.e. can web e certain that it did not change and go back to more regular cycles a few years later)?

Kommentoinut [GSa56]: I am not sure I follow, if we find that none of the sites showed a linera change (i.e. no increase or decreas over time), why then should our conclusion on there being no overal trend or indication of decline during the last 25 years being considered cautiosly? To me it is the opposite – almost none of the sites showed a linear trend which is a good indication that lemming numbers are not declining (or increasing) over the last 25 years! I am probably missing something though but that may be an indication to clarify this statement.

Kommentoinut [GSa57]: Maybe consider using a different transition – to me «at the same time» suggest something that goes against what we said in the previous sentence whereas what we say in the rest of this sentence follows what we talked about in the previous sentence. I therefore replaced this with «In fact, …».

Kommentoinut [L58]: the proper term is apparent competition areas (Reid et al. 1995; Killengreen et al. 2007), contributed to the observed declines in lemming populations at these sites. In addition, climate change may lead to more frequent melt and freeze events in winter (Sokolov et al. 2016), which have been hypothesized to be detrimental to the subniveal life of lemmings, but less so to voles (Kausrud et al. 2008; Ims et al. 2011; Berteaux et al. 2016). A climate-driven increased growth of meadows and tall shrubs (Myers-Smith et al. 2011; Elmendorf et al. 2012) at the detriment of more typical moss-graminoid and dwarf shrub tundra, which are the preferred habitats of arctic lemmings, may also contribute to vole expansion and lemming population decline.

The primarily oroartic populations of the Norwegian lemming did not show a similar negative trend, although they always occur together with several species of voles. This could be due to the fact that they live in mountainous areas, where they have the possibility to exploit altitudinal gradients in winter temperature and productivity (Oksanen 1993; Ims et al. 2011). Several of the monitored populations which were characterized by a large proportion of years without lemming captures may indeed be areas to which lemmings disperse only in peak years, while their permanent habitats might be at higher altitudes (Kalela ?), where harsh winters and scarce vegetation prevent voles from establishing.

CONCLUSIONS AND RECOMME0NDATIONS

Overall, the available time series for lemmings in the Arctic and sub-Arctic did not show any consistent population trend. Hence, at present the data do not support the contention that climate change so far negatively affects lemmings in general, but the low precision of the data limits the reliability of this conclusion. Negative trends were detected in low arctic populations co-occurring with one or several species of voles and, at the same time, voles also appeared for the fist time in some of these areas during our study period which is in accordance with predictions of a northward displacement of arctic specialist species (Loarie et al. 2009).

Considering the important environmental changes that are predicted to affect the Arctic in the near future and the critical importance of lemmings in the tundra food web (REF, Ims and Fuglei 2005), it is very important to continue and improve monitoring of this group as a whole. Based on the present review, we recommend harmonizing as far as possible the collection of abundance data at one site to obtain longer time series, but also to aim at circumpolar harmonization, making it easier to compare patterns across different regions (see Berteaux et al 2017 for similar suggestion). While

Kommentoinut [RA59]: I would recommend « alpine », instead of « oroarctic ».

Kommentoinut [GSa60]: What about skipping oroarctic and call it «mountainous sub-arctic» insetad(easier to understand as it describes what it is)? One reason I am suggesting this is that I got confused at first when reading this sentence as the previous paragraph talked about Norwegian lemmings in sub-arctic areas and I had forgotten what oroarctic areas was so had to go back and look at the definition again (which breaks the reading up and will likely be similar to most readers except for arctic people).

Kommentoinut [L61]: we (TO and LO) are quite insistent with the term « oroarctic ». Subarctic is a different thing, it refers to northern forests. The term « alpine » is inappropriate in the context of the altitudinal extensions of the tundra in northern areas such as Fennoscandia. These exensions have much more in common with the arctic than with truly alpine habitats see Virtanen et al. 2016. Alpine populations of lemmings do not exist; the domianting small herbivores of the alpine tundra are marmots and pikas. Notice that northern altitudinal extensions of the tundra are regarded as integral parts of the arctic tundra in all global biogeogeography systems known to us (e.g. Olson et al. 2001, various global biome maps of Prentice et al. and Kaplan et al.) it is also customary to pool corresponding altitudinal extensions of other zones (e.g. north, middle and south boreal) with the latitudinal zone in question).

Kommentoinut [GSa62]: I like it better to say that we did not find any evidence of a population decline over the last 25 years as we say in the abstract (more clear than no change in trend)!

Kommentoinut [GSa63]: We use sub-arctic and low arctic – better to be consistet and use only one term (I think sub-arctic is better).

Kommentoinut [GSa64]: DETAIL but probably good to say that these changes are predicted to occur.

Kommentoinut [GSa65]: «among sites», right? Or perhaps both within and among sites if harmonizing means gathering corrections factors when changing from one to another method.

Kommentoinut [GSa66]: Ahh, among sites as well. So perhaps shorten this to say «harmonizing methodology both withina and among sites».

continuing existing time series is a first priority, improving the spatial coverage of monitoring in underrepresented areas such as Russia, the Canadian Arctic archipelago, and the sub-Arctic regions, would be highly desirable. Considering that standardized incidental observations provide a comparable measure of abundance (REF) and can be easily implemented, this simple method is recommended for sites where more time-consuming methods can not be applied, at least in areas where only lemmings are present. To monitor species-rich low arctic communities, live and snap trapping can be used when possible.. The development of new non-invasive methods such as camera tunnels, which have the potential to provide year-round information including phenology of winter breeding, should also be continued (see REF). In addition to abundance, collection of data on potential drivers of change and on parasites/diseases should be encouraged (Christensen et al. 2013).

Kommentoinut [GSa67]: Again, syick to one term and I suggest sub-arctic.

Kommentoinut [GSa68]: Need a reference suporting this – use the one from above.

Kommentoinut [GSa69]: A bit redundant with earlier stuff and may not need to be repeated in the summary.

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Kommentoinut [DE70]: We name only the funding sources which supported our work with the review, otherwise it will be too much

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Kommentoinut [DE71]: Please add a small bioscetch

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Kommentoinut [GSa72]: DETAIL – that is my official address even if I am based in Sweden.

References: (There is still some fixing to do here – I will do it in the next round)

Kommentoinut [DE73]: We can have max 50 references, and the text of the references counts in the 6000 words we have for the manuscript – suggest rather to remove a few, than adding many

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Kommentoinut [RA74]: I added teh citation for Samelius and Alisauskas 2017, if you decide to keep it.

Table 2. List of lemming monitoring sites with the site number, site name, region and country indicated.

Site number and name	Region and country
1. Barrow Utgiagvik	Alaska, USA
2. Barrow	Alaska, USA
3. Komakuk	Yukon, Canada
4. Herschel Island	Yukon, Canada
5. Tuktuk	North-western Territories, Canada
6. Daring Lake	North-western Territories, Canada
7. Walker Bay	Nunavut, Canada
8. Karrak Lake	Nunavut, Canada
9. Churchill	Manitoba, Canada
10. Rankin Inlet	Nunavut, Canada
11. Aulavik	North-western Territories, Canada
12. Alert	Nunavut, Canada
13. Bylot Island	Nunavut, Canada
14. Igloolik	Nunavut, Canada
15. East Bay	Nunavut, Canada
16. Karupelv Valley	Greenland
17. Zackenberg	Greenland
18. Hochstetter Forland	Greenland
19. Møsvatn	Telemark, Norway
20. Finse	Hordaland, Norway
21. Helags	Jämtland, Sweden
22. Vålådalen-Ljungdalen	Jämtland, Sweden
23. Åmotsdalen	Trøndelag, Norway
24. Børgefjell TOV	Trøndelag?, Norway
25. Børgagfjäll	Västerbotten, Sweden
26. Børgefjell	Nordland, Norway
27. Ammarnäs	Västerbotten, Sweden
28. Vindelfjällen	Västerbotten, Sweden
29. Padjelanta	Norrbotten, Sweden
30. Stora Sjøfallet	Norrbotten, Sweden
31. Sitas	Norrbotten, Sweden
32. Abisko	Norrbotten, Sweden
33. Dividalen	Troms, Norway
34. Kilpisjärvi	Lapland, Finland
35. Joatka	Finnmark, Norway
36. Ifjord	Finnmark, Norway
37. Nordkyn Peninsula	Finnmark, Norway
38. Varanger Peninsula	Finnmark, Norway
39. Laplandskiy Zapovednik	Murmansk Obl., Russia
40. Nenetskiy	Nenetskiy AO, Russia
41. Erkuta	Yamal, Russia
42. Sabetta	Yamal, Russia
43. Belyi Island	Yamal, Russia
44. Meduza Bay	Taimyr, Russia
45. Mys Vostochnyi	Taimyr, Russia
46. South-eastern Taimyr	Taimyr, Russia
47. Jukarskoe	Yakutia, Russia
48. Chaun	Chukotka, Russia
49. Wrangel Island	Chukotka, Russia

A.

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Figure 1. Map showing time series of lemming numbers and the location of monitoring sites. The map shows the delimitations of the high Arctic, low Arctic and subarctic according to CAFF, and the oroarctic according to Virtanen et al. (2016). Numbers refer to the sites (see table S1) and symbols indicate small rodent community composition. Time series of annual variation in small rodent abundance estimates are presented for selected sites. Triangles on the maps represent lemmings (black for *Lemmus* and white for *Dicrostonyx*), circles represent data not identified to species such as winter nests, qualitative indices or incidental observations, whereas grey squares represent voles (all species pooled). The colour of the y-axis indicates the data type: black refers to individuals caught per 100 trap nights, light blue to density in individuals per ha (13, 16, 17), green to winter nest density in nests per ha (11), orange to incidental observations (number seen per observer-day, 1, or observer-hour, 15) and pink to qualitative indices. Smoothed trend lines for the total abundance of lemmings are shown in light blue. A. Circumpolar region. The grey square indicates the area covered by B. Fennoscandia.

Kommentoinut [GSa75]: Might not need this if saying «time series» in the first sentence.

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Figure 2. Length of time covered by lemming monitoring programs that have collected data after 2000. Sites are ordered according to site numbers given in Table S1 and Fig. 1. Colours refer to geographic regions: brown – North America west of the Mackenzie River; red – mainland North America east of the Mackenzie River; orange – Canadian Arctic Archipelago; green – Greenland; light blue – Fennoscandia including the Kola Peninsula; blue – Russia east of the White Sea. Thick lines indicate sites from which data were included in the status and trends analysis, whereas thin lines refer to sites from which data were not available. The dotted vertical line shows 1993 and highlights the start of the last 25 years which is the period for which trends were calculated.

Kommentoinut [GSa76]: Need to reparse this a bit (if no data available at all, the nit would not be included). I am guessing that you mean where data was to sparse to be included in the analyses.

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Figure 3. Number of sites where the the core attributes defined by CBMP for small mammals were or are monitored broken into whether data was collected All years, Most years, Some Years, or Never (following ESM Table S2).

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Figure 4. Methods used to assess lemming abundance. For each method the number of sites where it was or is used is plotted against whether data collection occured All years, Most years, Some Years, or Never following ESM table S).

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Figure 5. Boxplots of s-index values and the proportion of years with abundance estimates of 0 according to species (Dicro = *Dicrostonyx* spp.; Lem = *Lemmus* spp. except *L. lemmus*; Llem = *L. lemmus* and tot = two lemming species together) and to observation method (live = live trapping; nests = winter nest counts; obs = incidental observations; snap = snap trapping). Boxes represent the middle 50% of the data with the median. Whiskers extend to the extreme values.

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Figure 6. Predicted mean scaled linear trends of lemming abundance as estimated from linear models with 95% confidence intervals (units of standard deviation per year). Linear trends were analysed with respect to biogeographic zone (High Arctic, Low Arctic and Subarctic, including the oroarctic), species (Dicro = *Dicrostonyx* spp.; Lem = *Lemmus* spp. except *L. lemmus*; Llem = *L. lemmus* and tot = two lemming species together), region (Fen = Fennoscandia; Gre = Greenland; NAm = North-America; Rus = Russia east of the White Sea), and the community composition at each site (L = only one or two species of lemmings; N+V = *L. lemmus* and several species of voles; A+V = arctic lemmings and one or several species of voles; see ESM table S1 for details).

Kommentoinut [L77]: We think that oroarctic should be pooled with low arctic since it is the altitudinal extension of the low arctic zone and has quite similar vegetation, see Virtanen et al. 2016.

Kommentoinut [GSa78]: Where were the oroarctic (subarctic mountain regions) placed here – included in low arctic or excluded? Should clarify this here as the oroarctic has been talked about as its own region in the discussion.