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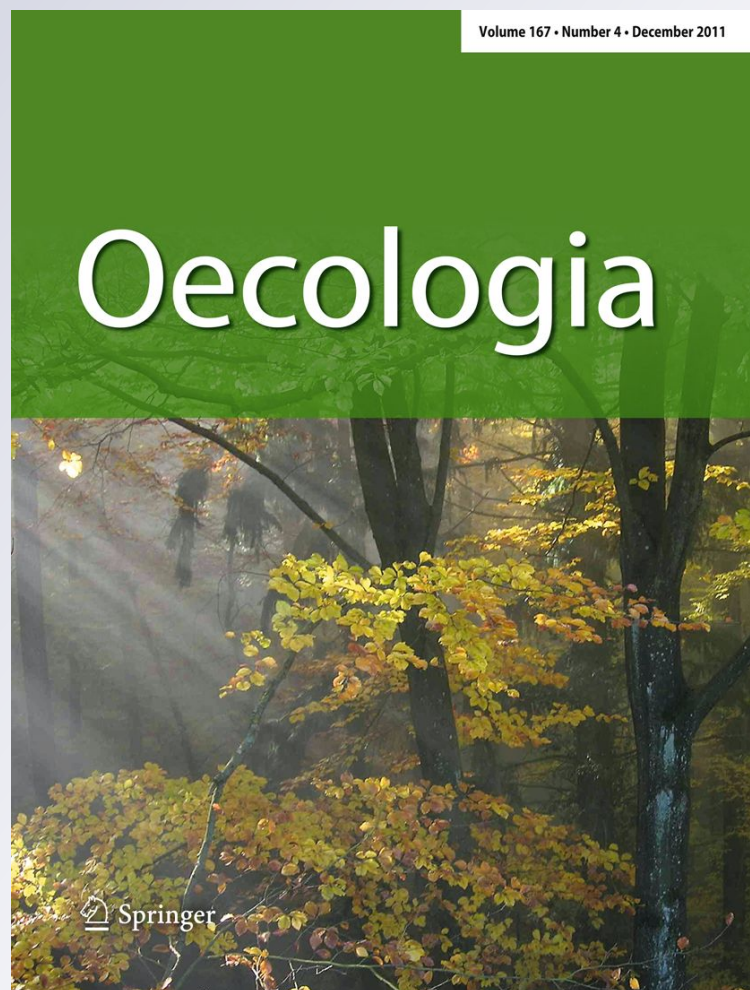Irina E. Menyushina, Dorothée Ehrich, John-André Henden, Rolf Anker Ims & Nikita G. Ovsyanikov

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The nature of lemming cycles on Wrangel: an island without small mustelids

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Abstract Lemming cycles are a key process in the functioning of tundra ecosystems. Although it is agreed that trophic interactions are important in causing the cycles, the actual mechanism is disputed. Some researchers attribute a major role to predation by small mustelids such as stoats and least weasels. Here we present a 40-year time series of lemming dynamics from Wrangel Island and show statistically that lemmings do exhibit population cycles in the absence of small mustelids. The observed density fluctuations differed, however, from those observed elsewhere, with long cycles and possibly higher densities of lemmings during the low phase. These differences in the shape of the population cycles may be related to the unique species assemblage of Wrangel Island, where arctic foxes are the only year-round resident lemming predator, and to the high diversity of landscapes, microclimatic conditions, and plants on the island. Both spectral analysis and wavelet analysis show a change in period length from five years in the 1970s to nearly eight years in the 1990s and 2000s. This change in dynamics coincides with reports of dampening or fading out of lemming cycles that have been observed in several regions of the Arctic in recent decades. As in the other cases, the changed lemming dynamics on Wrangel Island may be related to ground icing in winter, which could delay peak years.

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Introduction

Lemmings are a key species in tundra, and their characteristic population cycles are important for many processes in terrestrial arctic ecosystems (Ims and Fuglei 2005). The dynamics of lemmings are cyclic in most regions of the Arctic (Oksanen et al. 2008; Krebs 2011). However, one population with constantly low and stable densities has been described from northern Canada (Reid et al. 1995), and the regularity and frequency of lemming outbreaks is presently low in northern Fennoscandia (Ims et al. 2011). Population cycles in lemmings typically have a period of 3–5 years, but there are considerable spatial and temporal variations in cycle period (length) and amplitude (difference in the population density between low and peak years) (Angerbjorn et al. 2001; Krebs et al. 2002; Gilg et al. 2003; Gruyer et al. 2008; Kausrud et al. 2008). While many possible causes for lemming cycles have been suggested (Stenseth and Ims 1993), the main focus is on trophic interactions at present. According to classical models, specialist predators are dynamically strongly coupled to their prey. In particular, year-round resident specialist predators can cause population cycles in their small rodent prey by introducing delayed density dependence, whereas generalist or nomadic predators stabilize the prey's population dynamics, creating direct density dependence (Hanski et al. 1991, 2001). Considering northern small rodents, weasels and stoats are resident specialist predators (Andersson and Erlinge 1977) which hunt lemmings year round, following them into their tunnels under the snow in winter. They have been attributed a key role in generating small rodent cycles, particularly

those of Fennoscandian voles (Hanski et al. 1991), but also those of arctic lemmings (Sittler 1995; Gilg et al. 2003; Gauthier et al. 2009). They are considered essential for generating the characteristic low phase of the cycle, when voles or lemmings are virtually absent for one or more years (Boonstra et al. 1998). Other researchers think that plant–herbivore interactions cause the lemming cycles (Turchin et al. 2000; Oksanen et al. 2008) owing to the low plant productivity of tundra ecosystems, which cannot sustain a tritrophic food web. In this case, lemming crashes are expected to be steep and deep, owing to mass starvation after food resource depletion. The ongoing controversy over bottom-up and top-down processes is based on time series from only a few sites, most of which are rather short (Oksanen et al. 2008; Krebs 2011). The ecosystems in which these series have been observed differ in their geographic and climatic conditions, overall productivity, and food web structure, but represent only part of the variation present in lemming-dominated tundra ecosystems. Long time series from other parts of the circumpolar tundra region and from ecosystems with a different trophic structure are thus very valuable for obtaining a more complete understanding of the pattern present.

During the last few decades, small rodent dynamics, especially those involving some species of voles, have changed in several regions in Europe (Ims et al. 2008). Cycles have dampened or entirely collapsed, sometimes preceded by a period of change in length of the cycle (period lengthening or shortening; Ims et al. 2008). In the case of lemmings, a collapse of cycles was first reported from Fennoscandia (Kausrud et al. 2008). Moreover, lemming cycles have recently also disappeared from some areas in Greenland (Gilg et al. 2009). These changes are most likely due to changes in snow conditions during winter (Korslund and Steen 2006; Ims et al. 2008, 2011), and can have dramatic consequences for other species in the tundra ecosystem, particularly predators that depend on lemmings to reproduce, such as snowy owls (*Bubo scandiaca*) or arctic foxes (*Vulpes lagopus*) (Ims and Fuglei 2005). In order to better understand climate-related changes and their effects in the arctic ecosystem, it is important to analyze all available long-term data on lemming dynamics from different regions of the Arctic to cover the range of circumpolar variation in tundra food webs and climates.

Wrangel Island harbors a unique ecosystem characterized by particularly high biodiversity for the Arctic and several endemic species. However, the terrestrial food web comprising lemmings and their predators involves relatively few species. Several typical tundra predators, notably small mustelids and rough-legged buzzards (*Buteo lagopus*), are absent from the island. Nevertheless, other lemming predators can be numerous in some years. The whole island has been a nature reserve since 1976. It has a long

history of biological investigations and continuous data from the island on lemming dynamics have been available since 1971. However, lemming dynamics have so far only been discussed qualitatively (Travina 2002; Menyushina 2007), and earlier research has focused on the processes that generate lemming cycles (Chernyavsky and Tkachev 1982; Dorogoi 1987).

The aim of the work described in this paper was to statistically analyze the density fluctuations of lemmings on Wrangel Island over the last 40 years, combining new data with published data from earlier years. Our main objective was twofold: First, given the perceived importance of small mustelids in generating lemming cycles (Gilg et al. 2003), we aimed to assess what type of population dynamic pattern lemmings exhibit in an ecosystem without such predators. Second, given the long-term data available, we also assessed whether the population dynamics of lemmings on Wrangel Island have changed over the last few decades, as has been reported from other regions of the Arctic. We used modern statistical methods to describe the cyclical pattern of these populations and to document possible changes over the four decades covered by the data. The total time series consists of qualitative index values, which is not unusual for longer time series (Stenseth and Ims 1993; Steen et al. 1990; Angerbjorn et al. 2001), but quantitative data obtained from snap trapping and winter nest counts, and counts of active burrows exist for shorter time periods. The quantitative data were analyzed separately to validate the pattern shown by the qualitative data.

Materials and methods

Wrangel Island

Wrangel Island is a large island (7,608.7 km^2) situated in the far east of the Eurasian Arctic between the Chukchi Sea and the East-Siberian Sea, about 140 km north of the coast of Chukotka (Fig. 1). It is part of a vast continental shelf and was connected to mainland Beringia during the last ice age until about 10,000 years ago. The island was not glaciated during at least the whole of the last Pleistocene glaciation (Stauch and Gualtieri 2008) and was not flooded during late Pleistocene ocean transgressions (Bauch et al. 2001). It harbors a large diversity of landscapes. Mountains reach up to 1,096 m, cover about 70 % of the surface, and support a wide gradient of biotopes, including inland valleys with favorable microclimate. The northern part consists of a tundra plain with numerous lakes, marshes, and meandering river valleys. The climate is relatively continental, as the island lays in a zone of climatic collisions between continental air masses arriving from Siberia, Arctic air masses arriving from the Central Arctic Basin, and

Fig. 1 Map of the circumpolar area showing the location of Wrangel Island in the far east of the Eurasian Arctic (*black square*)

Pacific Ocean air masses that often invade the island as wet and warm cyclones (Svatkov 1970). The island belongs to bioclimatic zone B according to Walker et al. (2005). It is dominated by Rush/grass, forb, cryptogam tundra in the north, graminoid, prostrate dwarf shrub, forb tundra and prostrate dwarf shrub, herb tundra in the central and southern parts, and carbonate mountain complexes at higher altitudes (Walker et al. 2005). Biodiversity is exceptionally high for the Arctic (Gorodkov et al. 1987; Pulyaev 1988). A total of 417 species and subspecies of vascular plants, 31 species of spiders, 58 species of beetles, and 31 species of lepidopterans have for example been reported, including several endemic species. In addition, 62 species of birds breed on the island, among which 18 are common (Gorodkov et al. 1987).

Despite the high biodiversity on the island, its terrestrial mammalian fauna consists of only eight species. Four of them are long-time residents: Siberian lemmings (*Lemmus sibiricus portenkoi*), collared lemmings (*Dicrostonyx vinogradovi*), arctic foxes, and polar bears (*Ursus maritimus*). Reindeer (*Rangifer tarandus*) were introduced to the island around 1950 (Gruzdev and Sipko 2007a), and muskox (*Ovibos moschatus*) in 1975 (Gruzdev and Sipko 2007b). Following the establishment of ungulates, the island was colonized by wolverines (since the 1970s) and wolves (arrived for the first time in the late 1970s; were then eliminated in 1982–83, but they recolonized and settled in 2000). The red fox (*Vulpes vulpes*) has been observed as a rare visitor. The guild of lemming predators consists of three specialists—snowy owl, arctic fox, and pomarine skua (*Stercorarius pomarinus*)—the less specialized long-tailed

skua (*S. longicaudus*) and the generalists arctic skua (*S. parasiticus*) and glaucous gull (*Larus hyerboreus*). Despite being a lemming specialist in some parts of the Arctic, such as in Greenland and Scandinavia, long-tailed skuas are less specialized than pomarine skuas and snowy owls in the Siberian Arctic, and notably on Wrangel Island (Chernyavsky and Dorogoi 1988). Typical tundra species such as small mustelids (weasel and stoat) and rough-legged buzzards are absent from the island. This is also the case for ptarmigan (*Lagopus* spp.) and hare (*Lepus timidus*).

Lemming data

Systematic investigations of lemming dynamics on Wrangel Island started with the work of Chernyavsky and colleagues in 1972 (Chernyavsky 1979; Chernyavsky et al. 1981; Chernyavsky and Tkachev 1982). From 1972 to 1982, snap trapping was carried out every summer between June and September (Chernyavsky 1979; Chernyavsky and Tkachev 1982; Dorogoi 1987). Trapping was carried out in the area of Bukhta Somnitelnaya on the southern shore of the island from 1972 to 1975, and in the middle reaches of the River Neizvestnaya in the central part of the island from 1976 to 1982. Snap traps were set in lines at ~5 m intervals, on runways, or close to the entrances of lemming holes in several habitats favored by each species (Chernyavsky 1979). The data are reported as the total number of lemmings of each species trapped per month and year for all habitats combined, given the number of trap nights. The intensity of the trapping and the months in which trapping was carried out varied from year to year. As July is the only month in which trapping was carried out each year, we only used data from July (Fig. 2d). Trapping efforts in July varied between 100 (1981) and 8,300 (1974) trap nights (Dorogoi 1987). Snap trapping was also carried out in the southern and central parts of the island by staff from the nature reserve from 1981 to 1985 (Fig. 2b; Denisenko 1986; Travina 2002).

Some qualitative information on the period before 1972 is available in the literature. Referring to Belyaev and Shamurin (1967) and Chernyavsky (1969, 1979) writes that there were peak densities in 1966 and 1971 (Fig. 2f). Referring to a personal communication and data on the reproductive success of snowy owls (Litvin and Baranyuk 1989), Travina (2002) writes that densities peaked in 1970 and were already decreasing in 1971. Krechmar and Dorogoi (1981) and Dorogoi (1987), however, report that lemming numbers in 1971 were clearly higher than in 1970.

Based on these literature data and the field data of IEM and NGO, a qualitative time series spanning the period from 1971 to 2010 was assembled using an index from 0 to 6 that refers to total lemming densities (Table 1; Fig. 2f). Between 1980 and 1989, the values were based on visual
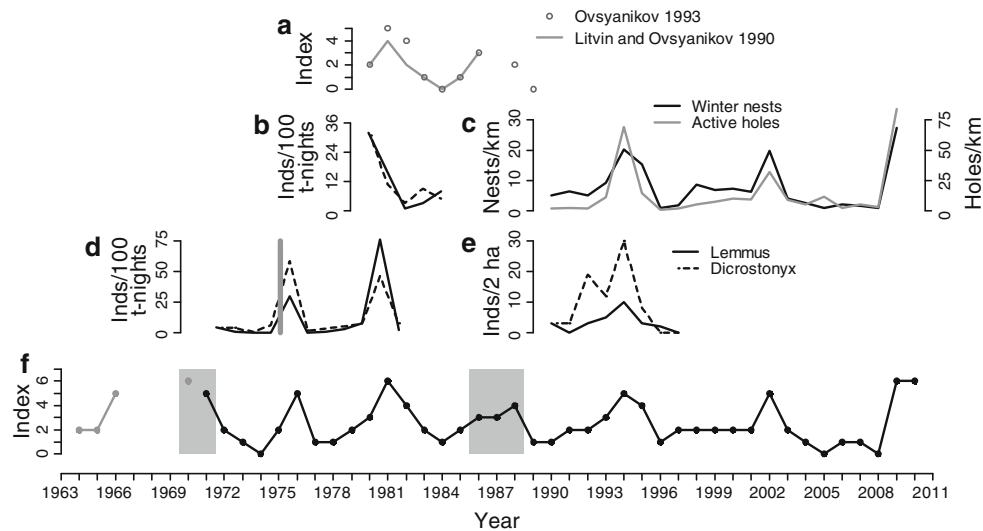
Fig. 2 Time series of lemming dynamics on Wrangel Island. **a** Two series of qualitative estimates using indices ranging from 0 to 4 (Litvin and Ovsyanikov 1990) and from 0 to 5 (Ovsyanikov 1993). **b** Data from snap trapping in the southern part of the island (Denisenko 1986; Travina 2002). **c** Winter nest counts and counts of active lemming burrows. **d** Data from snap trapping (Chernyavsky and Tkachev 1982; Dorogoi 1987). The *vertical line* marks the change in trapping locality from Bukhta Somnitelnaya to the middle reaches of the Neizvestnaya River. **e** Live trapping data (Travina 2002). **f** Qualitative time series using an index ranging from 0 to 6. The *gray boxes* mark years where there were discrepancies in the dynamics between different sources (see main text)

Table 1 Description of the qualitative index how it relates to quantitative observations of lemming presence and activity

Qualitative index value	Corresponding quantitative parameters	Description
0	Lemming observations: a total of 1–2 per 3 month Lemming winter nests: 1–2 per km Active lemming burrows: 1–2 per km Lemmings per snowy owl nest: 0	Depression
1	Lemming observations: 0–0.1 per km Lemming winter nests: 2–6 per km Active lemming burrows: 2–5 per km Lemmings per snowy owl nest: 0.5–0.6	Very low
2	Lemming observations: 0–1 per km Lemming winter nests: 4–9 per km Active lemming burrows: 2–8 per km Lemmings per snowy owl nest: 0.5–0.8	Low
3	Lemming observations: 0–5 per km Lemming winter nests: 7–9 per km Active lemming burrows: 10–11 per km Lemmings per snowy owl nest: 0.6–0.8	Medium
4	Lemming observations: 3–8 per km Lemming winter nests: 20 per km Active lemming burrows: 40–70 per km Lemmings per snowy owl nest: 1.0–1.3	High
5	Lemming observations: >10 per km Lemming winter nests: >20 per km Active lemming burrows: >70 per km Lemmings per snowy owl nest: >5	Very high
6	Lemming observations: >20 per km Lemming winter nests: >25 per km Active lemming burrows : >100 per km Lemmings per snowy owl nest: >10	Exceptionally high

These observations have only been carried out systematically since 1990. If not indicated otherwise, winter nests, active burrows, and lemming observations are reported per km of 10-m-wide line transects

estimations of lemming abundance and on detailed studies of the reproduction of arctic foxes by NGO and IEM (except for 1987, for which literature data were used).

Starting from 1990, the index is based on counts of winter nests and active burrows along line transects, as well as on the number of lemmings found in snowy owl nests and a

general evaluation of the situation of the ecosystem in a particular year (Menyushina 2007, 2011). For the period preceding 1980, the index is based on literature data, as detailed above.

For the sake of completeness, we also assembled all other data published on lemming densities on Wrangel Island during the study period. Qualitative data in the form of index values based on visual evaluations of lemming abundance are available from Litvin and Ovsyanikov (1990) for the years 1980 to 1986 and from Ovsyanikov (1993) for the years 1980 to 1989 (except 1987; Fig 2a). In addition, lemming dynamics from 1980 to 1987 are described qualitatively by Litvin and Baranyuk (1989). Moreover, live trapping of lemmings was carried out on the island in the years 1990–1997 (Travina 2002; Fig. 2e).

From 1990 to 2010, lemming abundance in winter was monitored by counting winter nests along line transects. Counts were performed in a permanent study area in the upper reaches of the River Neizvestnaya, in the center of the island. Line transects were 10 m wide and covered on average 25.9 km each year (range 9–61 km). They crossed all habitat types present in the area and slopes with different exposures (Menyushina 2007, 2011). Active lemming burrows were counted on similar transects (mean length per year 8.5 km, range 5–13 km) to obtain an indicator of lemming abundance in summer (Fig. 2c). On Wrangel Island, according to our observations, both species of lemmings use burrows in summer.

The qualitative data and the winter nest and active burrow counts do not distinguish between the lemming species. Therefore, our analyses explored the dynamics of both species together. We do not focus on the biology of the individual species here, but instead investigate the role of lemmings as a key species in the dynamics of the terrestrial tundra food web, so pooling the species seems an adequate approach considering the questions asked. On Wrangel Island, both species can reach very high densities, and neither is systematically dominant. Indeed, sympatric lemming species or voles often fluctuate in synchrony in a particular locality (Stenseth and Ims 1993; Krebs 2011).

Statistical analysis

We used spectral analysis (Kendall et al. 1998) to determine whether the time series showed a pattern of population cycles and to estimate the cycle length. Spectral analysis was applied to four quantitative series: the trapping data for each of the two lemming species (Chernyavsky and Tkachev 1982; Dorogoi 1987), winter nests (Menyushina 2011), and active burrows (Fig. 2c). The periodograms were calculated using a fast Fourier transformation as implemented in the function spec.pgram in R (R Development Core Team 2011). Because the series were relatively

short, zeros were added to the end (option pad = 0.2 in the function spec.pgram). The length of the cycle was determined as the location of the dominant spectral peak. In order to detect possible changes in the cycle length over the study period, we carried out spectral analysis of the qualitative series using a sliding window of 16 years with the default settings of the function spec.pgram. The window size was chosen so as to encompass at least two cycles in all parts of the time series. The locations of the dominant spectral peaks were then plotted against time.

To further assess whether the dominant period of the fluctuations changed with time, the qualitative time series was subjected to wavelet analysis. Wavelet analysis employs timescale and/or time–frequency signal decomposition (Torrence and Compo 1998), and it has been shown to be an ideal tool for detecting changes in ecological time series, as it has been developed to deal with time series with varying signal periods and the nonstationary, aperiodic, and noisy signals often found in ecological time series (Torrence and Compo 1998; Saitoh et al. 2006; Cazelles et al. 2008; Brommer et al. 2010). Wavelet analysis was performed using the continuous wavelet transform (CWT), function *wt* (provided by Aslak Grinsted at http://www.pol.ac.uk/home/research/waveletcoherence/), implemented in MATLAB R2010b (The Mathworks Inc. 2010).

Results

The assembled qualitative time series and the shorter quantitative series all showed clear multiannual fluctuations (Fig. 2). The trapping data showed that the difference in abundance between the two lemming species was not very pronounced and that they generally fluctuated in synchrony (Fig. 2d). Only the live-trapping data from Travina (2002) showed a certain degree of asynchrony between the species in 1992 (Fig. 2e).

For the trapping data covering the years 1972–1982 (Fig. 2d), the spectral analysis resulted in a dominant spectral peak at a frequency of 0.2 in both species. Thus, during that period, the cycle length was five years and the abundance of the two species fluctuated according to a similar pattern. Analyzing the winter nest counts for the period 1990–2009 (Fig. 2c) resulted in a dominant spectral peak at a frequency of 0.125, corresponding to a period of eight years. A similar cycle length was determined from the counts of active burrows (dominant spectral peak at a frequency of 0.125).

Wavelet analysis of the 40-year qualitative time series (Fig. 3) clearly documented a significant cyclic signal throughout most of the period, as well as a gradual change in period length from about five years in the beginning to approximately eight at the end. This change in periodicity
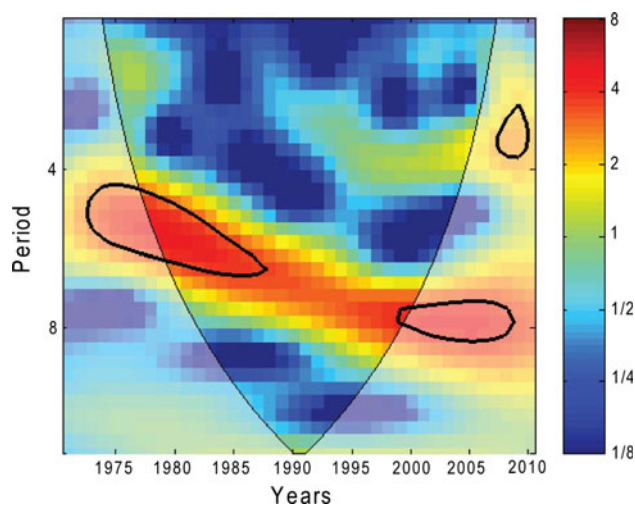
Fig. 3 The normalized wavelet power spectrum for the time series showing the statistical significance of the change in periodicity. The likelihood of the power spectrum increases from *blue* to *red*. The *black contour line* encloses the region with >95 % confidence, thus showing a significant approximate five-year periodicity at the beginning of the series that gradually changes to an eight-year periodicity at the end of the series. The *shaded* (*v-shaped*) envelope indicates the cone of influence. Outside this cone, interpretations are uncertain, because the inferences are weaker at the end and start of the time series
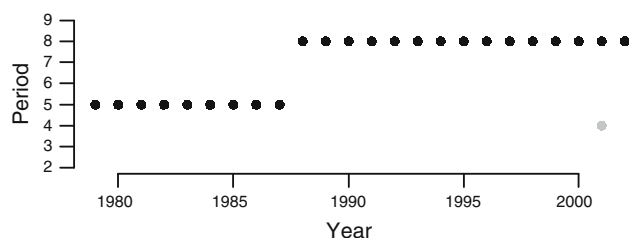

Fig. 4 Temporal changes in the periodicity of the lemming cycles on Wrangel Island based on analyses of a 16-year window. The period determined by spectral analysis is plotted against the midpoint of the time window. The *gray point* indicates that a period of four years was equally well supported by the spectral analysis for this particular time window

was further confirmed by the spectral analysis of the qualitative series (Fig. 4). The spectral analysis showed—more coarsely than the wavelet analysis—that the time series retained its cyclic nature throughout the entire study period, albeit with a sharp switch in cycle period length from about five to eight years in the early to mid 1990s. Note that in the second last time window of the spectral analysis (i.e., 1993–2009), there were two equally dominant spectral peaks in the spectral periodogram: one equivalent to a four-year period (Fig. 4; gray point) and one equivalent to an eight-year period. The spectral peak representing the four-year periodicity arises due to the small increase in 2006–07; i.e., it created two seemingly "four-year" cycles between 2002 and 2009.

Discussion

We found statistical evidence for cyclicity in multi-annual population fluctuations in the lemmings on Wrangel Island over the last 40 years. We have thus demonstrated that lemming populations can also cycle in the absence of small mustelid predators such as stoats or weasels, as had previously been reported based on a much shorter time series (Chernyavsky and Tkachev 1982; Boonstra et al. 1998). However, the assembled data also show that the dynamics of lemmings on Wrangel Island differ from those observed in other regions of the Arctic. In addition to particularly long periods, the lemming cycles on Wrangel seem to be characterized by a relatively high number of years with intermediate densities, in particular after 1990. Such years are rarely observed in other cyclic lemming populations (Turchin et al. 2000; Pitelka and Batzli 2007; Kausrud et al. 2008; Oksanen et al. 2008; Gilg et al. 2009; Ims et al. 2011).

Recently, Krebs (2011) pointed out that lemming peak densities may differ vastly between different regions of the Arctic, and that the importance of such differences has been underrated in the literature. Except for some estimates obtained by exhaustive snap trapping on open plots (up to 245 collared lemmings per ha and up to 308 Siberian lemmings per ha; Chernyavsky and Tkachev 1982), the data from Wrangel Island provide little information about the absolute density of lemmings. However, both the available trapping data and information about snowy owl breeding suggest that lemming densities are relatively high on Wrangel Island compared to other regions in the Arctic. The trapping data reported by Chernyavsky and Tkachev (1982) and Dorogoi (1987) indicate high lemming abundances, at least locally; compared, for instance, to the central Canadian Arctic (Krebs 2011) or Bylot Island (Gruyer et al. 2008), where indices were considerably lower. Trapping indices were, however, not higher on Wrangel Island than what has been reported for several sites in Eurasia (Oksanen et al. 2008). Densities per ha estimated by Travina (2002; Fig. 2e) were of the same order of magnitude as those reported from the central Canadian Arctic by Wilson et al. (1999), and somewhat higher than in eastern Greenland (Gilg et al. 2009). The exceptional regularity of snowy owl breeding on Wrangel Island also supports the conclusion that lemming densities are higher, or that years of low lemming densities are rarer, than in other regions of the Arctic. From 1980 to 2006, snowy owls bred on the island every year except in 1989, 1996, and 2005 (Menyushina 2007, 2011). The average number of fledglings per pair was 2.2 (SD 1.5) for the years 1990 to 2006 (no data for 1997). In other areas of the Arctic, snowy owls breed only in years with relatively high lemming densities (three out of ten years on Bylot Island (Gauthier et al. 2004); five out of

fifteen years in eastern Greenland (Gilg et al. 2006); several sites in the Russian Arctic (Volkov et al. 2005). Also, arctic foxes breed successfully during most years on Wrangel Island, although litter sizes fluctuate in close correlation with lemming abundance (Menyushina 2011).

Although the data presented here clearly show that lemming populations also cycle in the absence of small mustelids, it is tempting to relate the specificities of the lemming dynamics on Wrangel to the composition of the predator guild on the island. In the absence of small mustelids, arctic foxes are the only lemming predators that are regularly present during winter when little alternative prey are available (no ptarmigan and no hares). Foxes that remain on the island feed mostly on lemmings, but cached eggs (Careau et al. 2008) and carrion represent additional resources. In years with low lemming densities, the foxes leave the island in fall and in winter. Due to the richness of the surrounding marine habitat, it is likely that they can stay close to the island. Therefore, they can return early to their tundra territories and start to predate on lemmings early in spring. Arctic foxes are thus an important predator—maybe more so than in other areas of the Arctic—but not a true specialist, which may be important for the dynamics observed on Wrangel. In particular, arctic foxes are not as effective as small mustelids at hunting lemmings in winter, and may allow them to retain higher densities and to avoid the steep population crashes typical of other regions (e.g., in Finse; Kausrud et al. 2008). Regulating mechanisms other than predation may, however, determine the dynamics of lemmings on the island. Attributing them to interactions with the food plants (Oksanen et al. 2008) would point to another hypothesis for the possibly high average densities. They could be related to the high diversity in habitats and microrelief, which provides the lemmings with good feeding opportunities in most winters. Indeed, the Wrangel time series do not indicate that a rapid and strong depletion of food resources takes place, as the population crashes appears to be more gradual and shallow in the Wrangel populations than in most other lemming populations (Oksanen et al. 2008).

Over the 40 years of study, the period of the lemming cycles on Wrangel Island increased from about five to eight years. The results of the spectral analysis clearly revealed a lengthening of the cycle period in the time span covered by the study. Wavelet analysis showed the same pattern, although the wavelet power was not significant in the middle of the series during the time of the shift in period length (Fig. 3). Although the main analyses are based on qualitative index data, both the five-year cycle in the 1970s and the more recent eight-year cycle were also apparent in the quantitative time series (snap trapping, winter nests, and active burrow counts). The change in dynamics thus coincides with a change in observation methods. However,

because lemming cycles are an obvious phenomenon that have a considerable influence on many conspicuous components of the tundra ecosystem (in particular the guild of lemming predators), we are confident that the different observation methods used over the 40 years were equally able to reflect the main pattern of the fluctuations. A period of eight years is the longest period that has ever been reported for lemming cycles, which typically have a period of 3–5 years (Krebs 2011; Stenseth and Ims 1993).

Population cycles of small rodents have been reported to change and fade out in several boreal and Arctic regions over the last few decades (Hörnfeldt 2004; Ims et al. 2008; Gilg et al. 2009). A lengthening of the period, together with a weakening of the delayed density dependence has been observed for field voles in Scotland (Bierman et al. 2006). There it preceded the collapse of the cycles and was related to shorter winters. Changes in rodent population dynamics have also been related to climate change in winter and changing snow conditions in other regions (Kausrud et al. 2008; Gilg et al. 2009; Ims et al. 2008, 2011). However, as yet, the scarcity of long time series has restricted the assessment of effects of climate change on lemming dynamics to only a few localities within the Arctic region. On Wrangel Island, effects of climate change have been observed since the end of the 1990s. The frost-free season has increased by about one month, and sea ice forms later. Warm spells in winter followed by icing have become more common. Icing on the ground was observed in winter 2003–2004 and to a much larger extent in the following winter, when it caused a major crash in the reindeer population (Gruzdev and Sipko 2007a). In fall 2007, strong rain was followed by freezing, leading again to extensive icing. As lemming populations seem to be dependent on stable winter conditions to reproduce and reach peak densities (Ims et al. 2011), such icing events may delay peaks by preventing growth and thus lead to a longer period. Visual inspection of the shape of the qualitative series may indicate that populations did indeed start to grow in 1991 or 2006–2007, but the increase stopped, possibly because of unfavorable winter conditions. If such climatic events prevent an increase in the lemming population, the coupling between the lemmings and their predators, in particular the arctic fox, may be weakened, because the lemming population may be kept below the threshold where the predator population responds numerically (Ims et al. 2008). However, the last two years, when lemming densities peaked in two successive summers, provide hope that the cycles on Wrangel are not close to fading out.

Although the change in lemming dynamics coincided with observed changes in winter weather on Wrangel Island and climate-related fading of small rodent cycles in other parts of the Arctic, it is important to keep in mind that short-term alterations in cycle characteristics may result

from transient dynamics of nonlinear food web interactions. This has been shown by mathematical models and experimental work on simple laboratory model systems (Hastings 2004), and has been proposed as an explanation for periods of acyclic dynamics in boreal rodents (Hanski and Henttonen 1996; Brommer et al. 2010). We cannot therefore firmly exclude alternative explanations to climate-induced change based on the data available from Wrangel Island.

Conclusions

To the best of our knowledge, we have here for the first time demonstrated statistically that lemmings exhibit population cycles in the absence of small mustelids. However, the cycles on Wrangel Island are perhaps characterized by a higher frequency of years with intermediate densities compared to other regions in the Arctic. This is likely to be related to the different structure of the predator guild in combination with a complex of factors that make the island habitats favorable/optimal for lemmings, such as high plant diversity and productivity, high diversity of landscape, and microclimatic conditions. In the first part of the 40-year time series the cycles had a period and population density levels that are not unusual considering what has been found in other regions of the Arctic. Towards the latter half of the period analyzed, the original five-year cycle drifted into an era with exceptionally long periods between the peaks, most likely indicating a loss of intermittent peaks. Thus, it appears that lemmings on Wrangel Island have been subjected to changes similar to those recently demonstrated for lemmings and voles in other boreal and arctic regions.

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