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Cycles and synchrony in the Collared Lemming (*Dicrostonyx groenlandicus*) in Arctic North America

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Abstract Lemming populations are generally characterised by their cyclic nature, yet empirical data to support this are lacking for most species, largely because of the time and expense necessary to collect long-term population data. In this study we use the relative frequency of yearly willow scarring by lemmings as an index of lemming abundance, allowing us to plot population changes over a 34-year period. Scars were collected from 18 sites in Arctic North America separated by 2–1,647 km to investigate local synchrony among separate populations. Over the period studied, populations at all 18 sites showed large fluctuations but there was no regular periodicity to the patterns of population change. Over all possible combinations of pairs of sites, only sites that were geographically connected and close (<6 km) showed significant synchrony in fluctuations. The populations studied may not even be cyclic, at least for the time period 1960 to 1994, and although fluctuating, randomisation tests could not reject the null hypothesis of random fluctuations. These data have implications for the testing of hypotheses regarding lemming cycles and highlight the need for long-term trapping data to characterise the lemming cycle.

Keywords Lemming cycle · Synchrony · *Dicrostonyx groenlandicus*

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Introduction

Lemmings are generally known for their multiannual density fluctuations known as cycles. Occurring in a number of different species, these cycles are thought to have a fairly regular periodicity between 3 and 5 years, although the amplitude of the fluctuations can vary dramatically. The collared lemming, *Dicrostonyx groenlandicus*, is no exception, with earlier studies suggesting that this species shows a strong cyclic nature in its population fluctuations (e.g. Chitty 1950; Shelford 1943). However, later studies have shown separate populations to be cyclic (Mallory et al. 1981; Pitelka and Batzli 1993) or with little or no population fluctuations (Krebs et al. 1995; Reid et al. 1997). Differences in fluctuations found in different populations lead directly to the question of geographic synchrony. Krebs and Myers (1974) suggest that lemming populations are synchronous across large geographic areas and this has been supported largely by data from northern Europe (e.g. Henttonen et al. 1977; Myrberget 1973). A number of studies have, however, shown a general lack of synchrony (e.g. Myrberget 1973), including studies from North America (Pitelka and Batzli 1993).

The question of synchrony has clouded much of the debate regarding the relative merits of various hypotheses proposed to explain lemming cycles. Many intrinsic hypotheses (e.g. the Chitty hypothesis, Chitty 1960) at their core would suggest asynchrony among geographically separated populations. However, synchronising factors such as weather (Chitty 1996) are often included in order to explain apparent geographic synchrony, creating difficulties in formulating precise, testable predictions.

Nearly all past work on lemming cycles suffers from a common problem of ecology, namely a lack of long term data. Often statements are made regarding population fluctuations based on time series of less than 10 years. For populations that are thought to have a cyclic periodicity of 3–5 years, such data allow for only two, possibly three, complete cycles, and time series of at least 30 years are necessary for rigorous analysis.

Studies containing long time-series tend to use indirect estimates of lemming abundance. For example, Elton (1942) used the sales of Arctic fox skins over a 53 year period as an estimate of lemming abundance and Steen et al. (1990) analysed a 79-year time series based on reports of hunters, foresters and locals of the abundance of lemmings. However, in the case of using fox skins this covers very broad geographic areas and may be affected by variations in the fox populations independent of lemming fluctuations. Similarly, using anecdotal evidence is open to potential bias.

In this paper we use an indirect method to record former fluctuations in populations of the collared lemming (*Dicrostonyx groenlandicus*). During winter months, while living in subnivean spaces, collared lemmings eat the bark of willow stems (Batzli 1993). As long as stems are not ring-barked they will continue to grow and lay down yearly growth rings, apart from at the point where bark was removed, hence creating a scar. By taking a cross-section through a living stem at the point of the scar and counting growth-rings, it is possible to date the winter during which the bark was removed (Danell et al. 1981). Based on the assumption that when there are more lemmings there will be more scars, changes in the relative frequency of scars among years will reflect changes in the lemming population. The validity of this assumption has been supported by studies looking at temporal variation in vole numbers (Danell et al. 1981) and others looking at spatial variation in Siberian lemming populations (Danell et al. 1999; Erlinge et al. 1999). To test this assumption for populations of *D. groenlandicus*, in this study we compare the phases of the population fluctuations as derived from the frequency of scars with available trapping data. We then apply the dendrochronological analysis to 17 sites in the Canadian high Arctic and one site in Alaska. The resulting data allow us to test for periodicity and geographic synchrony in the lemming cycle over relatively long time periods and large geographic areas.

Materials and methods

Patterns of past population change were estimated at 18 sites (Fig. 1). Sites included mainland, peninsula and island locations and were chosen primarily for their ease of access, but some were chosen for specific comparisons, such as between island and nearby mainland sites (e.g. Fig. 1, sites O and P). At each of the 18 sites, estimates of past lemming population change were made using the techniques of Danell et al. (1981). Approximately 300 scarred willow stems were collected from each site in areas of dry hummocky tundra with a high cover of willows, the preferred habitat of *D. groenlandicus* (Morris et al. 2000). A sample of 300 scars gives a good representation of the past population patterns (K Danell, unpublished data). Scars were found by haphazardly moving through a patch of Arctic willows (*Salix lanata*), with the scars easily seen on stems. Stems were cut so that the entire scar was included in the section of stem for closer examination in the laboratory. Stems were stored in a mesh bag and air dried before being taken to the laboratory. *Salix lanata* usually has numerous stems arising from the soil and so the sampling did not kill the plants.

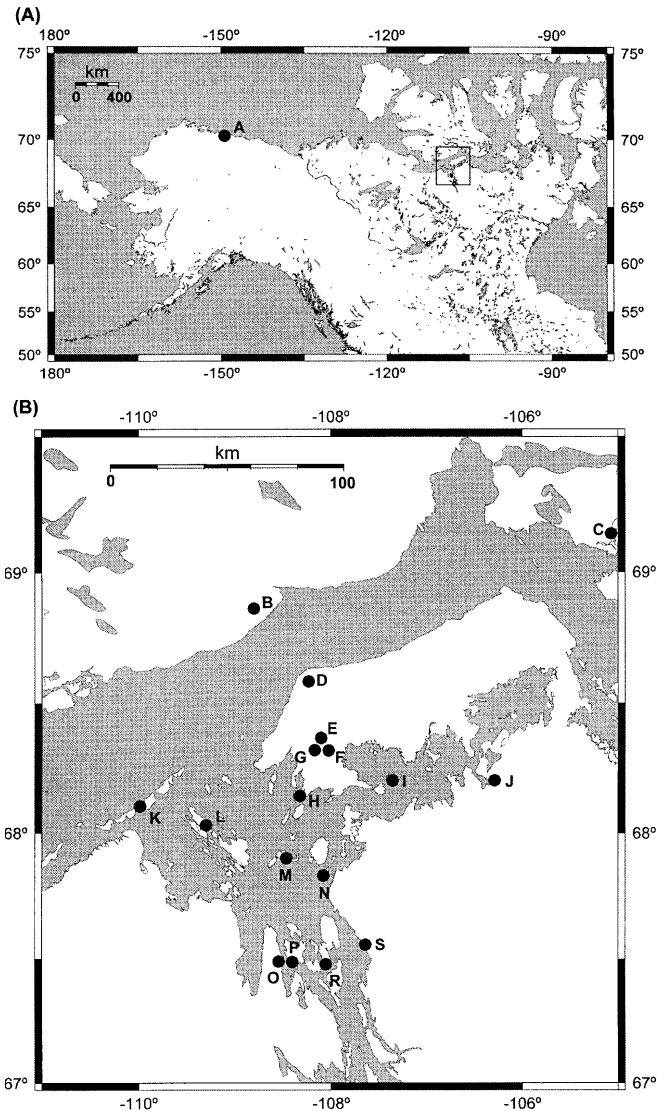


Fig. 1 A Map showing Northern Canada and Alaska. A is the location of Deadhorse. The *rectangle* shows the magnified area in map B. B Map showing the main study locations in the Canadian High Arctic. B Byron Bay; C Cambridge Bay; D Turnagain Point; E Walker Bay Camp; F Old Den; G Walker Bay South; H Cockburn Island; I Hurd Island; J Hope Bay; K Jameson Island; L Wilnot Island; M Breakwater Island; N Fishers Island; O Banks Peninsula; P Algak Island; R Ekalulia Island; S Bay Chimo

Scars were collected during the summers of 1994 and 1995, either at the start of summer, before the yearly growth of willows had started, or towards the end of summer after the yearly growth period, allowing us to distinguish precisely in which winter scars were made.

In the laboratory, scars were examined under a dissecting microscope and assigned to one of two categories based on their appearance. Many scars had rodent teeth marks still visible and these were assigned to the "sure" category. Scars that were not clearly created by rodents were assigned to the "unsure" category. Stems were discarded if a rodent clearly did not create the scar, for example if a branch had been pulled off. Seventy percent of stems were assigned to the "sure" category. Using an electric band saw, stems were cut across the grain, through the scar. If more than one scar was present on a single stem then these were kept together during the following process. Cut stems were placed in warm wa-

ter for about 5 min to soften the wood and then the cut surface of the stem was cleaned using a scalpel blade. Stems were allowed to dry for at least 12 h before the prepared cut surface was smeared with a thin film of yellow-coloured zinc cream, which highlighted the growth rings. Using a dissecting microscope we counted the number of growth rings laid down since the scar was made. Aged stems were assigned to either a "sure" category if the number of rings was clearly visible, or an "unsure" category if the age of the scar was in any doubt. Ninety percent of scars were assigned to the "sure" category. For stems that had more than one scar, only those scars with different ages were counted separately.

For each site, frequency distributions were constructed of the number of scars against the age of the scar. Distributions were firstly constructed using data excluding stems that fell into either of the two "unsure" categories and then including these data. There was no difference in the distributions comparing the two and hence the "unsure" data were included in further analyses.

Statistical analysis

Estimating population patterns

In order to age scars it was necessary to cut living stems. Because stems naturally die and with increasing age there is an increased cumulative chance that a stem will die, there were fewer old scars than there were young scars. Further, as stems grow, older scars tend to be grown over and hence hidden. Combined, these two factors were reflected in an overall increasing trend in the frequency histograms, with the number of scars increasing as the age of the scar decreased. Also, as noted by a number of authors, amplitude of the scar fluctuations varied over time. To overcome these two problems, data were transformed using logarithms [$\log(X+1)$] to stabilise the variation and smoothed using a kernel smoother (Siminoff 1996, see Appendix). To further overcome the problems of variation in amplitude, time series were converted into binary series. Past studies have used a variety of techniques to identify population peaks in a time series, including visual estimates (Krebs 1993) and statistical techniques (Steen et al. 1990). In this study we used two different methods to distinguish population peaks and hence derive a binary time series. In the first technique we used a modification of the methods of Steen et al. (1990) and derived the binary time series from the kernel smoothed average. The population in any year was assigned a "1" if it was above the smoothed mean and a "0" if it was below (see Appendix). The derived binary time series is herein referred to as the kernel estimate. In the second method, three of the authors (M.P., C.K. and K.D.) independently identified visually what we thought were peaks. Where agreement occurred between at least two of us, that year was coded as a peak ("1" in the binary series) and the remainder of years were coded as non-peak years ("0" in the binary series). The derived binary time series is herein referred to as the visual estimate. Because we generally felt more confident of our estimates of peak years for the last 15 years of data than for the entire data set, time series were further split into the last 15 years of data (1980–1994) and also the complete data set (the year in which the first scar was recorded after 1960 until 1994). All statistical analyses were carried out on the complete time series as well as the 15-year series.

Testing the methods

To test the reliability of the methods we compared the binary time series from one site (Hope Bay) with available trap data (Carriere and Obst 1999). Trap data covered 10 years (1984–1991 and 1994–1995) and were converted to binary time series based on whether or not captures were above ("1") or below ("0") average for the 10 years of data for comparison with the kernel estimate, and based on visual estimates of peaks for comparison with the visual estimate. Time series were compared statistically using a binary correlation (simple matching, Gower 1985) with the signifi-

cance level determined by a randomisation test based on 1,000 random permutations of the original series.

Testing for cyclicity

Based on the binary time series, if the data showed cyclicity we expected a regular sequence of 1 s and 0 s. For example, if the population cycled with a peak every 3 years we expected to see 0-runs of length 2 and 1-runs of length 1 at a greater frequency than would be found with a random pattern (e.g. 001001001001001...). This was tested using a randomisation test modified from Steen et al. (1990, see Appendix). The time series was considered to start at the earliest date to which a scar was aged for that particular site. We further carried out tests of combined runs of length 1, 2 and 3 to account for the vague qualifier in the definition of a cycle. We tested for both 1-runs and 0-runs for the kernel estimates, but only 0-runs for the visual estimates, since these can only have 1-runs of length 1, by their definition.

We further applied an index of the amplitude of population fluctuations, which is the standard deviation (s) of the logarithms of the smoothed mean data. Past studies have suggested that cycling populations have values of $s > 0.50$ and non-cycling populations values of $s < 0.50$ (Henttonen et al. 1985; Pitelka and Batzli 1993).

Testing for synchrony

We again used the binary time series and applied binary correlations (simple matching, Gower 1985) to test for any relationship between the high and low populations among all possible pairs of sites. We tested for the significance of the correlations using a randomisation test based on 1,000 random permutations of the original series.

To test the hypothesis that the degree of synchrony between pairs of sites is related to their distance apart, the straight-line distance in kilometres between each pair of sites was correlated with the binary correlation coefficients using Spearman's rank correlation.

Results

A total of 5,011 scars were aged from the 18 sites, an average of 278 per site. The oldest aged scar was 73 years, with an average age across all sites of 12 years. Scars older than 35 years were not included in further analysis because of their scarcity and hence we were able to estimate population fluctuations between 1960 and 1994. The numbers of stems of each age are shown for the 18 sites in Fig. 2, which also shows the derivation of the binary time series for both the kernel and visual estimates. All sites showed large fluctuations in scar abundance over time.

For the single site for which trap data is available (Hope Bay, Fig. 2J, Table 1), 9 out of 10 years showed matching between the trap and scar data using the visual estimates (simple matching = 0.9, $P < 0.05$) and 8 out of 10 using the kernel estimates (simple matching = 0.8, $P < 0.05$).

Of the 18 sites, very few showed significant patterns of 0-runs. Using the visual estimates, only 2 sites showed significant runs of zeros using all the data and 4 sites when using only the last 15 years of data (Table 2). Only one site, Deadhorse, showed significant runs using

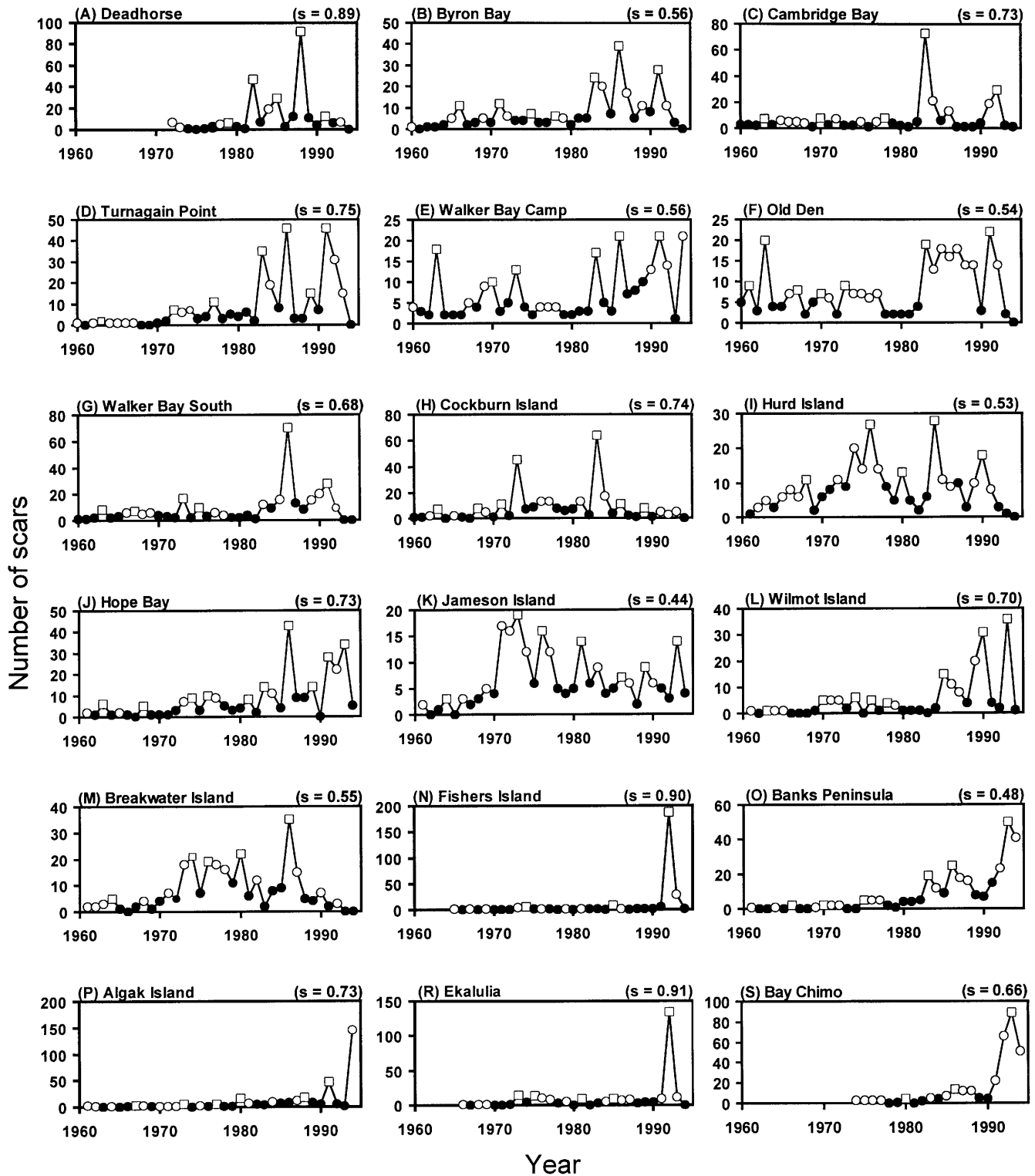


Fig. 2 Frequency distributions of willow scars for the 18 study sites for the period 1960 to 1994. *Open points* are points above the kernel smoothed mean and hence 1 *s* in the binary time series, *closed points* are points below the kernel smoothed mean and hence 0 *s* in the kernel binary time series. *Square points* are peaks in the visual time series, *circular point* shows trough (0) years in the visual time series. The letters of each figure correspond with Fig. 1. *s* is the index of cycling (standard deviation of log transformed data)

both length time series, at 0-runs of length 2 (Table 2). The mean probability of the visual estimates and 0-runs was 0.48 ± 0.28 (1SD) using the complete time series and 0.78 ± 0.30 using the last 15 years. Using the kernel estimates for the time series, only 2 sites showed significant 0-runs using all available data and only 1 site using the last 15 years of data. Algak Island showed significant 0-runs of length 2 using both length time series

(Table 2). Again using the kernel estimates, 5 sites showed significant 1-runs using all data and 6 sites using the last 15 years (Table 2). Byron Bay with 1-runs of length 2 and Cockburn Island with combined 1-runs of length 1, 2 or 3 were significant using both length of time series. The mean probability of the kernel estimates and 0-runs was 0.54 ± 0.35 using the complete time series and 0.67 ± 0.32 using the last 15 years. Using 1-runs and the kernel time series the mean probability was 0.56 ± 0.36 using the complete time series and 0.65 ± 0.35 using the last 15 years. The significant results should be interpreted cautiously because multiple tests are being carried out. Furthermore, the tests are not independent, and so adjusting for the multiplicity of tests is not simple and has not been done here. Instead, we note that to find nine significant results out of 648 tests is well within what is to be expected even if there is no real cyclicity in the data.

All sites, apart from Jameson Island and Banks Peninsula, had *s*-values greater than 0.50 (Fig. 2). Values

Table 1 Binary time series representing the phases of the lemming cycle at Hope Bay as derived using visual and kernel estimates of high ("1") and low ("0") years comparing trap data with dendrochronological techniques. Trap data are reported in Carriere and Obst (1999)

| Year | Visual | | Kernel | |
|------|--------|------|--------|------|
| | Trap | Scar | Trap | Scar |
| 1983 | 1 | 1 | 1 | 1 |
| 1984 | 0 | 0 | 1 | 1 |
| 1985 | 0 | 0 | 0 | 0 |
| 1986 | 1 | 1 | 1 | 1 |
| 1987 | 0 | 0 | 0 | 0 |
| 1988 | 0 | 0 | 0 | 0 |
| 1989 | 1 | 1 | 1 | 1 |
| 1990 | 0 | 0 | 1 | 0 |
| 1993 | 0 | 1 | 1 | 0 |
| 1994 | 0 | 0 | 0 | 0 |

Table 2 Significant 0-runs and 1-runs occurring in the binary time series as derived from the visual and kernel estimates of peak years

| Site | Type of series | Type of run | Length of runs | Number of runs | <i>P</i> |
|------------------|----------------|-------------|----------------|----------------|----------|
| Algak Is | Kernel (All) | 0-runs | 2 | 6 | 0.00 |
| | Kernel (15) | 0-runs | 2 | 4 | 0.00 |
| Bay Chimo | Kernel (All) | 0-runs | 2 | 3 | 0.02 |
| Byron Bay | Kernel (All) | 1-runs | 2 | 6 | 0.00 |
| | Kernel (15) | 1-runs | 2 | 3 | 0.03 |
| Cockburn Is | Kernel (All) | 1-runs | 1, 2 or 3 | 11 | 0.03 |
| | Kernel (15) | 1-runs | 1, 2 or 3 | 5 | 0.05 |
| | Visual (15) | 0-runs | 2 | 3 | 0.04 |
| Deadhorse | Kernel (15) | 1-runs | 1, 2 or 3 | 5 | 0.03 |
| | Visual (All) | 0-runs | 2 | 4 | 0.00 |
| | Visual (15) | 0-runs | 2 | 3 | 0.01 |
| Hope Bay | Kernel (15) | 1-runs | 1, 2 or 3 | 5 | 0.01 |
| | Visual (15) | 0-runs | 1, 2 or 3 | 5 | 0.03 |
| Hurd Is | Kernel (All) | 1-runs | 4 | 3 | 0.01 |
| Jameson Is | Kernel (15) | 1-runs | 1, 2 or 3 | 5 | 0.05 |
| Old Den | Kernel (15) | 1-runs | 7 | 1 | 0.03 |
| | Visual (15) | 0-runs | 7 | 1 | 0.04 |
| Walker Bay South | Kernel (All) | 1-runs | 4 | 2 | 0.04 |
| Wilmot Is | Visual (All) | 0-runs | 6 | 2 | 0.04 |
| | Kernel (All) | 1-runs | 3 | 3 | 0.03 |

ranged from 0.44 (Jameson Island) to 0.91 (Ekalulia) with a mean of 0.67 ± 0.14 , suggesting a high degree of fluctuation in numbers and hence, in contrast to the time-series analysis, highly cyclic populations.

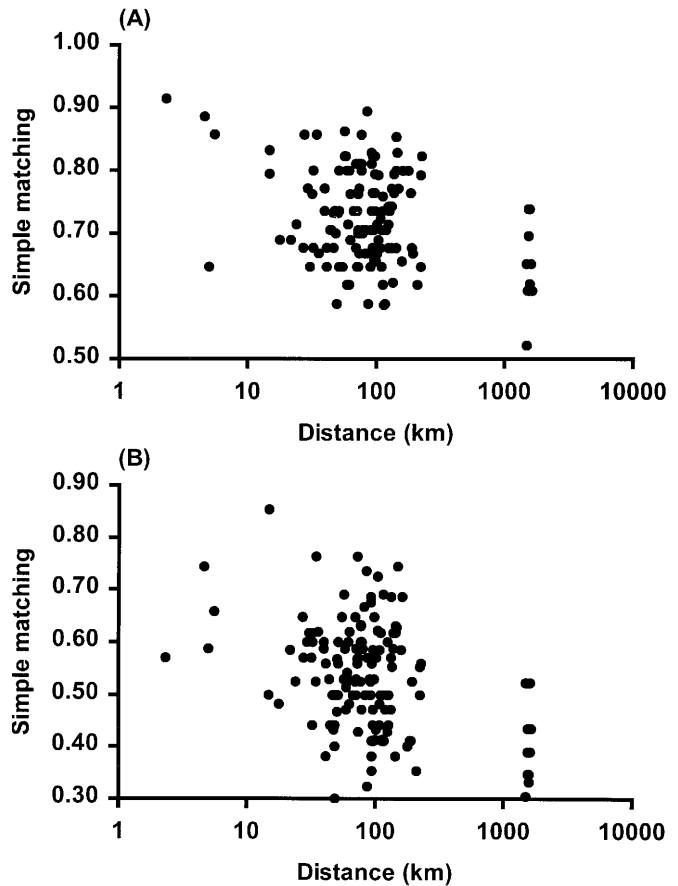


Fig. 3 The relationship between the distance between sites and the degree of matching of the binary time series as calculated using simple matching. **A** Visual estimates of time series ($r = -0.24$, $P < 0.01$), **B** Kernel estimates of time series ($r = -0.30$, $P < 0.01$). Distance is shown on a log scale for clarity

Comparing all sites with each other, there was a fair degree of synchrony across sites that were close to each other and on the same land formation (e.g. Old Den and Walker Bay Camp, visual estimate simple matching =0.93, $P < 0.01$), but this did not hold across sites that were close but separated by water (e.g. Banks Peninsula and Algak Island, visual estimate simple matching =0.65, $P > 0.05$). Overall, there was very little synchrony using either the visual or kernel peak estimates. Visual estimate mean simple matching =0.72±0.07 (1SD), kernel estimate mean simple matching =0.53±0.10, both of which are close to the expected means of random distributions. However, there was a significant relationship between the straight-line distance between sites and the degree of matching (Fig. 3; Visual: $r = -0.24$, $P < 0.01$; Kernel: $r = -0.30$, $P < 0.01$) with the closer the sites the higher the degree of matching.

Discussion

In the present study there was significant matching between scar data and available trap data, suggesting that the techniques provide a good estimation of lemming population phases. A similar matching between trap and scar data was found in a study of vole populations through time (Danell et al. 1981) and in Siberian lemmings across sites (Erlinge et al. 1999). However, it should be noted that in the present study traps sampled the summer population whereas the scar data is an index of winter abundance and this may in part explain the small discrepancy between the two data sets. Another factor that may influence the technique is the presence of secondary rodent species. At all sites sampled other species of rodent were present, the most common being the brown lemming, *Lemmus lemmus* (Carriere and Obst 1999). However, we are confident that our present data reflect the population dynamics of *D. groenlandicus* due to a number of points. Firstly, deciduous shrubs such as *S. lanata* predominate in the diet of the collared lemming, whereas they do not feature heavily in the diet of the brown lemming (Batzli 1993; Rodgers and Lewis 1985). Secondly, willow stems were sampled from the preferred habitat of the collared lemming, namely relatively dry and hummocky tundra (Morris et al. 2000; Pitelka and Batzli 1993). Finally, trap data from a number of sites where willows were sampled suggest that populations of different rodent species fluctuate in synchrony (Carriere and Obst 1999). Hence, we feel that the use of the willow browse technique is justified and that it gives a good representation of the population phases of the collared lemming.

All 18 sites showed large yearly fluctuations in the number of willow stem scars and hence lemming populations, yet there does not appear to be regular periodicity in the fluctuations. True cycles are defined as “a pattern of periodic fluctuations in the size of the population with rather constant period” (Stenseth and Ims 1993b, p 63), with the periodicity usually stated as being between 3

and 4 years, hence the qualifier “rather” in the above definition. Regular cycles with a periodicity of 3–4 years have been previously demonstrated for *D. groenlandicus*. For example, Shelford (1943) showed population peaks in the Churchill area in 1929, 1933, 1936 and 1940. Similarly, Chitty (1950) showed in Eastern Victoria Island (Cambridge Bay in the present study, Fig. 2C) increasing or peaked populations of lemmings in 1933/34, 1936/37, 1941/42, 1944/45 and 1947/48. In contrast to these studies that suggest fairly regular periodicity in the population fluctuations, Krebs et al. (1995) and later Reid et al. (1995) showed no population fluctuations at Pearce Point over 6 years, with population numbers remaining low during this period. Data in the present study appear to lie somewhere between these extremes, with clear fluctuations, yet with no regular periodicity and there are a number of possible explanations for these apparent differences. Although populations may be cyclic for a length of time, cycles may not be indefinite. In an analysis of a 79-year time series from Norway, Steen et al. (1990) showed that although cyclic with a fairly regular periodicity for most of the time, populations lost their cyclicality for a period of 20 years at the start of the century. The period 1960 to 1994 in the present study may be a non-cyclic period in this particular geographic area. Alternatively, the time-series of past studies may have simply not been long enough to detect true patterns. For example, looking at Turnagain Point in the present study (Fig. 2D) there appear to be regular peaks in the data during the 12-year period 1982 to 1994. However, taken in a longer-term context of a 34-year time series these fluctuations fit a random pattern. Similarly, looking at data from Old Den (Fig. 2F) for the period 1983 to 1989 suggests few or no fluctuations, yet again in the context of the full time series, there are in fact fluctuations, although no cycling. These data reconfirm earlier suggestions that it is necessary to have a long time series in order to detect overall patterns.

As an alternative to long time series, it has been suggested that the standard deviation (s) of the log transformed time series can give an indication of cycling (Henttonen et al. 1985; Pitelka and Batzli 1993), with values of $s > 0.50$ generally found in cycling populations (Henttonen et al. 1985). However, in the present study 16 of the 18 sites showed s -values greater than 0.50 and reaching as high as 0.91. Eleven of the sites had values greater than 0.64, the s -value presented by Pitelka and Batzli (1993) as sufficient to justify an inference of cycling in the collared lemming. These values are in direct contrast to the time-series analysis in the present study, which showed no pattern of regular cycling. It has been suggested that s -values increase the longer the time series used to calculate them, due to long term population trends (Pimm and Redfearn 1988). However, in the present study long-term trends were eliminated using the kernel smoothing technique, so it is unlikely that this would have caused the increase in s -values. The use of s -values to investigate the relative degree of cycling has been used to great effect in a number of studies (e.g. Hansson

and Henttonen 1985), yet the present study indicates that it may not be applicable across all species of lemming and care should be taken when applying these methods.

Overall, there was a significant negative relationship comparing the distance between sites and the degree of matching of populations; the closer the sites the higher the degree of matching. This would suggest that a synchronising factor is at work, either driving the population changes or occasionally resetting a number of populations to a common level. However, this analysis was heavily influenced by the inclusion of Deadhorse in Alaska. Removing Deadhorse from the analysis resulted in no pattern being displayed between the distance apart and the degree of matching. When looking at the pairs of sites individually, this study found only a small degree of synchrony among the 18 populations studied, which was particularly evident among the geographically close and connected populations. Chitty (1950) showed a similar degree of asynchrony in the same general region as the present study, Erlinge et al. (1999) showed asynchrony in Siberian lemming populations across the Palaearctic tundra and Pitelka and Batzli (1993) demonstrated asynchrony in populations of *Lemmus* only 150 km apart in Alaska. These patterns of asynchrony fit with the predictions of Ims and Steen (1990), that areas such as the Arctic tundra, with relatively few non-migratory predators, should have relatively asynchronous populations of microtines.

Within the present study, two types of comparisons prove most interesting, namely those sites that are both geographically close to each other with potentially continuous populations and those sites that are again close, but have potentially separated populations. Three sites (Walker Bay Camp, Walker Bay South and Old Den) are all within 6 km of each other on a continuous piece of land and showed strong synchrony among the three populations using the visual estimates. However, this was not perfect synchrony, with between 86% and 91% of the years matching. This is likely to be a real mismatch in these areas, rather than a problem with the techniques. Live-trapping on two of the sites (Walker Bay Camp and Old Den) during 1994 supported this asynchrony (M. Predavec, C.J. Krebs and D. Wilson, unpublished data). Captures of lemmings at Walker Bay Camp were increasing and at medium density during the summer of 1994 and traps locked open for the winter showed a high degree of usage. In contrast, only 2 traps out of 100 at Old Den showed signs of winter usage and only a single juvenile male was captured.

Within the possible comparisons made among the 18 sites, a number allowed for testing for synchrony between sites that were geographically close, but separated by water (Fig. 1B). Even over relatively short distances, such as 5-km (O and P of Fig. 1B) there was no evidence of synchrony. Such comparisons allow for testing of hypotheses regarding causes of lemming cycles. A large number of different hypotheses have been put forward to explain why lemmings go through large population fluctuations with a fairly regular periodicity (see Norrdahl

1995; Stenseth and Ims 1993a). These hypotheses can generally be split into intrinsic hypotheses (e.g. Charnov-Finerty hypothesis, Charnov and Finerty 1980) and extrinsic hypotheses (e.g. the nutrient recovery hypothesis, Pitelka 1964; Schultz 1964). Extrinsic hypotheses can be further split into those with localised effects (e.g. the quantity of available food) and those with wider geographic effects (e.g. weather). Taken at their most basic level, these groups of hypotheses make specific predictions regarding synchrony of geographically isolated populations. Intrinsic hypotheses and localised extrinsic hypotheses predict asynchrony, whereas wider ranging extrinsic factors predict synchrony. However, this dichotomy is confused by the inclusion of synchronising agents; an environmental factor (either biotic or abiotic) that through its irregular influence can reset the population cycles so that they appear synchronous. An example of this may be weather, which in a particularly severe year may reduce all populations of lemmings, over a wide geographic range, to their minimum levels (Moran effect). Synchronising agents have been included in the Chitty hypothesis as an explanation of geographic synchrony (Chitty 1996). With the inclusion of synchronising agents in the hypotheses, all can explain synchrony, making it difficult to test many hypotheses using pattern analyses. However, in the present study we found little evidence of synchrony among the 18 sites we looked at, even with geographically close, but isolated, populations. This is good evidence against synchronising agents having major influence and also against wide ranging extrinsic hypotheses. If weather, sunspots or nomadic predators were influencing lemming populations, one might expect a high degree of synchrony among populations separated by only 5 km of water. Predators such as snowy owls can easily travel such distances and have been suggested as factors synchronising microtine population fluctuations (Ydenberg 1987). Nomadic predators such as snowy owls and arctic foxes are known to be present at the sites mentioned in this study. This is certainly not *sufficient* evidence (c.f. Underwood 1990) to suggest that weather and nomadic predators are unlikely to be influencing the lemming fluctuations, but it is *necessary* evidence. A lack of synchrony among close and isolated populations cannot distinguish between intrinsic factors and extrinsic localised factors. It does, however, leave the way open for real tests of a number of these hypotheses. For example, one test of the Chitty hypothesis is to take individuals from an increasing population and transfer them into a decreasing population (Chitty 1960; Krebs 1978). If cycles are driven by intrinsic factors then the transplanted "population" should continue to increase. The presence of isolated populations only 5 km apart in the present study, that are asynchronous, suggest an ideal opportunity for such experiments. Pattern analyses such as the present study will not give us the answer to the question of lemming cycles, but can hopefully point us in an appropriate direction.

So how well do the willow browse techniques work? Firstly it should be noted that they cannot be used to re-

place long-term trapping data. The methods described in this paper give us only an index of relative population size from year to year, but tell us nothing of the demography or the environment during that time. However, the cost of carrying out long-term trapping studies is often prohibitive, and this is a relatively easy way of obtaining long-term data, from a large number of sites, within a short period of time. The advantages of these techniques over other indirect estimates is that they can be employed over relatively small, localised areas and they are unlikely to be biased by density-dependent factors (see Xia and Boonstra 1992). In this study we used two different techniques to distinguish peak years and hence patterns in the time series. Both methods have their advantages, the kernel method because it is free of bias and the visual estimates because they better reflect what we would generally define as a peak year in a binary time series, namely a single peak year with lower numbers either side (0–1–0 in a binary series). We recommend that in future a better statistical technique is developed to distinguish peak years in cycles, that better reflects our definitions of peaks and cycles, while at the same time being free of potential bias. Long-term data sets, such as this one, combined with judicious pattern analyses may in the future provide relatively inexpensive and robust preliminary tests of hypotheses concerning lemming cycles.

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Appendix

Estimating the lemming population

Let Y_t be the number of scars of age t from a site. We transformed the data using logarithms to stabilise the variation and then used a kernel smoother to estimate the mean of the transformed data over time. Define $X_t = \log(Y_t + 1)$ (the addition of 1 to all observations prevents problems with years where $Y_t = 0$). The mean of the transformed data for year t is calculated as

$$\hat{m}(t) = \sum_{j=1}^n w_j(t) X_j \quad (1)$$

where

$$w_j(t) = \frac{K\left(\frac{t-j}{h}\right)}{\sum_i^n K\left(\frac{t-i}{h}\right)} \quad (2)$$

and $K(u)$ is a kernel function. The parameter h controls the smoothness of the estimated mean curve. In this paper we used the standard normal kernel, $K(u) = \frac{1}{\sqrt{2\pi}} \exp(-u^2/2)$ with $h=2.6$.

If we assume that the lemming population fluctuates about a constant mean, then we can scale the scar data by this estimated mean. The lemming population in year t is then proportional to $\exp(\hat{m}(t))$.

Testing for cyclicity

Because of the uncertainty in the true estimate of the lemming population as a result of variance in amplitude and long-term trends, we used binary data rather than the numerical values calculated as above. We formed the binary series as

$$L_t = \begin{cases} 1 & \text{if } Y_t > \exp(\hat{m}(t)) \\ 0 & \text{if } Y_t \leq \exp(\hat{m}(t)) \end{cases} \quad (3)$$

So let $L_t=1$ when the population is above the long trend and $L_t=0$ when the population is below the long run trend. If the data shows cyclicity, we expect regular sequences of 1 s and 0 s to occur. We call a run of i 0 s a "0-run of length i " and a run of i 1 s a "1-run of length i ".

Following the ideas of Steen et al. (1990) we tested for the occurrence of 1-runs and 0-runs in $\{L_t\}$. Let $r_1(i)$ be the number of 1-runs of length i and let $r_0(i)$ be the number of 0-runs of length i . We then used a randomisation test to compare the observed frequency of these quantities with what we would expect to see by chance given a sequence with the observed number of 1 s and 0 s. The observed frequencies were compared with the number of runs of each length obtained from 1,000 random permutations of the $\{L_t\}$ sequence.

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