Lemming density in Taimyr tundra and its influence on reproduction of birds

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Densities of Siberian Lemming *Lemmus sibiricus* and Collared Lemming *Dicrostonyx torquatus* have been studied for about thirty years on the Taimyr peninsula. There have been no previous summaries of long-term data on fluctuations in lemming density on the Taimyr in the different tundra subzones. A two-way correlation shows that the most dissimilar cycles occur in the arctic and southern tundra subzones (r=0.75). Differences between these two subzones and the typical tundra are also comparatively large (r=0.87). Lemming density cycles in western and eastern parts of typical tundra strongly correlated (r=0.92). Lack of cycles of longer than four years duration results in intensive migration exchange between different lemming populations. Migrants are probably the source of the increase in lemming density in the arctic tundra. Three regions can be distinguished on the Taimyr, characterized by differences in the structure and duration of their lemming cycles. In areas where there is a close correlation between predators and lemmings an increase in lemming density usually starts in the most successful breeding year for birds. This is the year before peak lemming numbers. A lack of synchronicity in the start of the increase in lemming numbers in different areas, and a gradual increase in densities, results in generally better breeding success of tundra birds in lemming peak years on the Taimyr.

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Плотность сибирского *Lemmus sibiricus* и кольчатого *Dicrostonyx torquatus* леммингов изучается на Таймырском полуострове около 30 лет. До настоящего времени не было опубликовано сводок долгосрочных данных по колебаниям плотности леммингов на Таймыре в различных тундровых подзонах. Двусторонней корреляцией показано, что самые несходные циклы встречаются в арктической и южной тундровых подзонах (r=0.75). Различия между этими двумя подзонами и типической тундрой также сравнительно велики (r=0.87). Циклы плотности в западной и восточной частях типической тундры демонстрируют сильную корреляцию (r=0.92). Отсутствие циклов длительностью больше четырех лет ведет к интенсивным миграционным обменам между различными популяциями леммингов. Увеличение численности леммингов в арктической тундре происходит, вероятно, за счет мигрантов. На Таймыре возможно различить три района, характеризующиеся разными структурами и длительностью циклов леммингов. В районах, в которых существует тесная корреляция между хищниками и леммингами, увеличение плотности леммингов обычно начинается в самом удачном году для размножения птиц, т.е. в году перед пиком численности леммингов. Отсутствие синхронности в начале роста численности леммингов в различных районах и постепенное увеличение плотности обычно ведут к более успешному гнездованию тундровых птиц в годы обилия леммингов.

Introduction

Changes in lemming density have been studied for about thirty years on the Taimyr peninsula. These data are used for predicting when to hunt Arctic Fox *Alopex lagopus* and bird breeding success. However, there have been no attempts to summarise these long-term data and to compare the periodicity of changes in lemming densities in different tundra subzones of the Taimyr. Knowledge of these cycles is important for a better understanding of how the lemming cycles influence the density of predators and the consequences for breeding birds.

Data from the archives of the Institute of Extreme Northern Agriculture in Norilsk were used for this analysis as well as personal observations on the Taimyr between 1990-1993. These data were collected by many different methods. Therefore it is necessary to review and compare all the methods of obtaining data on lemming densities used in Russian tundras to set the context for their interpretation.

Methods

Principal methods used to determine lemming density

There are two groups of methods used to determine lemming density: methods of absolute calculation and methods of relative calculation. The first generates data about the rodents' presence in numbers per hectare. The other provides data on the number of animals per 100 trapping days (td) or 100 cone days (cd).

Absolute calculation methods

Density calculations are made by catching lemmings by hand or with dog on a 0.25 ha study plot. This method was described by Romanov & Dubrovsky (1937) for the purpose of forecasting Arctic Fox densities. Usually it was used with other methods such as transect observations in the area. All holes in a plot are dug by hand or with a specially trained dog. Out of all the absolute calculation methods this one is the most inaccurate, with an estimated error of 20%.

Absolute calculation in closed plots. There are a lot of variations in the use of this method by Russian and foreign researchers. The principle idea is the use of a 0.25 ha plot fenced in with plastic. The plastic is buried as deep as the permafrost and rises 40-50 cm above the ground. The area is divided in 5 x 5 m squares and 100 traps are placed on the ground, each 5 m apart. All lemmings in the plot are caught over a period of 10-15 days. This method, like the previous one, is comparatively difficult and time-consuming.

Absolute calculation in open plots. The originators of this method (Tupikova & Emel'yanova 1975) recommend it because of its simplicity and the possibility it gives for widescale, rapid, density assessments. As in previous methods, 0.25 ha plots are used. As densely as possible 400 traps are put on the ground near holes and, if possible, on all trails. The data can be considered to be reliable when the number of trapped lemmings decreases sharply after the first or second day. In this case after three or four days (the usual period of catching on the plot) the number of caught lemmings on the plot is the same as the number of migrants entering the plot. Apart from economy of time, this method allows other studies because lemmings are mainly caught near their nest holes.

Relative calculation methods

These methods have been used for about 50 years and it is not clear who was the first to use them. Considerable work concerning quantitative methods for the field study of animals began in the different biological institutions of the former USSR in the late 1930s. Some results and instructions were published in the mid 1940s (Formozov 1952). Two relative calculation methods have particularly been used on the Taimyr.

Density calculation with trap-lines. "Break-back" traps of various kinds are used. The traps are put on the ground in a straight line at a distance apart of 5m., but may be changed by ±1 m to give a better trap position near a lemmings' hole or a track. The direction of the line is fixed, except when the configuration of the studied habitat is narrow and winding (*e.g.* stream valleys). The number of traps in a line has to be divisable by 25. The optimal working time for one line is four days. The number of trap-lines in a certain type of habitat is determined by the size and significance of it for lemmings. The aim is to obtain a number of trapped animals per 100 trap days for a specific type of habitat. This is considered to be the "available lemming population".

Density calculation with capturing cones. Metal cones to trap lemmings are put in the ground on the main trails of animals. Sometimes, when there is no system of trails visible or there are a lot of migrants, the cones are connected by a ditch (5-6 cm deep). The length of the ditch can vary, but as a rule, one cone needs 10 m of ditch. The number of ditches in the habitat is determined as for density calculation with trap lines. The aim is to obtain the number of trapped lemmings per 100 cone-days. Unlike the first method, the majority of lemmings caught this way are migrants.

Range of densities

All the data collected on Taimyr since 1960 given in this paper use the scale of estimated lemming densities developed in the Institute of Extreme Northern Agriculture (Kuksov 1975) :

1) Extreme low density. There are no lemmings trapped in 100 td. Predators do not breed. Seagulls concentrated on large waterbodies.

2) Low density. Less than 3 lemmings/100 td. Predators do not breed.

3) Average density. Less than 10 animals/100 td. Rodents inhabit only perfect habitats. Density per hectare is about 70-80 animals. Predators breed rarely and their brood size is small.

4) High density. Relative density is about 30 lemmings/100 td. Absolute density is 170-200 animals per hectare in perfect habitats. Occupation of Arctic Fox dens is high, all predators breed successfully.

5) Very high density. This is usually a seasonal peak at the end of the summer breeding season. More rarely it is a result of two consecutive good years.

Availability in perfect habitats increases to 80 animals/100 td. Predators breed in high densities, brood sizes are higher than usual.

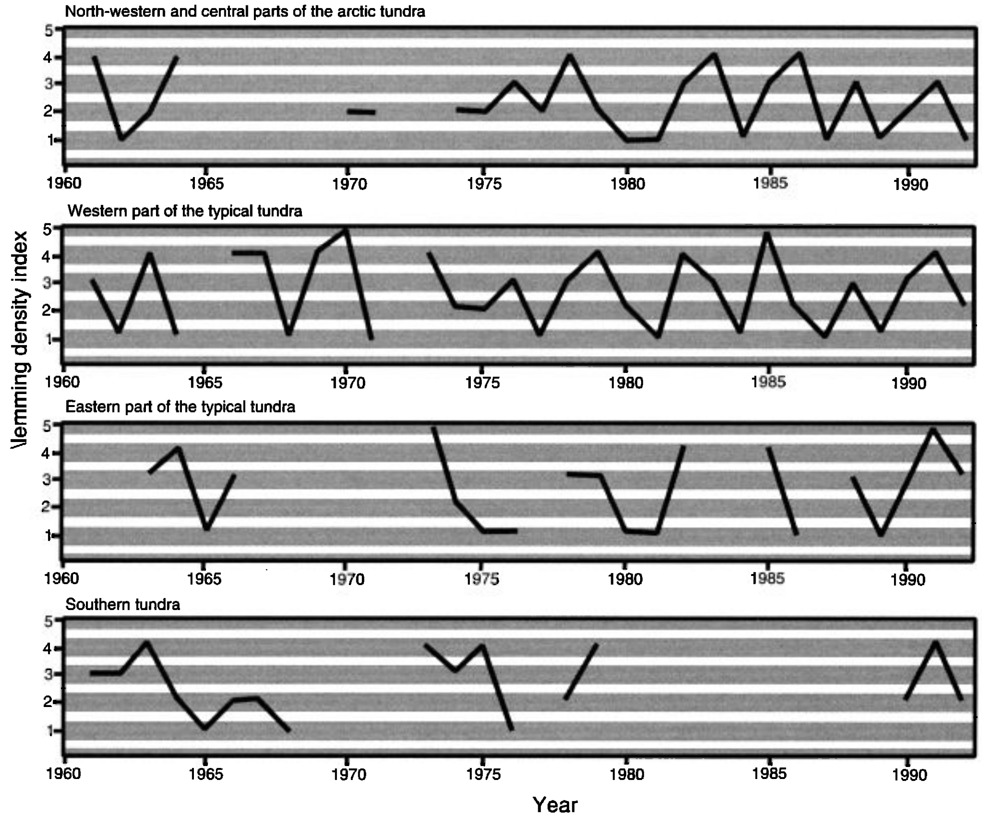

Figure 1. Lemming density variation in different subzones of the Taimyr tundra. The lemming density index (for further details see text) is:1. extremely low density; 2. low density; 3. average density; 4. high density; 5. very high density.

Lemming densities in different parts of Taimyr

Data on the variations in lemming density in the different subzones of Taimyr (zonation according to Chernov 1985) are shown in Figure 1. The data are not complete, but there are obvious differences in the structure and duration of lemming cycles in different regions.

Two-way correlations show that the most dissimilar cycles occur in arctic and southern tundra (r=0.75). The difference between these two subzones and typical tundra is also comparatively large (r=0.87). Cycles in the western and eastern parts of the typical tundra are very similarly timed (r=0.92).

An autocorrelation-test (Figure 2) shows that, in general, a three-year cycle of lemming density

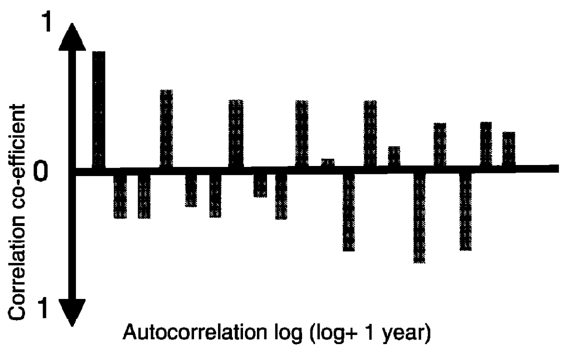

Figure 2. Autocorrelation function of average lemming density fluctuation in Taimyr.

occurs on the Taimyr peninsula. Analysis of average data from 16 cycles on Taimyr over 30 years has shown that four four-year cycles, ten three-year and two two-year cycles occurred. Mathematical models of lemming populations show that there are no cycles longer than four years in groups of populations where there is active migratory exchange (Benenson 1982). It can be seen from Figure 1 that in the arctic tundra a population has lower peaks than in the typical tundra and an increase in lemming density over two years is more usual. This is because in the Arctic the influence of climate on an unstable population is high (Cherniavsky & Tkachov 1980) and a population cannot restore itself. Migrants contribute to increases in lemming density in the arctic tundra. This explains the absence of high peaks there and a longer period of increase.

Our observations on Taimyr during recent years demonstrate the lemming migration exchange between typical and arctic tundras. In summer 1990, the lemming density in upper Pura River, Western Taimyr (72°55'N, 86°40'E) was rather high. At the same time the density on Eastern Taimyr was low: in the arctic tundra that year less then 10 animals were trapped during a month near the mouth of Pyasina River (74°06'N, 86°50'E) (M. Rykhlikova pers. comm.) and no lemmings were found near the mouth of Lower Taimyra River (76°04'N, 98°32'E). In 1991 lemming density increased to a peak in the typical tundra, but the increase stopped in the western and southern part of subzone in spring. In the north-western part of

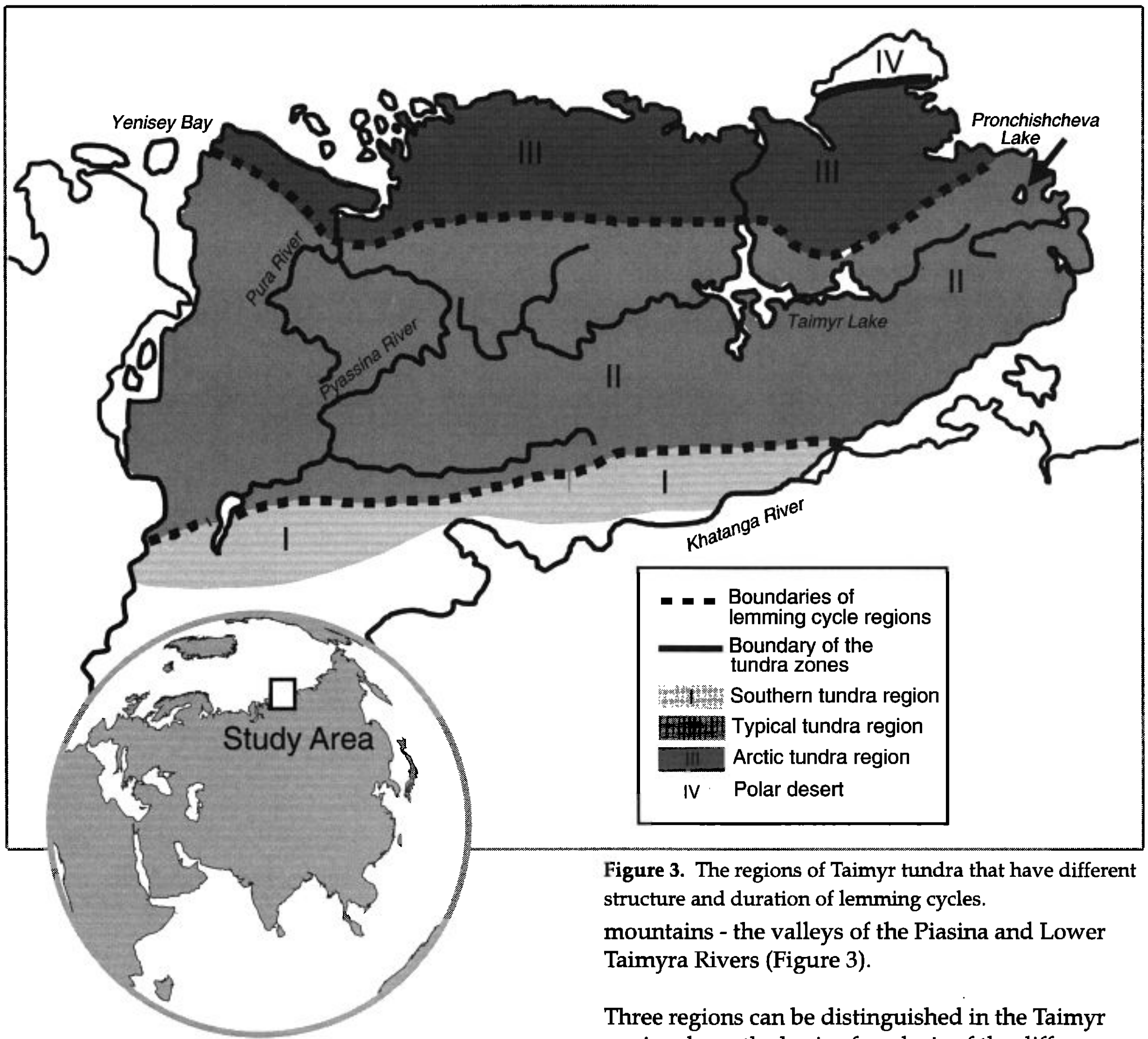

Figure 3. The regions of Taimyr tundra that have different structure and duration of lemming cycles.

the arctic tundra the density of lemmings was average until the spring of 1991, but the cold and damp spring of that year concentrated animals on snow-free patches where many of them were depredated. The density then fell to a low level and did not increase until the beginning of August (M. Rykhlikova unpubl.). Near the Lower Taimyra River mouth the density of lemmings increased slowly during the entire summer to an above average level (P. Tomkovich pers. comm.). The same increase took place in the north-eastern part of the typical tundra near Pronchishcheva Lake (75°16'N, 112°28'E) but the density was much higher. At the same time a team led by P. Prokosch saw no lemmings at all during the summers of 1990 and 1991 working in the area of Cape Sterlegov (75°25'N, 89°15'E) (on shore between the Piasina and the Lower Taimyra Rivers).

Kuksov (1975) noted that the lemming density in typical tundra does not increase uniformly. It begins to increase in some regions of the typical tundra and is followed by the occupation of a great variety of habitats to a very high density. In this situation, after several breeding cycles a part of the population is obliged to migrate because of shortage of food and habitats. Gradually, a wave of increased density fills all habitats in the subzone and penetrates into the arctic tundra through passes in the Byrranga mountains - the valleys of the Piasina and Lower Taimyra Rivers (Figure 3).

Three regions can be distinguished in the Taimyr peninsula on the basis of analysis of the differences in structure and duration of lemming density cycles (Figure 3).

The south tundra region occupies the entire subzone of the southern tundra. Lemming density dynamics there are complicated by the occurrence of other rodents. There is not enough suitable habitat there for the Collared Lemming to reach a high density and therefore the density is relatively more stable. For the Siberian Lemming, density fluctuations have an opposite trend to that of Middendorf's Vole *Microtus middendorffi* (Kuksov 1975). The main cycles are generally in correspondance with the three-year cycle of the peninsula, but they are smoother.

The typical tundra region is the largest region of Taimyr. It occupies the entire typical tundra subzone and the south-eastern section of the arctic tundra, south from the Burranga mountains. This area of arctic tundra is included because of the presence of mountains which have a barrier effect. It is typical here for lemming densities to increase to a peak in one year, followed by a decrease for two years. Very occasionally (twice during thirty years), high densities have been recorded for two consecutive years. The density increases gradually from the west to the east, but the difference in time is no more than a few months. This region is evidently

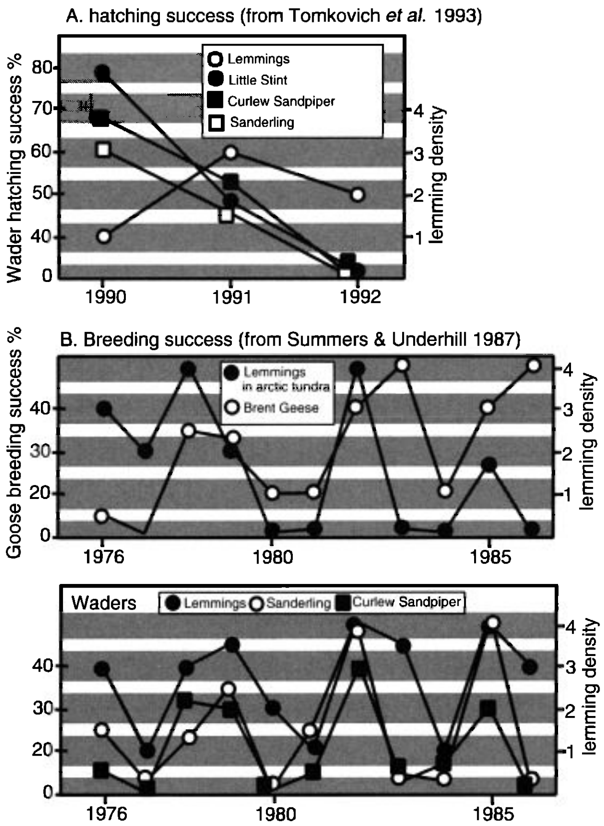

Figure 4. Comparison of a) hatching success in the Lower Taimyra River mouth region (Tomkovich *et al.* 1993), and b) breeding success (Summers & Underhill 1987) of some tundra birds with density of lemmings. Levels of lemming density are 1. extremely low density; 2. low density; 3. average density; 4. high density; 5. very high density.

the optimal area for both species, but a decreasing humidity from west to east makes the western part of Taimyr better for the Siberian Lemming and the eastern part better for the Collared Lemming. Distribution at more or less the same density and a preference of typical tundra subzone is characteristic for lemmings in adjacent regions (Dunaeva 1948).

Our data collected in 1991-1992 near Pronchishcheva Lake illustrate the typical tundra distribution of lemmings in both a high peak and decreasing year. The year of 1991 had an extreme peak in lemmings densities. The increase started in winter and continued until August. Highest densities of Siberian Lemmings were found in damp habitats and of Collared Lemmings in comparatively dry, upland habitats.

The highest density of 400 lemmings per hectare was found in lake basins occupied by uniform marshes. This type of habitat was inhabited almost exclusively by the Siberian Lemming (98-100% of animals found). Steep slopes of these basins were inhabited by rather low densities of animals of both species.

Less steep slopes formed by loam and loamy sand with "baydjarakhs" (tundra hills covered with hummocks left after permafrost clines have melted) were inhabited as densely as the lake basins: 312 ha^{-1} already in June. Collared Lemmings (66.5% of animals) were found twice as often as Siberian Lemmings. Collared Lemmings also dominated on hill tops with spotty tundra, but their density was lower there: 232 ha^{-1} in July (63.8% *D. torquatus*, 36.2% *L. sibiricus*).

A similar density (216 ha^{-1} in July) was recorded on the gentle slopes of valleys formed by loam. Siberian Lemming was the more abundant (55.5% of trapped animals) because of the damp conditions.

Water-logged habitats with thermokarst were the most sparsely inhabited. The density of lemmings here in July was 152 ha^{-1} (94.7% L. sibiricus).

Studies in 1992 (a year of rapid density decrease) showed large changes in lemming distrbution. The main wintering areas of Siberian Lemmings were lake basins, where they ate about 90% of plant biomass in some places. Collared Lemmings spent the early winter in their summer holes, where they had food stocks (about 12 kg for one group at the beginning of August). Later, they inhabited mainly south-facing slopes. Collared Lemmings had one brood under the snow.

The long, cold spring of 1992 caused a concentration of lemmings on snow-free patches. Their density was about 72 ha^{-1} on damp valley slopes, which led to active predation. After the snow-melt Lemmings did not inhabit the spotty tundra on hill tops and gentle slopes, nor low-lying habitats. There was a uniform distribution of both species on slopes with baydjarakhs and with dales. Density in July was about 28-32 ha^{-1}. Populations could increase seasonally, since all females were pregnant.
The north-western arctic tundra region differs from the other regions on Taimyr due to its higher humidity, caused by the mountain barrier of Burranga. This is why Collared Lemmings have a lower density here than in typical tundra. High densities are reached only in local areas (Heptner 1937; Sdobnikov 1955; Rybkin 1993). The increase in density there continues usually for two years, with influxes of migrants from typical tundra. In most cases decreases are rapid, and very low densities remain. The high humidity and usually cold springs result in a decrease in density before the highest peak is reached.

Modeling the influence of lemming density on the local breeding success of birds

The relationship between bird breeding success and lemming density has been previously noted (Summers 1986; Summers & Underhill 1987; Martin & Baird 1988). These studies have shown that the relationship is very complicated. Other factors such as weather conditions and migrations of predators influence the system.

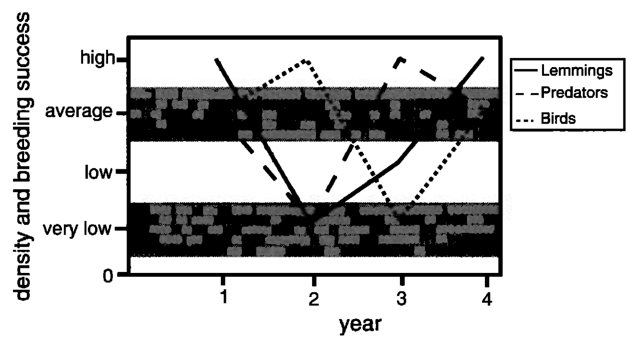

Figure 5. General relationship between density of lemmings (A) and predators (B) and breeding success of birds (C) for the regions where initial growth in lemming numbers occurs.

The three-year studies of Tomkovich *et al.* (1993) have shown that the highest breeding success of several common bird species in the Arctic Taimyr coincides with those years before peak lemming abundance in any area (Figure 4a). The results are similar if comparisons are made between lemming densities and the percentage of first year birds in migrating and wintering flocks of Brent Geese Branta bernicla (Figure 4b). Such links between lemming density and fluctuations in the productivity of Brent Geese, which have a restricted, mainly coastal breeding range, is not the same for those bird species which have broader breeding ranges (*e.g.* waders in Figure 4b). Available data lead to a preliminary conclusion that, in general, the relationship between birds' breeding success, lemmings and predators is a direct one based on the unevenness of lemming density distribution on the peninsula.

Locally, however, the situation is more complex. This is summarised below and in Figure 5. Predators breed very successfully in a peak lemming year. Lemmings form their basic food in such years. The breeding success of other birds is also comparatively high. Due to the abundance of food most Arctic Foxes (the main bird egg predators) stay on the breeding grounds for the following winter. This is why in the following year, although lemming densities decrease, the abundance of predators remains rather high. Because of the lack of lemmings predators then switch to feeding on bird eggs and chicks, resulting in very low bird breeding success.

The following year is characterised by a low density of Arctic Foxes: these have died or migrated in the preceding winter to areas with higher densities of lemmings. As a result bird breeding success is rather successful. But the best year for birds coincides with the growth of lemming populations, especially in those regions in which this growth starts. In spite of the rather high breeding activity of Arctic Foxes and birds of prey in these regions, their abundance and breeding success are still low. The correlation between densities of lemmings and predators in this year is better than during peak years probably because the increase in lemming density continues throughout the whole of the summer whilst in a peak year it usually stops in July-August. The lower breeding success of birds in a year when lemming numbers are increasing, compared with the following year, is a result of the variable distribution of those areas which have increasing lemming numbers. These regions are occupied by territorial predators which limit the density of migrant conspecifics. As a result the breeding success of birds declines in the neighbouring regions where migrant predators concentrate. We recorded such a situation around Medusa Bay, north-western Taimyr (73°15'N, 83°40'E), in summer 1993.

Conclusions

Three regions can be distinguished on the Taimyr peninsula on the basis of differences in structure and duration of lemming cycles. These are: the southern tundra; typical tundra regions including the south-eastern part of arctic tundra, and a region of north-western and central parts of arctic tundra.

Active migration exchange between lemming populations is a factor important in determining density fluctuations.

The reproductive success of birds in local areas is determined not so much by the absolute number of predators, but by the relationship between numbers and their basic food - lemmings. The most successful breeding of birds occurs in those years following a peak of lemming density. Due to the patchy distribution of such areas, bird breeding success is, however, highest in peak lemming years for the Taimyr in general.

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