

# Cyclic dynamics of sympatric lemming populations on Bylot Island, Nunavut, Canada

Nicolas Gruyer, Gilles Gauthier, and Dominique Berteaux

**Abstract:** We characterized the fluctuations (amplitude, periodicity) of two sympatric species, the brown lemming (*Lemmus sibiricus* (Kerr, 1792)) and the northern collared lemming (*Dicrostonyx groenlandicus* (Traill, 1823)), in a High Arctic area. Our objective was to determine if these populations were cyclic, and if fluctuations in numbers were synchronized between the two species temporally and spatially. An annual index of lemming abundance was obtained using snap-traps at two sites 30 km apart on Bylot Island (Nunavut, Canada) over 13 years (1993–2005) and 9 years (1997–2005), respectively. The time series were analyzed by spectral analyses and autoregressive modelling. At the site with the longest record, brown lemming showed regular population fluctuations of large amplitude (>40-fold), but collared lemming fluctuations were of much smaller amplitude (4-fold). At the other site, the collared lemming population was higher than at the main site, but brown lemmings were still most abundant in the peak year. Models with a second-order function obtained from a spectral analysis were highly correlated with the observed abundance index in both species at the site with the longest time series, and provide evidence of cyclic dynamic. The periods of the cycles were estimated at  $3.69 \pm 0.04$  (SE) years for brown lemmings and  $3.92 \pm 0.24$  (SE) years for collared lemmings, but the amplitude of the cycle was weak in the latter species. Fluctuations in abundance at the same site were relatively well synchronized between the two species, but the evidence for synchrony between sites was equivocal.

**Résumé :** Nous avons étudié les fluctuations des cycles (amplitude, périodicité) de deux espèces sympatriques, le lemming brun (*Lemmus sibiricus* (Kerr, 1792)) et le lemming variable (*Dicrostonyx groenlandicus* (Traill, 1823)) à une localité du Haut Arctique. Notre objectif était de déterminer si les populations étaient cycliques et si les fluctuations en abondance étaient synchronisées entre les deux espèces dans le temps et l'espace. Un indice annuel d'abondance a été obtenu par piégeage mortel à deux sites distants de 30 km à l'île Bylot (Nunavut, Canada) durant respectivement 13 ans (de 1993 à 2005) et 9 ans (de 1997 à 2005). Les séries temporelles ont été analysées par analyses spectrales et modèles autorégressifs. Au site avec la série temporelle la plus longue, le lemming brun présentait des fluctuations régulières avec des variations d'abondance de grande amplitude (par un facteur de plus de 40), alors que les fluctuations du lemming variable étaient plus faibles et de moindre amplitude (par un facteur de 4). À l'autre site, la population de lemmings variables était plus élevée qu'au site principal, mais le lemming brun était plus abondant lors de l'année de pic. Des modèles prédictifs de deuxième ordre obtenus par l'analyse spectrale étaient fortement corrélés aux indices d'abondance observés pour les deux espèces au site avec la plus longue série temporelle et apportent des évidences d'une dynamique cyclique. Les périodes du cycle ont été estimées à  $3,69 \pm 0,04$  (ET) ans pour le lemming brun et  $3,92 \pm 0,24$  (ET) ans pour le variable, mais l'amplitude du cycle était faible chez cette dernière espèce. Les fluctuations d'abondance à un même site étaient relativement bien synchronisées entre les deux espèces, mais les preuves d'une synchronie entre les deux sites étaient équivoques.

## Introduction

Lemmings are recognized for their multiannual fluctuations in density known as cycles. These cycles typically have a fairly regular periodicity between 3 and 5 years, although the amplitude of these fluctuations can vary considerably (Elton 1924; Stenseth and Ims 1993). Moreover, the regularity of these oscillations may vary spatially and temporally (Krebs et al. 1995; Stenseth et al. 1996, 2003; Angerbjörn et al. 2001). Thus, "cyclic" species are not necessarily cyclic throughout their range; for example, southern populations tend to be less cyclic than more northern ones in Europe (Hanski et al. 1994; Stenseth 1999). However, there

is as yet no clear evidence of such latitudinal gradient in North America. Additionally, populations that have been cyclic for several decades may not continue to do so indefinitely, whereas the reverse can also be true (Stenseth and Ims 1993; Angerbjörn et al. 2001; Predavec et al. 2001).

Krebs et al. (2002) suggested that rodent cyclic fluctuations in the Canadian Arctic were synchronized at both the local scale and over large geographic areas, and that sympatric species were locally synchronized. Two aspects of synchrony must be distinguished: spatial synchrony, which refers to populations of the same species fluctuating in phase over small or large geographic regions, and interspecific synchrony, which refers to several rodent species present at

Received 20 December 2007. Accepted 18 April 2008. Published on the NRC Research Press Web site at [cjz.nrc.ca](http://cjz.nrc.ca) on 24 July 2008.

**N. Gruyer and G. Gauthier.**<sup>1</sup> Département de biologie et Centre d'études nordiques, pavillon Vachon, 1045 avenues de la Médecine, Université Laval, Québec, QC G1V 0A6, Canada.

**D. Berteaux.** Chaire de recherche du Canada en conservation des écosystèmes nordiques et Centre d'études nordiques, Université du Québec à Rimouski, QC G5L 3A1, Canada.

<sup>1</sup>Corresponding author (e-mail: [gilles.gauthier@bio.ulaval.ca](mailto:gilles.gauthier@bio.ulaval.ca)).

a given site fluctuating in phase (Krebs et al. 2002). Climate is one factor that may contribute to impose synchrony in rodent cyclic fluctuations. Interactions with specialist predators, which is currently one of the most popular hypotheses to explain rodent population cycles, may also contribute to impose both spatial and interspecific synchrony (Stenseth and Ims 1993; Viljugrein et al. 2001). However, the scale of spatial synchrony in lemming cycles remains poorly known, although it apparently does not extend to whole continents (Erlinge et al. 1999; Krebs et al. 2002).

Long time series of lemming population fluctuations are essential to characterize these fluctuations and to examine questions related to spatial and interspecific synchrony. However, such data sets are scarce in the Nearctic (Krebs et al. 2002) compared with the Palearctic (e.g., Stenseth et al. 1996; Framstad et al. 1997; Stenseth 1999; Angerbjörn et al. 2001). In this study, we used a long-term data set to examine features of population fluctuations for two sympatric species of lemmings, the brown (*Lemmus sibiricus* (Kerr, 1792)) and the northern collared (*Dicrostonyx groenlandicus* (Traill, 1823)) lemmings, in the Canadian Arctic. Trapping was conducted at two sites 30 km apart over 13 and 9 years, respectively. Our objectives were first to determine whether these species were cyclic at our study area by characterizing the amplitude and periodicity of the oscillations. Secondly, we examined the degree of spatial and interspecific synchrony in fluctuations. Thirdly, we determined the order of density dependence (i.e., direct or delayed density dependence) present in the data for each species at our study area. Delayed density dependence (i.e., second order) has been found in many cyclic populations and is often an indication that specialized trophic interactions is a cause of the observed cycles (Stenseth 1999; Turchin and Hanski 2001; Jiang and Shao 2003).

## Materials and methods

### Study area and species

Fieldwork was carried out on the south plain of Bylot Island, Sirmilik National Park of Canada, Nunavut, Canada (73°N, 80°W). This area covers ca. 1600 km<sup>2</sup>, and is bordered to the south and west by the sea and the north and east by high mountains (2000 m) and glaciers. The landscape is a mixture of wetlands dominated by graminoids and mosses in lowland areas, mesic tundra dominated by shrubs, forbs, and some graminoids in both lowlands and rolling-hill areas, and by xeric tundra at higher elevations (Gauthier et al. 1996). Data were collected at two sites 30 km apart: site 1 (Qarlikturvik Valley) and site 2 (located in the centre of a large greater snow goose (*Chen caerulescens atlantica* Kennard, 1927) nesting colony).

Two species of rodents are found on Bylot Island: the collared and brown lemmings. Brown lemmings are typically found in wetlands where they feed primarily on sedges and grasses, as well as mosses in winter. In contrast, collared lemmings prefer drier habitats where they mainly feed on forbs and shrubs (Rodgers and Lewis 1986; Batzli and Jung 1980). The two species present different levels of adaptation to the arctic environment, which is reflected in their distribution range. The range of collared lemmings extends to the northernmost land mass in the Arctic (Golley

et al. 1975). On the other hand, brown lemmings reach the northern limit of their geographical range precisely on Bylot Island in eastern North America (Banfield 1974).

### Trapping protocol

Lemming abundance was estimated annually with snap-traps from 1994 to 2005 at site 1 and from 1997 to 2005 at site 2. Trapping was conducted between 21 and 31 July at site 1 and between 5 and 15 July at site 2. At site 1, trapping was simultaneously conducted in two plots: one located in wet meadow habitat and one located in drier mesic habitat. At site 2, trapping took place in only one plot located in a mixed wet-mesic habitat. In each plot, 50 Museum special traps baited with peanut butter and rolled oats were set every 10 m on two parallel transects lines (100 m apart) and checked daily for 10 days following the protocol of Shank (1993). Traps were set within 1–2 m of each station, preferably near a lemming burrow if one was found within this radius. One trapping day was added when the number of misfired traps was >25. The total number of trap-nights was thus around 1000 at site 1 and 500 at site 2 each year. The date, trapping station, and species were noted for each capture. The methods were approved by the Animal Care Committee of Université Laval following guidelines of the Canadian Council on Animal Care.

Although no trapping was conducted in 1993, a quantitative estimate of lemming abundance is nonetheless available based on winter nest surveys, which were conducted at our site 1 in 1993 and 1996 (O. Gilg, personal communication). The ratio of winter nest to lemming abundance index obtained in 1996 was applied to the nest survey data in 1993 to estimate lemming abundance that year. Both 1993 and 1996 were peak lemming years in our study area and thus data should be comparable. To obtain the species composition of the estimated abundance in 1993, we applied the mean ratio of brown lemmings to collared lemmings observed in other peak years at our study site.

Even though snap-trap data are commonly used to estimate abundance of small mammals (e.g., Hanski et al. 1994; Stenseth 1999), they only provide an index of abundance, not a true abundance. Such indices should thus be validated against true abundance data. Since 2004, we have live-trapped lemmings at site 1, which allowed us to obtain true abundance estimates using capture–recapture data. Over the period 2004–2006, the live-trapping and snap-trapping annual abundance estimates showed a very good correlation, with a peak abundance in 2004, a large decline in 2005, and a further decline in 2006 (Gruyer 2007). Thus, although we consider our annual snap-trap data as indices of abundance, we believe that they accurately tracked annual fluctuations in abundance at our study site.

### Statistical analyses

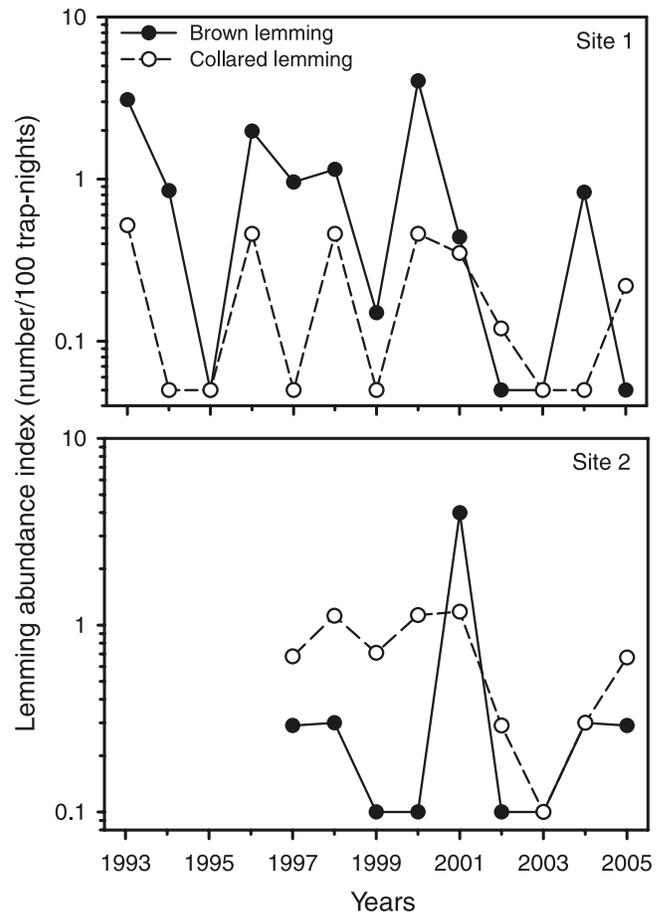
We calculated the number of individuals caught per 100 trap-nights (lemming abundance index:  $N$ ) by dividing the total number of lemmings trapped by the standardized total number of trap-nights (STN) over the whole period multiplied by 100, where  $STN = \text{total number of trap-nights} - [(\text{number of lemmings caught} + \text{number of misfires}) \times 0.5]$ . We subtracted 0.5 night for each sprung trap to improve estimates of sampling effort (Beauvais and Buskirk 1999).

Trapping data from the two plots were pooled at site 1. Annual time-series data are presented in the form of  $N_1, N_2, \dots, N_T$ , where each  $N$  is the number of individuals caught per trapping effort in a particular year and  $T$  is the total number of years for which we have such data. The level of synchrony for both species at each site was quantified with Spearman's rank correlations ( $r_s$ ) over the period 1994–2005 at site 1 and 1997–2005 at site 2.

We used spectral analysis to determine to what extent fluctuations in abundance were regular and to estimate their period. The spectral density function is a natural tool to examine the properties of periodic processes (Priestley 1981). This analysis was carried out with Proc SPECTRA (SAS Institute Inc. 2002). The Fisher's  $\kappa$  statistic (Fuller 1976) tests the null hypothesis of no cycle and the periodogram provides a graphic representation of the period in the time series. The spectral function uses Fourier transformations to describe the time series by transforming it into a sum of sine and cosine functions of different period lengths. It is then possible to use this sum to determine a frequency or range of frequencies in the periodogram that best describe the cyclic process present in the time series (Henttonen et al. 1985; Bjørnstad et al. 1996; Ranta et al. 2006). In a similar analysis, Bjørnstad et al. (1996) used a Parzen smoothing window to estimate the periodogram because results based on raw data may not be always consistent. However, the periodograms obtained with the raw data and a smoothing window were virtually identical, hence we only report the results based on the raw data. The significance of the period detected was tested by adjusting the spectral density function to the data taking into account the serial correlation between observations. This was done with the Proc MODEL (SAS Institute Inc. 2002). We use Godfrey's statistic to test the assumption of independence of the data. In presence of nonindependent data, we added a term accounting for an autoregressive process of the order one, AR (1). The order of the process corresponds to the number of lags included in the model. The AR (1) term allowed us to correct the model for nonindependence. Adjustment of the model to the data was tested using Pearson's correlation coefficient ( $r$ ).

We also analysed each population for direct and delayed density dependences (Bjørnstad et al. 1995; Stenseth 1999). We used autoregressive modelling (Proc REG, maximum likelihood option; SAS Institute Inc. 2002) to explore the dynamic properties of our time-series data. All series were logarithmically transformed with  $X_t = \ln(N_t + C)$ , where  $C$  is a constant because of zero in some years. For the value of  $C$ , we used half of the smallest abundance estimate that could be obtained at each site: 0.05 (1 lemming for 1000 night-traps) for site 1 and 0.1 (1 lemming for 500 night-traps) for site 2. Our conclusions were not sensitive to the  $C$  value used because using different values did not change our results. A second-order log-linear autoregressive model was chosen based on previous work (Turchin 1993; Bjørnstad et al. 1995; Stenseth 1999) and the shortness of the time series (Erb et al. 2000). When defining the growth rate as  $R_t = X_{t+1} - X_t$ , the second-order autoregressive model takes the following form:  $R_t = \beta_0 + \beta_1 X_t + \beta_2 X_{t-1}$  or equivalently  $X_t = \beta_0 + (1 + \beta_1)X_{t-1} + \beta_2 X_{t-2}$ , where  $\beta_0$  is the intercept with no dynamic effects and  $\beta_1$  and  $\beta_2$  are the first- and second-order autoregressive coefficients, respectively.  $\beta_1$  is

**Fig. 1.** Fluctuation in our index of abundance ( $N$ , i.e., number of lemmings/100 trap-nights) for brown (*Lemmus sibiricus*) and northern collared (*Dicrostonyx groenlandicus*) lemmings at two sites on Bylot Island, Nunavut, Canada, over 13-year (site 1) and 9-year (site 2) periods. Because we used a log scale and some abundance estimates were 0, we added a constant ( $C = 0.05$  at site 1 and 0.1 at site 2) calculated as half the smallest number of lemmings that could be trapped (see Materials and methods) to all values.

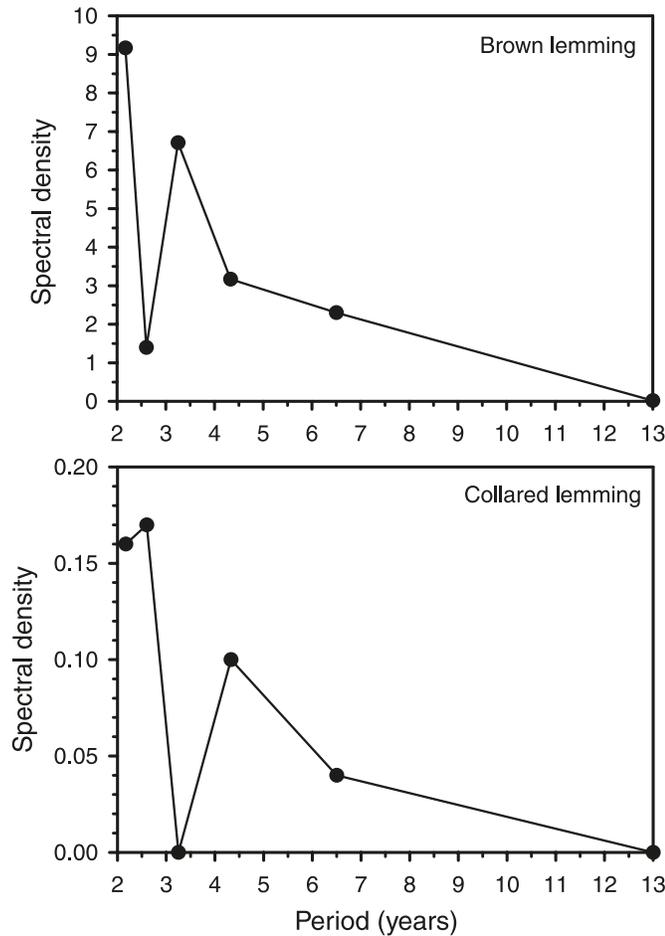


the direct annual density-dependent effect and  $\beta_2$  is the delayed annual density-dependent effect (Bjørnstad et al. 1995; Stenseth 1999). Hence, absence of direct annual density dependence corresponds to  $\beta_1 = 0$ , whereas increasing direct annual density dependence corresponds to  $\beta_1$  being progressively more negative (i.e.,  $1 + \beta_1$  being progressively  $< 1$ ; Bjørnstad et al. 1995).

## Results

Temporal variation in brown lemming abundance index at site 1 was indicative of cyclic variations with peak populations occurring in 1993, 1996, 2000, and 2004, i.e., at approximately 3- or 4-year intervals (Fig. 1). Our annual abundance index ranged from 0 to 3.99 brown lemmings/100 trap-nights. Considering the resolution of our trapping index (i.e., 1 lemming for 1000 trap-nights), our annual abundance index could vary by more than 40 times. Interestingly, the year of peak abundance always followed the year of lowest abundance since the previous peak. Thus, abundance appears to build up abruptly (i.e., within 1 year),

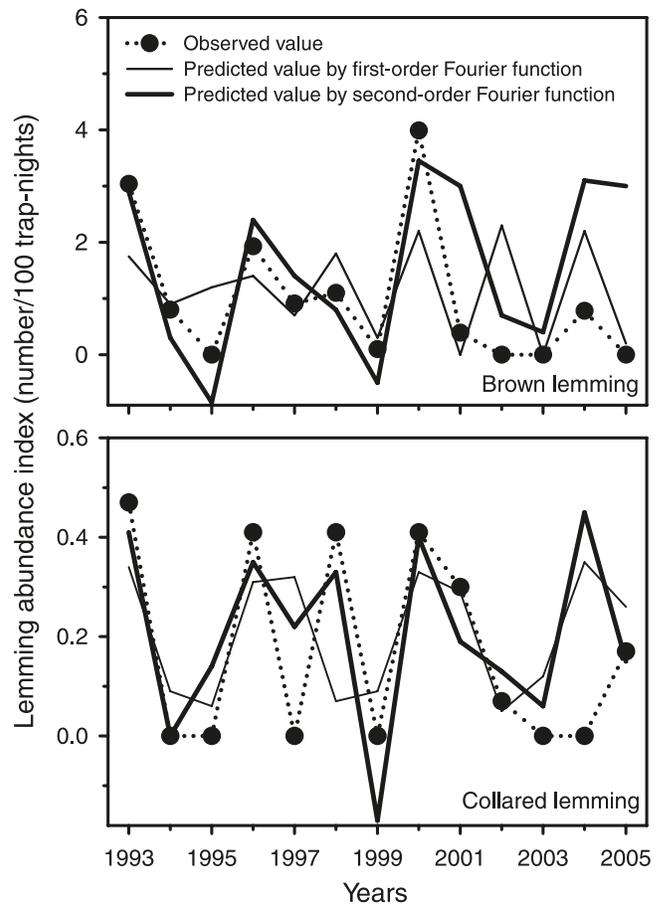
**Fig. 2.** Spectral density of the time series obtained by Fourier transformations of the abundance index for brown (*Lemmus sibiricus*) and northern collared (*Dicrostonyx groenlandicus*) lemmings over a 13-year period at site 1, Bylot Island, Nunavut, Canada.



whereas the decline, though rapid in the year following the peak, was not complete until at least 2 years after the peak, and was thus more gradual. At site 2, where the time series was shorter (9 years), only one peak of abundance of brown lemmings was recorded. Although its amplitude was similar to that seen in site 1, surprisingly, it occurred 1 year later (2001) than the corresponding peak in site 1 (2000) (Fig. 1). The weak peak in 2004 at site 1 was not detected at site 2.

Population fluctuations of collared lemmings at site 1 were weaker than those of brown lemmings (Fig. 1). Our annual abundance index ranged from 0 to 0.41 collared lemmings/100 trap-nights, indicating only a 4-fold variation in the annual abundance index. Overall, the brown lemmings abundance index was about 5.8 times higher than the one for collared lemmings at site 1, although both species were generally equally scarce in years of low abundance. Collared lemmings were more abundant at site 2 (index ranging from 0 to 1.08 lemmings/100 trap-nights), and if we exclude the 2001 peak in brown lemming abundance, their abundance index was 5.3 times higher than the one for brown lemmings. Considering the resolution of our trapping index, this index showed at least a 5-fold variation at site 2 for

**Fig. 3.** Time series of observed and predicted abundance index obtained by first- and second-order Fourier functions for brown (*Lemmus sibiricus*) and northern collared (*Dicrostonyx groenlandicus*) lemmings over a 13-year period at site 1, Bylot Island, Nunavut, Canada.



collared lemmings compared with a 19-fold variation for brown lemmings.

Both lemming species at site 1 were synchronized in their fluctuations ( $r_s = 0.67$ ,  $df = 11$ ,  $P = 0.02$ ). However, fluctuations were apparently not synchronized at site 2 ( $r_s = 0.40$ ,  $df = 8$ ,  $P = 0.28$ ), although the time series was relatively short.

The periodogram of both species showed some peaks (Fig. 2), although Fischer's  $\kappa$  tests were not significant, ( $\kappa = 2.42$  for brown lemmings and  $\kappa = 2.17$  for collared lemmings, both  $P > 0.05$ ), possibly owing to the shortness of the time series. We nonetheless examined how well the predictions derived from the Fourier functions fitted the observed data, correcting for the lack of independence detected (Godfrey's test;  $LM = 8.26$ ,  $P = 0.02$  for brown lemmings;  $LM = 5.30$ ,  $P = 0.07$  for collared lemmings). For brown lemmings, a first-order Fourier function estimated a period of  $1.87 \pm 0.07$  (SE) years, which corresponds to the first peak of the periodogram (Fig. 2), whereas a second-order function estimated a period of  $3.69 \pm 0.04$  (SE) years, which corresponds to the second peak. Observed data showed a much higher correlation with values predicted by the second-order Fourier function ( $r = 0.96$ ,  $df = 12$ ,  $P < 0.001$ ) than with those predicted by the first-order function ( $r =$

**Table 1.** Estimates of autoregressive coefficients ( $\pm$ SE) and their level of significance for brown (*Lemmus sibiricus*) and northern collared (*Dicrostonyx groenlandicus*) lemmings over a 13-year period at site 1, Bylot Island, Nunavut, Canada.

	$\beta_0$	<i>P</i>	$\beta_1$	<i>P</i>	$\beta_2$	<i>P</i>
Brown lemming ( $R^2 = 0.06$ )	-1.06 $\pm$ 0.55	0.09	-0.22 $\pm$ 0.36	0.56	-0.13 $\pm$ 0.34	0.71
Collared lemming ( $R^2 = 0.11$ )	-2.34 $\pm$ 0.93	0.04	-0.35 $\pm$ 0.35	0.35	-0.10 $\pm$ 0.33	0.76
Both species pooled ( $R^2 = 0.09$ )	-0.82 $\pm$ 0.48	0.12	-0.26 $\pm$ 0.34	0.48	-0.19 $\pm$ 0.32	0.57

**Note:** Coefficient  $\beta_0$  is the intercept,  $\beta_1$  is the direct density-dependent effect, and  $\beta_2$  the delayed density-dependent effect (see Materials and methods).

0.63,  $df = 12$ ,  $P = 0.02$ ; Fig. 3). For the collared lemmings, the first-order Fourier function estimated a period of  $3.87 \pm 0.26$  (SE) years, whereas the second-order function estimated a period of  $3.92 \pm 0.24$  years; both of which apparently correspond to the second peak of the periodogram (Fig. 2). It thus seems that the first peak in the periodogram of collared lemmings corresponded to noise in the data. Again, the observed data showed a higher correlation with values predicted by the second-order Fourier function ( $r = 0.86$ ,  $df = 12$ ,  $P = 0.002$ ) than with those predicted by the first-order function ( $r = 0.62$ ,  $df = 12$ ,  $P = 0.02$ ; Fig. 3).

The estimates of coefficients for direct ( $\beta_1$ ) and delayed ( $\beta_2$ ) annual density dependence were negative for both species as expected (Table 1). However, none of these were significant, possibly owing to the shortness of our time series. When the values of these coefficients were positioned in the parameter space graph of Bjørnstad et al. (1995), they fell in the portion of the graph characterizing populations with proper multiannual population cycle of periodicities between 3 and 4 years for both species; a result that is consistent with the previous analysis.

## Discussion

Our analysis supports the hypothesis that brown lemming populations showed typical fluctuations of large amplitude with a periodicity of 3–4 years as found in many other populations of the genus *Lemmus* Link, 1795 (Krebs 1964; Pitelka 1973; Erlinge et al. 1999; Angerbjörn et al. 2001). The cycle was not symmetrical on either side of the peak, as populations generally tended to have a rapid explosion of abundance lasting 1 year or less, followed by a period of decline over 1–3 years. In contrast, evidence for population cycles was weaker in the collared lemming, as their fluctuations were of much smaller amplitude compared with brown lemmings. Cyclical fluctuation in collared lemmings appeared to be confined to relatively low densities, unlike the dramatic fluctuations observed in brown lemmings. Comparing indices of lemming abundance across studies is difficult because trapping and analytical methods often differ (Hanski et al. 1994). Nonetheless, our abundance index appears comparatively low, even in years of peak abundance, for both species. In Fennoscandia, abundance indices derived from snap-traps can be as high as 30 in peak years (Hanski et al. 1994; Framstad et al. 1997), which is 7 times higher than our index in peak years. This also means that our abundance index should not have been affected by trap-saturation problems (Hanski et al. 1994).

The differential pattern between the two species is intriguing, especially the absence of irruptions of large amplitude

in collared lemmings. Indeed, cyclic fluctuations of large amplitude have been reported in this species at many sites (e.g., Greenland, Gilg et al. 2003; Kent Peninsula, Canada; Wilson et al. 1999; Devon Island, Canada; Fuller et al. 1975), although at other sites collared lemming populations appear to be limited at low density with little cyclicality (Pearce Point, Canada; Reid et al. 1995). When both species occur in sympatry, others have also reported that population fluctuations of brown lemmings tend to be of greater amplitude compared with collared lemmings (Baker Lake, Canada; Krebs 1964).

Interestingly, the predictions of the model proposed by Hanski and Henttonen (1996) to explain the dynamics of two competing vole species generally fit with our observations. This model explains the dynamic of multispecies rodent assemblage in the presence of predators. In their model, both species share the same predators, but one (*Microtus* Schrank, 1798) is competitively superior and more vulnerable to predation than the other (*Clethrionomys* Tilesius, 1850). Under these conditions, the model predicts multiannual oscillations with a shift from dominance of the competitively superior species near the peak of the cycle to dominance of the competitively inferior species during the low phase of the cycle because of the higher vulnerability to predation of the former. In lemmings, patterns of habitat use have been found to be density-dependent, with brown lemmings excluding collared lemmings from some habitats at high density presumably because they are superior competitors (Morris et al. 2000; Predavec and Krebs 2000). However, little information is available on relative vulnerability of the two species to predation.

Another factor that may promote greater fluctuations in brown lemmings is its higher potential for population growth (i.e., greater fecundity) compared with collared lemmings (Negus and Berger 1998). Although the mean litter size is generally the same, there is a difference in the age at first reproduction, with brown lemmings reaching maturity at a younger age than collared lemmings (Negus and Berger 1998). Collectively, these observations allow us to formulate a hypothesis to explain the difference in population dynamics of the two species at our study site. When populations start to increase as a result of low predator abundance, the brown lemming population could quickly outnumber the collared lemming population if its rate of population growth is higher. Being a superior competitor, brown lemmings could further limit the expansion of collared lemmings at high density and thus reach a much higher abundance. As predators build up owing to high prey abundance (Gilg et al. 2003), populations of both species may start to decline because of increased predation mortality in combination

with density-dependent effects. During the low phase of the cycle, both species may be equally low or the competitively inferior species (collared lemmings) may be relatively more abundant than its competitor if it is less vulnerable to predation (Hanski and Henttonen 1996). Admittedly, this explanation is speculative and needs to be tested but is consistent with recent evidence suggesting that predators may control lemming abundance in Greenland (Gilg et al. 2003). If this hypothesis is true, then the interaction between brown lemmings and predators could have a dominant impact on the dynamics of the system, forcing synchronous oscillations in the collared lemmings because of shared predation.

Our observation that populations of brown and collared lemmings fluctuated in temporal synchrony at one site is consistent with this hypothesis. In northern Fennoscandia, synchrony between microtine species occupying the same habitat is well documented (Heikkilä et al. 1994; Norrdahl and Korpimäki 1996; Angerbjörn et al. 2001; Huitu et al. 2004). Interactions with shared specialist predators have often been invoked as the causal factor behind interspecific synchrony in population fluctuations of small mammals (Stenseth and Ims 1993; Erlinge et al. 1999; Norrdahl and Korpimäki 1996). Indirect effects among prey (i.e., geese and lemmings) because of shared predators have previously been documented at our study site (Bêty et al. 2002; Gauthier et al. 2004).

Many studies have suggested that population cycles of northern rodents are generated by combined effects of delayed and direct density dependences (Hanski et al. 2001; Klemola et al. 2003; Turchin 2003). If lemming abundance is controlled by a specialized trophic interaction of the type predator–prey, then delayed density-dependent effects (i.e., second-order process) should be detected (Stenseth 1999). Our autoregressive model yielded negative second-order coefficients as expected, although they were not significant. Besides predator–prey interactions, specialized plant–herbivore interactions could also yield the same second-order effects. Although we cannot rule out entirely this hypothesis, long-term exclosures at our study site suggest that lemmings have little effect on plant biomass even in years of peak abundance, contrary to other herbivores at the site (Gauthier et al. 2004). Moreover, given that brown and collared lemmings eat different types of plants (Batzli and Jung 1980; Rodgers and Lewis 1986), it seems doubtful that food depletion could impose synchrony in density fluctuations of both species.

Our data suggest some level of asynchrony in the pattern of population fluctuations between our two study sites that were 30 km apart. Most notably, the 2000 peak in brown lemming abundance at site 1 apparently occurred 1 year later at site 2, which is surprising considering that there are no major physical barriers between our two sites. Although we have no satisfactory explanation for this result, one should be cautious in concluding a lack of spatial synchrony at the level of our two study sites. This conclusion is based on a single annual data point at each site and we cannot exclude the possibility that the actual peak in lemming density occurred before or after our annual mid-summer sampling. Hence, it is still possible that peaks in lemming abundance at our two study sites could have overlapped somewhat during the winter of 2000–2001 (i.e., the peak density at

site 2 may have been reached before the peak density at site 1 started to decline). Spatial synchrony in lemming population fluctuations has previously been reported at a relatively large scale (i.e., several hundred kilometres; Erlinge et al. 1999; Krebs et al. 2002).

We conclude that brown lemming fluctuations observed at our study site were cyclical in nature and typical of cyclic small-mammal populations, but that collared lemmings showed weak cycles of shallow amplitude. Both species nonetheless fluctuated in synchrony.

## Acknowledgements

We thank the large number of people who participated in the fieldwork over all these years; Marie-Christine Cadieux for managing the long-term data and for assistance during the preparation of the manuscript; Gaëtan Daigle for help with the spectral analyses; and Daniel Fortin, Steeve Côté, Charles Krebs, and Nigel Gilles Yoccoz for their comments on the manuscript. Funding was provided by grants from the Natural Sciences and Engineering Research Council of Canada to G. Gauthier, the Fonds québécois pour la nature et les technologies, the Canadian Network of Centres of Excellence ArcticNet, the Northern Ecosystem Initiative (Environment Canada), the Arctic Goose Joint Venture (Canadian Wildlife Service), the Canada Foundation for Innovation, and Indian and Northern Affairs Canada. Logistic supports were generously provided by the Polar Continental Shelf Project, Natural Resources Canada. We are indebted to the Pond Inlet Hunter and Trapper Association (Nunavut Territory) and to Parks Canada for allowing us to work on Bylot Island. This is Polar Continental Shelf Project contribution no. 018-08.

## References

- Angerbjörn, A., Tannerfeldt, M., and Lundberg, H. 2001. Geographical and temporal patterns of lemming population dynamics in Fennoscandia. *Ecography*, **24**: 298–308. doi:10.1034/j.1600-0587.2001.240307.x.
- Banfield, A.W.F. 1974. *The mammals of Canada*. University of Toronto Press, Toronto, Ont.
- Batzli, G.O., and Jung, H.J.G. 1980. Nutritional ecology of microtine rodents — resource utilization near Atkasook, Alaska. *Arct. Antarct. Alp. Res.* **12**: 483–499.
- Beauvais, G.P., and Buskirk, S.W. 1999. Modifying estimates of sampling effort to account for sprung traps. *Wildl. Soc. Bull.* **27**: 39–43.
- Bêty, J., Gauthier, G., Korpimäki, E., and Giroux, J.F. 2002. Shared predators and indirect trophic interactions: lemming cycles and arctic-nesting geese. *J. Anim. Ecol.* **71**: 88–98. doi:10.1046/j.0021-8790.2001.00581.x.
- Bjørnstad, O.N., Falck, W., and Stenseth, N.C. 1995. A Geographic gradient in small rodent density fluctuations: a statistical modeling approach. *Proc. R. Soc. Lond. B Biol. Sci.* **262**: 127–133. doi:10.1098/rspb.1995.0186.
- Bjørnstad, O.N., Champely, S., Stenseth, N.C., and Saitoh, T. 1996. Cyclicity and stability of grey-sided voles, *Clethrionomys rufocanus*, of Hokkaido: spectral and principal components analyses. *Proc. R. Soc. Lond. B Biol. Sci.* **351**: 867–875. doi:10.1098/rstb.1996.0081.
- Elton, C.S. 1924. Periodic fluctuations in the numbers of animals: their causes and effects. *J. Exp. Biol.* **2**: 119–163.
- Erb, J., Stenseth, N.C., and Boyce, M.S. 2000. Geographic varia-

- tion in population cycles of Canadian muskrats (*Ondatra zibethicus*). *Can. J. Zool.* **78**: 1009–1016. doi:10.1139/cjz-78-6-1009.
- Erlinge, S., Danell, K., Frodin, P., Hasselquist, D., Nilsson, P., Olofsson, E.B., and Svensson, M. 1999. Asynchronous population dynamics of Siberian lemmings across the Palaearctic tundra. *Oecologia (Berl.)*, **119**: 493–500. doi:10.1007/s004420050812.
- Framstad, E., Stenseth, N.C., Bjørnstad, O.N., and Falck, W. 1997. Limit cycles in Norwegian lemmings: tensions between phase-dependence and density-dependence. *Proc. R. Soc. Lond. B Biol. Sci.* **264**: 31–38. doi:10.1098/rspb.1997.0005.
- Fuller, W.A. 1976. Introduction to statistical time series. John Wiley, New York.
- Fuller, W.A., Martell, A.M., Smith, R.F.C., and Speller, S.W. 1975. High-arctic lemmings, *Dicrostonyx groenlandicus*. II. Demography. *Can. J. Zool.* **53**: 867–878. doi:10.1139/z75-100.
- Gauthier, G., Rochefort, L., and Reed, A. 1996. The exploitation of wetland ecosystems by herbivores on Bylot Island. *Geoscience Canada*, **23**: 253–259.
- Gauthier, G., Bety, J., Giroux, J.F., and Rochefort, L. 2004. Trophic interactions in a high arctic snow goose colony. *Integr. Comp. Biol.* **44**: 119–129. doi:10.1093/icb/44.2.119.
- Gilg, O., Hanski, I., and Sittler, B. 2003. Cyclic dynamics in a simple vertebrate predator–prey community. *Science (Washington, D.C.)*, **302**: 866–868. doi:10.1126/science.1087509. PMID:14593179.
- Golley, F.B., Petruszewicz, K., and Ryszkowski, L. 1975. Small mammals: their productivity and population dynamics. Cambridge University Press, Cambridge, UK.
- Gruyer, N. 2007. Étude comparative de la démographie de deux espèces de lemmings (*Lemmus sibiricus* et *Dicrostonyx groenlandicus*) à l'Île Bylot, Nunavut, Canada. M.Sc. thesis, département de biologie, Université Laval, Québec.
- Hanski, I., and Henttonen, H. 1996. Predation on competing rodent species: a simple explanation of complex patterns. *J. Anim. Ecol.* **65**: 220–232. doi:10.2307/5725.
- Hanski, I., Henttonen, H., and Hansson, L. 1994. Temporal variability and geographical patterns in the population density of microtine rodents: a reply to Xia and Boonstra. *Am. Nat.* **144**: 329–342. doi:10.1086/285678.
- Hanski, I., Henttonen, H., Korpimäki, E., Oksanen, L., and Turchin, P. 2001. Small-rodent dynamics and predation. *Ecology*, **82**: 1505–1520.
- Heikkilä, J., Below, A., and Hanski, I. 1994. Synchronous dynamics of microtine rodent populations on islands in Lake Inari in Northern Fennoscandia — evidence for regulation by mustelid predators. *Oikos*, **70**: 245–252. doi:10.2307/3545635.
- Henttonen, H., McGuire, A.D., and Hansson, L. 1985. Comparisons of amplitudes and frequencies (spectral analyses) of density variations in long-term data sets of *Clethrionomys* species. *Ann. Zool. Fenn.* **22**: 221–227.
- Huitu, O., Norrdahl, K., and Korpimäki, E. 2004. Competition, predation and interspecific synchrony in cyclic small mammal communities. *Ecography*, **27**: 197–206. doi:10.1111/j.0906-7590.2003.03684.x.
- Jiang, L., and Shao, N. 2003. Autocorrelated exogenous factors and the detection of delayed density dependence. *Ecology*, **84**: 2208–2213. doi:10.1890/02-0557.
- Klemola, T., Pettersen, T., and Stenseth, N.C. 2003. Trophic interactions in population cycles of voles and lemmings: a model-based synthesis. *Adv. Ecol. Res.* **33**: 75–160.
- Krebs, C.J. 1964. The lemming cycle at Baker Lake, Northwest Territories, during 1959–1962. Tech. Pap. No. 15, Arctic Institute of North America, Calgary, Alta.
- Krebs, C.J., Boonstra, R., and Kenney, A.J. 1995. Population dynamics of the collared lemming and the tundra vole at Pearce Point, Northwest Territories, Canada. *Oecologia (Berl.)*, **103**: 481–489. doi:10.1007/BF00328687.
- Krebs, C.J., Kenney, A.J., Gilbert, S., Danell, K., Angerbjörn, A., Erlinge, S., Bromley, R.G., Shank, C., and Carriere, S. 2002. Synchrony in lemming and vole populations in the Canadian Arctic. *Can. J. Zool.* **80**: 1323–1333. doi:10.1139/z02-120.
- Morris, D.W., Davidson, D.L., and Krebs, C.J. 2000. Measuring the ghost of competition: insights from density-dependent habitat selection on the co-existence and dynamics of lemmings. *Evol. Ecol. Res.* **2**: 41–67.
- Negus, N.C., and Berger, P.J. 1998. Reproductive strategies of *Dicrostonyx groenlandicus* and *Lemmus sibiricus* in high-arctic tundra. *Can. J. Zool.* **76**: 390–399. doi:10.1139/cjz-76-3-390.
- Norrdahl, K., and Korpimäki, E. 1996. Do nomadic avian predators synchronize population fluctuations of small mammals? A field experiment. *Oecologia (Berl.)*, **107**: 478–483. doi:10.1007/BF00333938.
- Pitelka, F.A. 1973. Cyclic pattern in lemming populations near Barrow, Alaska. In *Alaskan arctic tundra. Edited by M.E. Britton*. Tech. Pap. No. 25, Arctic Institute of North America, Calgary, Alta. pp. 199–215.
- Predavec, M., and Krebs, C.J. 2000. Microhabitat utilisation, home ranges, and movement patterns of the collared lemming (*Dicrostonyx groenlandicus*) in the central Canadian Arctic. *Can. J. Zool.* **78**: 1885–1890. doi:10.1139/cjz-78-11-1885.
- Predavec, M., Krebs, C.J., Danell, K., and Hyndman, R. 2001. Cycles and synchrony in the collared lemming (*Dicrostonyx groenlandicus*) in Arctic North America. *Oecologia (Berl.)*, **126**: 216–224. doi:10.1007/s004420000516.
- Priestley, M.B. 1981. Spectral analysis and times series. Vols. 1 and 2. Academic Press, New York.
- Ranta, E., Lundberg, P., and Kaitala, V. 2006. Ecology of populations. Cambridge University Press, Cambridge, UK.
- Reid, D.G., Krebs, C.J., and Kenney, A. 1995. Limitation of collared lemming population growth at low densities by predation mortality. *Oikos*, **73**: 387–398. doi:10.2307/3545963.
- Rodgers, A.R., and Lewis, M.C. 1986. Diet selection in Arctic lemmings (*Lemmus sibiricus* and *Dicrostonyx groenlandicus*): forage availability and natural diets. *Can. J. Zool.* **64**: 1684–1689. doi:10.1139/z86-253.
- SAS Institute Inc. 2002. SAS/STAT user's guide. Version 9. SAS Institute Inc., Cary, N.C.
- Shank, C.C. 1993. The Northwest Territories small mammal survey: 1990–1992. Manuscript Rep. No. 72, Department of Renewable Resources, Government of the Northwest Territories, Yellowknife.
- Stenseth, N.C. 1999. Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. *Oikos*, **87**: 427–461. doi:10.2307/3546809.
- Stenseth, N.C., and Ims, R.A. 1993. The biology of lemmings. Academic Press, London.
- Stenseth, N.C., Bjørnstad, O.N., and Saitoh, T. 1996. A gradient from stable to cyclic populations of *Clethrionomys rufocanus* in Hokkaido, Japan. *Proc. R. Soc. Lond. B Biol. Sci.* **263**: 1117–1126. doi:10.1098/rspb.1996.0164.
- Stenseth, N.C., Viljugrein, H., Saitoh, T., Hansen, T.F., Kittilsen, M.O., Bolviken, E., and Glockner, F. 2003. Seasonality, density dependence, and population cycles in Hokkaido voles. *Proc. Natl. Acad. Sci. U.S.A.* **100**: 11478–11483. doi:10.1073/pnas.1935306100. PMID:14504382.

- Turchin, P. 1993. Chaos and stability in rodent population dynamics — evidence from nonlinear time-series analysis. *Oikos*, **68**: 167–172. doi:10.2307/3545323.
- Turchin, P. 2003. Complex population dynamics: a theoretical/empirical synthesis. Princeton University Press, Princeton, N.J.
- Turchin, P., and Hanski, I. 2001. Contrasting alternative hypotheses about rodent cycles by translating them into parameterized models. *Ecol. Lett.* **4**: 267–276. doi:10.1046/j.1461-0248.2001.00204.x.
- Viljugrein, H., Lingjaerde, O.C., Stenseth, N.C., and Boyce, M.S. 2001. Spatio-temporal patterns of mink and muskrat in Canada during a quarter century. *J. Anim. Ecol.* **70**: 671–682. doi:10.1046/j.1365-2656.2001.00526.x.
- Wilson, D.J., Krebs, C.J., and Sinclair, T. 1999. Limitation of colored lemming populations during a population cycle. *Oikos*, **87**: 382–398. doi:10.2307/3546754.