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Seasonal demography of a cyclic lemming population in the Canadian Arctic

Dominique Fauteux[1]*, Gilles Gauthier[1] and Dominique Berteaux[2]

[1]Department of Biology and Centre d'études Nordiques, Université Laval, 1045 Avenue de la Médecine, Québec, QC G1V 0A6, Canada; and [2]Canada Research Chair on Northern Biodiversity and Centre d'études Nordiques, Université du Québec à Rimouski, 300 Allée des Ursulines, Rimouski, QC G5L 3A1, Canada

Summary

1. The causes of cyclical fluctuations in animal populations remain a controversial topic in ecology. Food limitation and predation are two leading hypotheses to explain small mammal population dynamics in northern environments. We documented the seasonal timing of the decline phases and demographic parameters (survival and reproduction) associated with population changes in lemmings, allowing us to evaluate some predictions from these two hypotheses.

2. We studied the demography of brown lemmings (*Lemmus trimucronatus*), a species showing 3- to 4-year population cycles in the Canadian Arctic, by combining capture–mark–recapture analysis of summer live-trapping with monitoring of winter nests over a 10-year period. We also examined the effects of some weather variables on survival.

3. We found that population declines after a peak occurred between the summer and winter period and not during the winter. During the summer, population growth was driven by change in survival, but not in fecundity or proportion of juveniles, whereas in winter population growth was driven by changes in late summer and winter reproduction.

4. We did not find evidence for direct density dependence on summer demographic parameters, though our analysis was constrained by the paucity of data during the low phase. Body mass, however, was highest in peak years.

5. Weather effects were detected only in early summer when lemming survival was positively related to snow depth at the onset of melt but negatively related to rainfall.

6. Our results show that high mortality causes population declines of lemmings during summer and fall, which suggests that predation is sufficient to cause population crashes, whereas high winter fecundity is the primary factor leading to population irruptions. The positive association between snow depth and early summer survival may be due to the protective cover offered by snow against predators. It is still unclear why reproduction remains low during the low phase.

Key-words: Bylot Island, fecundity, *Lemmus*, population cycles, population limitation, probability of survival, snow cover, winter nests

Introduction

Cyclic fluctuations in northern small mammal populations have been the focus of extensive research for almost 100 years (Krebs 2013), but a consensus on the predominant factors generating these cycles has not been reached (e.g. Gauthier *et al.* 2009). Although numerous long-term time series of fluctuations in small rodent abundance are available, detailed temporal changes in demographic parameters such as reproduction and survival remain scarce. Yet, such information is crucial to fully understand factors driving the dynamics of these populations (Krebs 2011).

Although social interactions may play an important role in the population dynamics of microtine species, the two most popular hypotheses for explaining lemming cycles are the bottom-up (i.e. food) and top-down (i.e. predators) limitation (Krebs 2013). According to the first hypothesis, population cycles should be controlled by

*Correspondence author. E-mail: dominique.fauteux.1@ulaval.ca

variations in food abundance or quality due to a delayed response of plants to grazing. High concentration of plant defensive compounds such as catechins, proteinase inhibitors or silica can affect food consumption and digestibility of small mammal (Seldal, Andersen & Hogstedt 1994; Berg 2003; Massey *et al.* 2008), but a link between grazing-induced levels of these compounds and population fluctuations was not found in several lemming and northern vole populations (Lindgren, Klint & Moen 2007; Dahlgren *et al.* 2009; Erlinge *et al.* 2011). Alternatively, overgrazing of plants during population peaks may cause the decline of small mammal populations, and low food abundance may limit subsequent population growth as plants need time to recover. Evidence for the food abundance hypothesis was found in both lemming and northern vole populations (Moen & Oksanen 1998; Turchin *et al.* 2000; Pitelka & Batzli 2007). According to the second hypothesis, delayed density-dependent effect of predation and the inability of the prey to compensate for the resulting high mortality could limit small rodent populations (Hanski *et al.* 2001; Gilg, Hanski & Sittler 2003).

One important difference exists between the predation and food abundance hypotheses as applied to the control of small tundra herbivores, namely the period of the year when conditions should be most limiting. The strong seasonality forces small herbivores like lemmings to survive on a limited food supply during the 9-month-long arctic winter when plants are dormant (Billings & Mooney 1968), and the accessibility may be hindered by ice crusts formed by melt–freeze events (Aars & Ims 2002; Korslund & Steen 2006). Thus, if food abundance is limiting, population decline should occur in winter, when food depletion will be most severe, as empirically shown in voles (Huitu *et al.* 2003; Ergon *et al.* 2004). In contrast, the predation rate on small mammals increases dramatically during the summer when birds of prey migrate to the Arctic to breed and the disappearance of snow increases access to prey for resident predators like foxes (Gilg *et al.* 2006; Bilodeau, Gauthier & Berteaux 2013b; Therrien *et al.* 2014). Therefore, if predation is the limiting factor, population decline should occur mostly during the snow-free period and especially in late summer when predator populations should be highest after the fledging/weaning of young. Determining the seasonal timing of each phase of lemming population cycles (i.e. growth and declines) and seasonal changes in vital rates is thus critical to establish what the most likely limiting factors are.

The demography of lemming and vole populations may differ between the phases of the cycle (Goswami *et al.* 2011). For instance, reproduction declined when lemmings were abundant at Barrow, Alaska (Pitelka & Batzli 2007), the proportion of juvenile collared lemmings (*Dicrostonyx groenlandicus*) was relatively low during the decline phase in Greenland (Gilg 2002), and the proportion of lactating Siberian brown lemmings (*Lemmus sibiricus*) was higher during the increase than the peak phase (Erlinge *et al.* 2000). As discussed by Goswami *et al.* (2011) for voles, phase-dependent demographic parameters may be indicative of future changes in densities. Other characteristics may also be associated with population density such as body mass, which is often highest during high abundance phases (Krebs 1964; Gilg 2002; Krebs *et al.* 2011b).

Snow quality affects both the amplitude and spatial synchrony of small mammal population cycles in Fennoscandia and eastern Greenland (Aars & Ims 2002; Kausrud *et al.* 2008; Gilg, Sittler & Hanski 2009). Even in northern Canada where the snow is dry, snow depth and density explain part of the annual variation in brown lemming (*Lemmus trimucronatus*) abundance, presumably because survival is higher under deep snow cover (Bilodeau, Gauthier & Berteaux 2013a). High summer rainfall may also negatively affect lemming survival through increased thermoregulation costs and burrow flooding, especially during snow melt (Shelford 1943; Reid, Krebs & Kenney 1995). However, few studies have analysed variations in lemming survival in relation to climatic factors.

On Bylot Island in the Canadian Arctic, annual summer trapping of brown lemmings has revealed large-amplitude fluctuations of abundance with a 3- to 4-year periodicity (Gruyer, Gauthier & Berteaux 2008). Since 2004, we have studied lemming summer demography with live-trapping data and their winter demography with winter nests (Duchesne, Gauthier & Berteaux 2011b). Lemming winter nests sampled after snow melt can provide an estimate of spring densities (Krebs *et al.* 2012), whereas the presence of small faeces in those nests can be used to infer winter reproduction (Duchesne, Gauthier & Berteaux 2011a). Thus, a combination of long time series of summer and winter demographic data can be used to pinpoint more accurately when population increases and declines occur, and determine which demographic factors are associated with seasonal population changes.

We had three objectives. First, we studied the seasonal timing of lemming population changes over three population cycles to determine whether declines occurred between the winter and early summer (as predicted by the food abundance hypothesis) or between summer and winter (as predicted by the predation hypothesis). Because lemmings consume a small proportion of the plant biomass at our study site in winter (Legagneux *et al.* 2012; Bilodeau *et al.* 2014) and summer predation is high (Therrien *et al.* 2014), we predicted that declines should occur mostly between the summer and winter periods. Our second objective was to identify changes in demographic parameters that are recurrent and associated with population fluctuations. We examined whether summer population growth was mostly related to change in survival, fecundity or proportion of juveniles and whether winter growth was related to fecundity and proportion of juveniles. We also investigated whether changes in demographic parameters and body mass could be due to direct density-dependent effects. Our third objective was to study the effects of selected weather variables on summer survival of lemmings. Based on the study of Bilodeau, Gauthier & Berteaux (2013a), we hypothesized that a deep snow cover in spring should increase early summer survival by extending the period during which lemmings are protected from predation under the snow. In contrast, we hypothesized that heavy summer rainfall should reduce summer survival, especially during spring thaw.

Materials and methods

STUDY AREA

Our study area was located in the Qarlikturvik valley (~50 km^2) on Bylot Island, Nunavut, Canada (73°08′ N; 80°00′ W). Two main habitats dominate the valley and are used by lemmings (Duchesne, Gauthier & Berteaux 2011b). The wet habitat consists primarily of a mosaic of tundra polygons, ponds and thaw lakes and is common in the valley bottom. The surrounding slopes and hills as well as higher grounds in the valley are characterized by mesic tundra, the dominant habitat. The vegetation of the wet habitat is composed of sedges (*Eriophorum* spp., *Carex aquatilis*), grasses (*Dupontia fisheri*) and brown mosses (such as *Limprichtia cossonii* and *Campylium stellatum*), while prostrate shrubs (*Salix* spp., *Cassiope tetragona*), grasses (*Arctagrostis latifolia, Alopecurus alpinus*), forbs (*Saxifraga* spp., *Ranunculus* spp.) and some mosses (such a *Polytrichum swartzii*) are dominant in the mesic habitat (Bilodeau *et al.* 2014). The average annual temperature is −15 °C, and the ground is generally covered by snow from early October to mid-June.

Only two rodent species are present on Bylot Island: brown and collared lemmings. Here, we focus on the former species because it is the most abundant and its abundance fluctuate >40-fold between the low and peak phases of its cycle (Gruyer, Gauthier & Berteaux 2008). Other herbivores include the snow goose (*Anser caerulescens*; during the summer only) and arctic hare (*Lepus arcticus*) and rock ptarmigan (*Lagopus muta*) at very low densities. The main predators are the ermine (*Mustela erminea*), arctic fox (*Vulpes lagopus*), snowy owl (*Bubo scandiacus*) and long-tailed jaeger (*Stercorarius longicaudus*).

SMALL MAMMAL TRAPPING

From 2004 to 2013, we live-trapped lemmings in two 11-ha permanent grids, one located in wet habitat and one in mesic habitat. Each grid was laid out in a 12 × 12 Cartesian plane (10 × 10 from 2004 to 2006) with 144 trapping stations (100 from 2004 to 2006) separated by 30 m. From 2007 to 2013, a third trapping grid of 7·3 ha (10 × 10) was located in mesic habitat and used for a snow fencing experiment (2008–2011). Although the enhanced snow depth on that grid increased the density of winter nests, it had no effect on summer population density (Bilodeau *et al.* 2013b). We thus used data from this grid to estimate summer demographic parameters, but not winter parameters. All trapping grids were separated by >500 m to minimize spatial dependence.

Trapping stations had one Longworth trap baited with a piece of apple and stuffed with a 10-cm ball of cotton batting to provide warmth and bedding material. Lemmings were trapped during four primary periods (mid-June, beginning and end of July and mid-August) from 2004 to 2007 and three periods afterwards (mid-June, mid-July and mid-August) according to Pollock's robust design (Williams, Nichols & Conroy 2002). During each primary period, we visited traps twice a day at 12-h intervals for three consecutive days (4 days from 2004 to 2006), for a total of six (or eight) secondary occasions. We activated one grid at a time and trapping was done consecutively on the three grids at each primary occasion. Traps remained in the field between primary periods for pre-baiting. All captured lemmings were identified to species, weighed, sexed, marked with a Passive Integrated Transponder (PIT, AVID®; Avid Identification Systems, Inc., Norco, CA, USA) tag, and the reproductive condition of females was noted. Females were noted as lactating or gravid when their mammary glands were visible or when foetuses were palpable. From 2010 to 2013, males were noted as reproductive if their scrotum was visible. All subsequent recaptures were noted. Manipulations were approved by the Animal Welfare Committee of Université Laval and Parks Canada (SIR-2013-13953).

ESTIMATION OF SUMMER DEMOGRAPHIC PARAMETERS

We estimated five demographic parameters during the summer: population density (D), survival (S), fecundity (B), proportion of juveniles (J) and body mass (M). Three separate estimates of each parameter were calculated for lemmings trapped on each grid in June, July and August, except for survival which was calculated for the two intervals. From 2004 to 2007, lemmings trapped during both periods of July were pooled as one July group for B, J and M estimations. Demographic parameters (except D, see below) could not be estimated at periods with <5 lemming captures, which frequently occurred during the low phases of the cycle. Sample sizes are provided in Appendix S1 (Supporting Information).

Population density was modelled with spatially explicit capture–recapture (SECR) analyses with the package 'secr' implemented in the R software (Efford 2014). This inferential approach uses the spatial structure of the trapping grids and the location of each trapped animal in the grids to estimate densities (lemming ha^{-1}) using a maximum-likelihood approach (Efford & Fewster 2013). We used the null SECR model with a 100-m buffer and the half-normal detection function to estimate densities and their standard errors (Krebs *et al.* 2011a). If <4 lemmings were trapped on a grid during a primary period, we used the minimum number of animals alive.

Capture–mark–recapture analyses (Williams, Nichols & Conroy 2002) were used to estimate survival probabilities between the primary periods (see Appendix S2, Supporting Information for methodological details). We estimated the fecundity of females as the proportion of adult females that were lactating or gravid, and the proportion of juveniles among all captured individuals. Females and males were considered adults if they weighed ≥28 g and ≥30 g, respectively (see Appendix S3, Supporting Information for criteria used to determine this threshold), and juveniles below these values (individuals became trappable at ~12 g).

ESTIMATION OF WINTER DEMOGRAPHIC PARAMETERS

Starting in 2007, we sampled winter nests after snow melt. During winter, lemmings are most abundant in mesic tundra and especially in small gullies along intermittent streams, which are conducive to deep snow accumulation (Duchesne, Gauthier & Berteaux 2011b). We sampled winter nests along forty 500-m-long permanent transects (evenly split between mesic tundra and stream gullies) randomly distributed over 40 km^2. While walking along each transect, we removed all winter nests found and recorded the perpendicular distance from the transect. Nests are easy to detect at our site due to the low vegetation height. All nests were classified as brown or collared lemmings according to the size, shape and colour of the faeces (Duchesne, Gauthier & Berteaux 2011b; Soininen *et al.* 2015). We eliminated from the analysis the small number of nests containing faeces of both species. We used the line transect method (Buckland 2001) and the software DISTANCE 6.0 (Thomas *et al.* 2010) to estimate overall densities of brown lemming nests and the associated variance.

The proportion of brown lemming nests with signs of reproduction (based on the presence of small faeces using the criteria of Duchesne, Gauthier & Berteaux 2011a) among those found across all transects provided an overall index of their reproductive activity during winter (a single value per year). To increase sample size in years of low lemming abundance, we also used nests collected along transects run in the wet areas (used to study winter habitat selection; Duchesne, Gauthier & Berteaux 2011b) and those found while walking on our trapping grids or opportunistically to determine reproductive activity.

WEATHER VARIABLES

We collected snow and rainfall data at the study site every year. Spring snow depth was monitored annually from ca 25 May to 3 June until disappearance (around 20 June). Snow depth was measured every two days at 50 stations spaced out by 10 m along two 250-m transects running parallel to each other and separated by 100 m. The transects encompassed the two main habitats, wet and mesic. We used the average snow depth observed between 5 and 7 June to obtain an annual measure in spring because these dates were available through all years of the study. Daily rainfall (mm day^{-1}) was measured with a rain gauge from early June until 20 August annually. We averaged daily rainfall for two periods: early (6 June–20 July) and late summer (21 July–20 August). The date of 20 July corresponds to the end of our mid-summer live-trapping period.

STATISTICAL ANALYSES

We used linear mixed-effects models (LMMs) to estimate the relationships between change in population density and demographic parameters. Trapping grids were used as a random factor because the same grids were sampled repeatedly. Coefficients and their standard errors (which are reported throughout the paper) were obtained with the packages 'lme4' (Bates *et al.* 2014) and 'contrast' (Kuhn *et al.* 2013) within the R software. Population growth rates were ln-transformed, as well as densities to respect normality if necessary, and homoscedasticity was determined visually by plotting the residuals in relation to fitted values. We checked for collinearity among independent variables with Pearson correlations and we avoided including highly correlated variables ($r \geq 0{\cdot}7$) simultaneously in models. Relationships were considered statistically significant when the 95% confidence interval of the slope excluded 0. To assess the amount of variation explained by our models, we report the marginal R_g^2 (for fixed effects) and conditional R_c^2 (for fixed and random effects) calculated with the method proposed by Nakagawa & Schielzeth (2013) for mixed-effects models.

We used two time units to study changes in population density: intraseasonal (between months, *m*) for summer analyses and interannual (*w*) for winter analyses. We first examined the relationships between the population growth rate (λ) on each trapping grid and various demographic parameters to verify which ones could explain changes in numbers. To study the effect of winter demography on λ, we examined the relationship between changes in population density from August of year *y* to June of year *y* + 1 and nest density (M1) or the fecundity index observed in winter nests (M2; Table 1). We also examined the relationships between winter λ and late summer demographic parameters (fecundity and proportion of juveniles, models M3–M4). We used separate models because several of these independent variables were highly correlated (see Results). We further assessed the relationship between annual change in winter nest density and population density measured in August (model M5). For intraseasonal analyses, we examined the relationship between λ during

Table 1. Candidate models for determining the effects of demographic parameters on lemming population growth rate and density-dependent effects on demographic parameters

Model ID	Response variables	Independent variables	Model description
M1	λ_w	D^{WN}	Effect of winter nest density on winter population growth rate
M2	λ_w	B^{WN}	Effect of winter reproduction on winter population growth rate
M3	λ_w	B^A	Effect of August fecundity on winter population growth rate
M4	λ_w	J^A	Effect of proportion of juveniles in August on winter population growth rate
M5	λ^{WN}	D^A	Effect of August population density on change in winter nest density
M6	λ_m	S_m	Effect of monthly survival (from *m* to *m* + 1) on monthly population growth rate
M7	λ_m	B_m	Effect of monthly fecundity on monthly population growth rate
M8	λ_m	J_m	Effect of monthly proportion of juveniles on monthly population growth rate
M9	S_m	D_m	Direct density dependence on monthly survival (from *m* to *m* + 1)
M10	J_m	D_m, *m*	Direct density dependence on monthly proportion of juveniles
M11	B_m	D_m, *m*	Direct density dependence on monthly fecundity
M12	M_m	D_m, *m*	Direct density dependence on monthly body mass

$\lambda_w = D^{Jn}_{w+1}/D^A_w$; $\lambda_m = D_{m+1}/D_m$; $\lambda^{WN} = D^{WN}_{w+1}/D^{WN}_w$; λ = population growth rate; *D* = population density; D^{WN} = winter nest density; *S* = survival; *B* = fecundity; *J* = proportion of juveniles; *M* = body mass; *Jn* = June; *A* = August; *m* = month; *w* = winter.

the summer months and demographic parameters observed during the interval (for survival, model M6) or at the start of the interval (for fecundity and proportion of juveniles, models M7 and M8) on each trapping grid.

In simple linear regressions between two variables measured with an error, such as survival and population density, the uncertainty associated with the slope should consider variance components of both variables. We thus used ranged major axis regressions to estimate the slope and its 95% confidence intervals when an error was present on both axes (models M1, M5 and M6) with the package 'lmodel2' (Legendre 2014) implemented in the software R. Coefficients estimated with ranged major axis regressions assume that the response and explanatory variables are correlated, which was verified.

We tested for direct density dependence on summer survival, proportion of juveniles, adult body mass (both sexes combined) and fecundity (i.e. relationships between demographic parameters and monthly population density on each trapping grid, models M9–M12, Table 1). We conducted analyses on fecundity if we had ≥5 adult females and on proportion of juveniles if we had ≥5 lemmings, regardless of age and sex. Post hoc multiple comparisons were conducted using Tukey's tests to determine whether there were differences between months.

We used LMMs to assess potential effects of weather variables on demographic parameters, also using trapping grid as a random variable. We examined the relationships between June–July survival (dependent variable) and spring snow depth or June–July rainfall, and between July–August survival and July–August rainfall.

Results

FLUCTUATIONS IN LEMMING ABUNDANCE

Brown lemmings showed large fluctuations in abundance (Fig. 1). During summer 2004, population density was high but declined to reach very low values in early summer 2005 until summer 2007. Nest density increased in winter 2007–2008 compared to the previous one. Population density was high in early summer 2008 but winter nest density indicated that it had declined to low levels by the following winter and remained low in summer 2009. Nest density increased in winter 2009–2010 as well as population density in summer 2010 compared to the previous year. Nest and population densities remained high during winter 2010–2011 and early summer 2011. Population density declined in summer 2011, and nest density was very low during the following winter. Lemming abundance was very low during summers 2012 and 2013 and the winter in between.

ESTIMATION OF DEMOGRAPHIC PARAMETERS

Sample size allowed an estimation of summer survival only in years of high abundance (2004, 2008, 2010 and 2011). The most parsimonious models for estimating probabilities of survival differed between years (see Appendix S2 for model selection). In 2004 and 2008, models with constant survival between months and trapping grids were preferred, but survival probabilities differed between trapping grids in 2010 and trapping grids and months in 2011. Model-averaged survival estimates in 2010 and 2011 were higher in the mesic trapping grids compared to the wet grid and higher in June–July than July–August (Table 2).

Estimation of summer fecundity was also possible only in years of high abundance. The average proportion of females with signs of reproduction was lowest in August 2008 ($B = 0{\cdot}07$, $n = 13$) and highest in July 2010 ($B = 0{\cdot}69$, $n = 60$). In winter, the proportion of nests with signs of reproduction averaged 0·25 ($n = 1534$). The lowest value occurred in 2007 ($B^{\mathrm{WN}} = 0{\cdot}12$, $n = 76$) and the highest in 2010 ($B^{\mathrm{WN}} = 0{\cdot}41$, $n = 497$). The proportion of juveniles could be estimated in most years except in 2013 and a few periods in 2006, 2009 and 2012. The lowest proportion of juveniles value occurred in June 2005 with no juvenile captured ($J = 0{\cdot}0$, $n = 11$) and the highest value in August 2008 ($J = 0{\cdot}72$, $n = 80$). The average body mass of adult lemmings could not be estimated in 2006, 2013 and some periods in 2007, 2009 and 2012. The

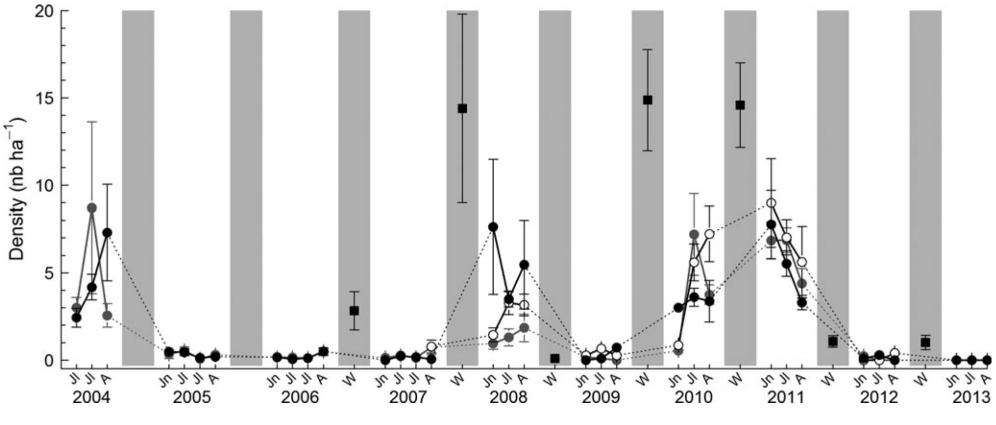

Fig. 1. Temporal fluctuations in brown lemming populations represented by monthly population densities in summer (circles) and nests densities in winter (squares) with their standard error on Bylot Island, NU, Canada. Population densities are presented for three trapping grids: wet (black circles), mesic 1 (grey circles) and mesic 2 (open circles, starting in 2007 only). Winter nest densities (black squares) are averaged values across the study area. Grey areas represent winters and stippled lines links late summer population density of year *y* with early summer population density of year *y* + 1. *Jn* = June; *Jl* = July; *A* = August; *W* = winter.

Table 2. Monthly survival probability estimates (S) of brown lemmings trapped on three different grids on Bylot Island. Periods extend from the middle of each month except in 2004. Survival was obtained by capture–mark–recapture analysis, which controls for capture probabilities, and mean and standard errors were averaged across models (see Appendix S2)

		Mesic 1		Mesic 2		Wet	
Year	Period	S	SE	S	SE	S	SE
2004	June–July[a]	0·32	0·06	[b]		0·30	0·06
	July–August[c]	0·31	0·06			0·29	0·05
2008	June–July	0·26	0·07	0·27	0·06	0·26	0·05
	July–August	0·28	0·07	0·28	0·06	0·27	0·05
2010	June–July	0·56	0·24	0·56	0·19	0·38	0·15
	July–August	0·41	0·07	0·45	0·09	0·31	0·08
2011	June–July	0·61	0·09	0·59	0·10	0·44	0·10
	July–August	0·28	0·06	0·34	0·09	0·13	0·07

[a] Survival estimates for the period of early July to end of July.

[b] Grid «Mesic 2» did not exist in 2004.

[c] Survival estimates for the period of end of July to mid-August.

lowest average body mass was observed in June 2012 (M = 35·4 g, n = 5) and the highest in July 2011 (M = 56·8 g, n = 230).

COVARIATE EFFECTS ON DEMOGRAPHIC PARAMETERS

Growth rate of lemming populations over winter was positively related to winter nest density (M1) and to reproductive activity in winter nests (M2, Table 3). Winter nest density and fecundity index were highly correlated (r = 0·89). Thus, when density of winter nests and reproductive rates were high, the population increased, but it decreased when these parameters were low (Fig. 2A). Similarly, population growth rate over winter was positively related to the proportion of reproductive females in August (M3, Fig. 2B), but not to the proportion of juveniles (M4, Table 3). Fecundity in August and in nests during the following winter were also positively correlated (r = 0·75). In contrast, annual change in winter nest density was negatively related with population density in late August (M5).

During the summer, monthly growth rate of lemming populations was positively related to their survival rate (M6, Fig. 3), but not to fecundity (M7) or proportion of juveniles (M8, Table 3). Although demographic parameters were variable during the summer, we found no direct density-dependent effect on survival, recruitment or fecundity (M9, M10 and M11, Table 3). The proportion of juvenile lemmings was higher (M10) in August (0·54) compared to June (0·25) and July (0·20), but fecundity of adult females was similar (M11) between months (June: 0·37, July: 0·44, August: 0·35). The only significant direct density-dependent effect was on body mass (M12, Table 3). Adult lemmings were heavier during high abundance years than in low years and heavier in July (57·5 g) than in June (36·8 g) or August (46·7 g; Fig. 4).

WEATHER EFFECTS

The snow depth observed at the beginning of melt and total rainfall in June–July had opposite effects on early summer lemming survival (R^2_c = 0·74, R^2_g = 0·85); survival probability increased with snow depth (β = 0·008, SE = 0·002) but decreased with daily rainfall (β = –0·39, SE = 0·08; Fig. 5). Daily rainfall did not have any effect on late summer survival (β = 0·00, SE = 0·02).

Table 3. Slope parameters and their 95% confidence intervals (CI) for all variables tested in the models described in Table 1. Variables and coefficients in bold have confidence intervals that exclude 0. Marginal R^2 for mixed-effects models are shown and were identical to conditional R^2 for all models except M9 (R^2_c = 0·07)

Model ID	Response variable	Explanatory variable	β	Low CI	High CI	R^2_g
M1[a]	$\ln(\lambda_w)$	$\boldsymbol{D^{WN}}$	**1·58**	**0·94**	**2·54**	0·55
M2	$\ln(\lambda_w)$	$\boldsymbol{B^{WN}}$	**25·6**	**17·3**	**33·9**	0·70
M3	$\ln(\lambda_w)$	$\boldsymbol{B^{A}}$	**7·53**	**3·76**	**11·3**	0·69
M4	$\ln(\lambda_w)$	J^{A}	–2·18	–6·96	2·60	0·07
M5[a]	$\ln(\lambda^{WN})$	$\boldsymbol{\ln(D^{A})}$	**–1·23**	**–3·28**	**–0·41**	0·29
M6[a]	$\ln(\lambda_m)$	$\boldsymbol{S_m}$	**4·95**	**0·33**	**14·8**	0·18
M7	$\ln(\lambda_m)$	B_m	–0·50	–1·43	0·44	0·02
M8	$\ln(\lambda_m)$	J_m	0·61	–2·13	3·35	0·01
M9	S_m	$\ln(D_m)$	–0·01	–0·08	0·06	0·00
M10	J_m	$\ln(D_m)$	–0·00	–0·05	0·04	0·49
		$\boldsymbol{m_{Jl}}$	**–0·39**	**–0·53**	**–0·26**	
		$\boldsymbol{m_{Jn}}$	**–0·37**	**–0·52**	**–0·22**	
M11	B_m	$\ln(D_m)$	0·14	–0·05	0·33	0·11
		m_{Jl}	0·08	–0·15	0·32	
		m_{Jn}	0·00	–0·29	0·29	
M12	M_m	$\boldsymbol{D_m}$	**1·02**	**0·34**	**1·70**	0·34
		$\boldsymbol{m_A}$	**–4·90**	**–9·26**	**–0·55**	
		$\boldsymbol{m_{Jn}}$	**–6·66**	**–11·28**	**–2·04**	

λ = population growth rate; D = population density; WN = winter nest density; S = survival; B = fecundity; J = proportion of juveniles; M = body mass; m = month; w = winter; A = August; Jl = July; Jn = June.

[a] Slope estimated with a ranged major axis regression.

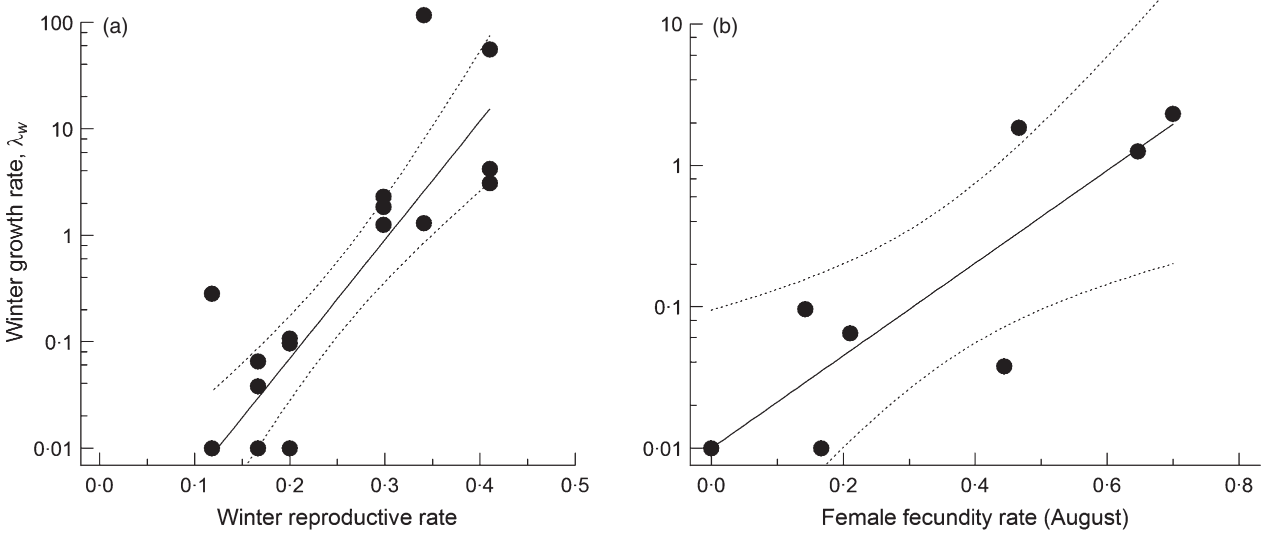

Fig. 2. Relationships between winter population growth rate (λ_w, from August of year y to June of year $y + 1$) of brown lemmings on each trapping grid and reproductive rate in winter nests (a) as well as fecundity of adult females measured in August (b). The regression (solid lines) and 95% confidence intervals (dotted lines) are presented.

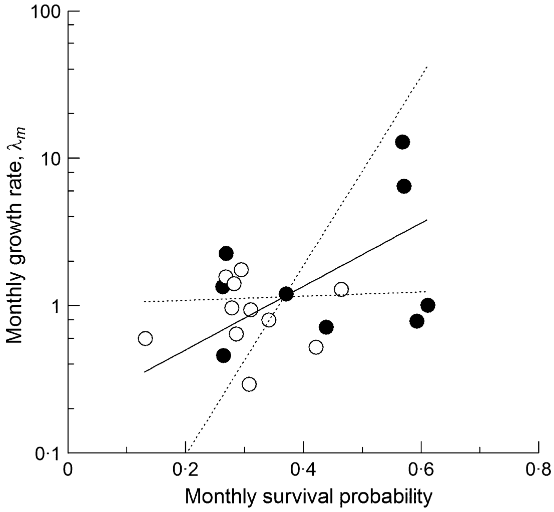

Fig. 3. Relationship between monthly population growth rate (λ_m) of brown lemmings and survival probability over the same period on each trapping grid. Monthly survival estimates are shown for the periods June–July (filled circles) and July–August (open circles). Regression (solid line) and 95% confidence interval (dotted lines) were estimated with a ranged major axis regression.

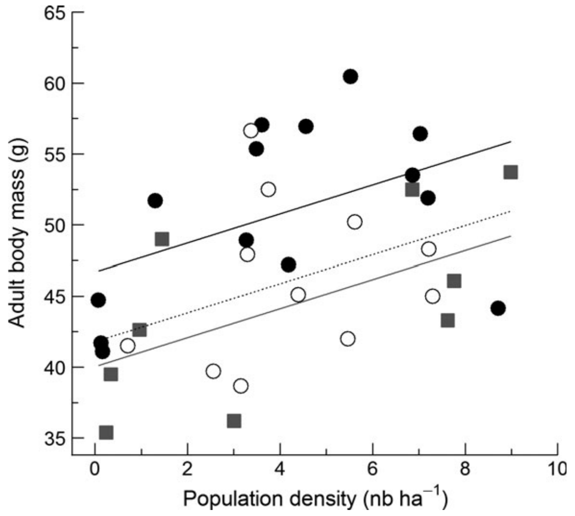

Fig. 4. Relationship between adult body mass of brown lemmings and population density measured in June (grey squares and line), July (black circles and line) and August (open circles and line) on each trapping grid.

Discussion

TIMING OF POPULATION CHANGE

Our results show that lemming population declines occurred between the late summer and winter periods on Bylot Island. Indeed, a large population decline between late summer and the following spring was associated with a very low abundance of winter nests and was further confirmed by the negative relationship between annual change in winter nests and late summer density. This is likely a general pattern as Krebs *et al.* (2012) reported that winter nest abundance was more strongly correlated with spring than late summer population size across several sites in the Canadian Arctic. In contrast, population build-ups during our study occurred in winter as high density of winter nests was associated with peak lemming densities in the following summers. Finally, periods of peak density were short-lived and were followed by a population decline before the onset of winter as evidenced by the low density of nests in winters following peak summer abundance.

Winter nests provide shelters for lemmings under the snow and are important for thermoregulation, rearing young and survival (Casey 1981; Duchesne, Gauthier &

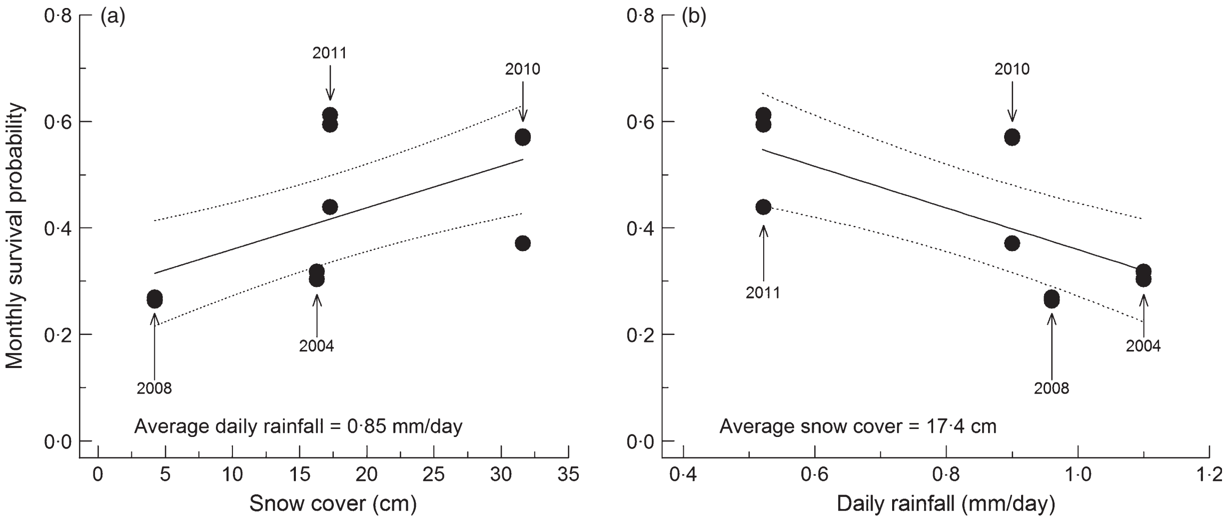

Fig. 5. Relationships between early summer (June–July) survival probability of brown lemmings on each trapping grid and spring snow depth (a) and mean daily rainfall (b). The regression (solid lines) and 95% confidence intervals (dotted lines) are presented.

Berteaux 2011b). Our results show that reproductive activity in those nests can be very high in some years. In certain areas, lemmings can apparently overwinter in natural sites with a high accumulation of litter, such as in tussock tundra in northern Alaska (Krebs *et al.* 2012). However, these features are absent from most of the Canadian High Arctic due to the sparse vegetation cover. Therefore, as the ground freezes in the fall and snow sets in, these nests become important shelters. The strong positive relationship between winter population growth rate and reproductive activity substantiates previous suggestions that lemming population growth is conditional to high winter reproduction (Millar 2001; Krebs 2011).

The seasonal pattern in brown lemming population changes that we document here differs from the one reported in northern Alaska. At this site, high winter nest density is generally associated with low population density at snow melt, which suggests that population crashes occur mostly during winter, possibly due to winter food limitation (Pitelka & Batzli 2007). Interestingly, peak lemming densities in northern Alaska can reach 100–200 ind ha^{-1}, much higher than peak densities elsewhere in the Canadian Arctic or Greenland, usually 10–15 ind ha^{-1} (Wilson, Krebs & Sinclair 1999; Gilg, Hanski & Sittler 2003; this study). Experimental and observational studies conducted at the latter sites suggest that delayed density-dependent effects of specialist predators (e.g. weasels) and direct density-dependent effects of generalist predators cause population declines (Wilson, Krebs & Sinclair 1999; Gilg, Hanski & Sittler 2003) or maintain populations at low density (Reid, Krebs & Kenney 1995). In northern voles, an experimental removal of predators allowed peak populations to exceed 150 ind ha^{-1} compared to <50 ind ha^{-1} on the control, which resulted in a population crash due to winter food limitation (Huitu *et al.* 2003).

Recent evidence shows that, unlike what has been reported for *Lemmus* elsewhere, brown lemmings on Bylot Island consume willows (*Salix* spp.) in high proportion during winter (56% of their diet), along with mosses (Soininen *et al.* 2015). They can take advantage of the high abundance of prostrate willows at our study site during the critical winter period without negatively affecting its biomass in snow beds, even during years of high abundance (Bilodeau *et al.* 2014). Thus, a lack of food during winter, as predicted by the food abundance hypothesis, is unlikely to explain the periodic declines of brown lemmings in the Canadian Arctic.

DEMOGRAPHY AND POPULATION CHANGES

We found a highly interesting contrast between summer and winter in the demographic factors associated with lemming population changes. During the summer, population growth was apparently driven by change in survival, but not in fecundity or proportion of juveniles, whereas in winter it was driven by changes in late summer and winter reproduction. Even though we used capture–recapture methods to estimate survival, we recognize that mortality is here confounded with permanent emigration, which includes dispersal, and could vary with phases of the cycle. However, given that survival could only be estimated in years of moderately high abundance, variations in dispersal rate with cycle phase should not be a serious issue here. Although we could not measure survival probability during winter, the contrasting effects of fecundity on summer and winter population growth rates indicate that factors limiting lemmings vary seasonally.

During summer, it is safe to say that predation is the main cause of mortality due to the high abundance of birds of prey, foxes and ermines (Reid, Krebs & Kenney 1995; Therrien *et al.* 2014). Because survival was the only demographic parameter related to summer population change, predation may thus be the main factor driving lemmings into a summer decline, as found in Greenland (Gilg *et al.* 2006). Young born in winter will have matured and should be able to reproduce during the summer, which could explain why the proportion of juveniles in the population peaked in late summer. Nonetheless, high reproductive activity did not prevent the summer population to decline. Although we have no data from mid-August until the onset of snow in October, predation is likely to remain high as the population of predators should increase with the addition of recently fledged and weaned juveniles.

At the beginning of winter, lemmings move under the snow and become less vulnerable to predation (Duchesne, Gauthier & Berteaux 2011b; Bilodeau, Gauthier & Berteaux 2013b). Furthermore, most avian predators have migrated southwards (Gilg, Sittler & Hanski 2009; Therrien *et al.* 2014). Thus, lemming survival should improve as soon as the snow cover settles, which may explain why fecundity then becomes a driver of lemming population change, unlike in the summer. Interestingly, winter population growth rate was also positively associated with fecundity in August. The reproductive output of lemmings during winter may thus be dependent upon their condition in late summer, as also reported by Wilson, Krebs & Sinclair (1999) and Krebs *et al.* (2011b). Nonetheless, we recognize that we have no data on winter survival, and nests only provide information on overall reproduction during the 9-month-long winter period. For instance, we have no information on the timing of winter reproduction, whereas breeding onset can be important in some vole population dynamics (Ergon *et al.* 2011).

We did not find any evidence for direct density dependence on summer demographic parameters, which indicates that density had little direct effect on summer growth. However, a limitation of our analysis was that these parameters, and especially survival, could only be estimated in years of moderate to high densities due to small sample sizes in other years. Therefore, density-dependent effects could still be present when considering all phases of the cycle (Goswami *et al.* 2011). The strong effect of weather on summer survival may also have weakened our ability to detect density dependence. Body mass of adult lemmings was the only density-dependent parameter, which supports the hypothesis that lemmings are generally larger during years of peak density (Krebs 1964; Gilg 2002).

If reproduction is driving population growth in winter, it is surprising that populations do not recover more quickly after a population crash. Clearly, the population must be exposed to delayed density dependence that prevents its quick recovery (Boonstra, Krebs & Stenseth 1998; Barraquand *et al.* 2014). A possible mechanism may be a delayed, negative neuro-endocrinological effect on fecundity, as recently shown in the snowshoe hares (*Lepus americanus*; Boonstra *et al.* 1998; Sheriff, Krebs & Boonstra 2009) and root voles (*Microtus oeconomus*; Bian *et al.* 2015). Chronic stress induced by high predator density or social interactions, either alone or in interaction with predation risk, may cause breeding suppression in small mammals and be carried over to the winter period due to maternal effects (Jochym & Halle 2012). However, we note that we did not find any density-dependent effect on fecundity, and Ylönen *et al.* (2006) found no change in corticosterone levels in bank voles (*Myodes glareolus*) exposed to weasel odours. In some vole populations, it has been suggested that a delay in the initiation of spring breeding due to grazing-induced change in plant quality (e.g. phenolic compounds or silica content) could be a mechanism leading to delayed density dependence (Massey *et al.* 2008; Ergon *et al.* 2011). However, considering that lemming reproduction occurs in winter when plants are dormant (Billings & Mooney 1968), it is difficult to imagine how such mechanisms could operate. It is also possible that poor snow condition limits access to food in some winters (Korslund & Steen 2006).

EFFECTS OF WEATHER ON SUMMER SURVIVAL

Our analysis suggests that climatic factors may also affect summer survival of lemmings. However, it is possible that the high early summer survival in years of deep snow cover is actually an indirect effect mediated through predation. Although deep snow cover in winter may provide benefits to lemmings in terms of improved insulation (Duchesne, Gauthier & Berteaux 2011b), this is unlikely at snow melt when temperatures are milder above the snow pack than underneath (Bilodeau *et al.* 2013a). A deep snow cover will delay snow melt and could allow lemmings to move for a longer period of time under the protective cover offered by snow during the melt period (Gilg, Sittler & Hanski 2009). The result is also consistent with the positive correlation between snow depth and the amplitude of lemming population cycles shown by Bilodeau, Gauthier & Berteaux (2013b).

High rainfall was another climatic factor that negatively affected early summer survival of lemmings. High precipitation during spring should accelerate the melting of snow, increase the run-off and cause streams to overflow. On one hand, this could reduce the period during which snow still offers a protective cover. On the other hand, high rainfall may flood lemming habitats in lowlands, including burrows, thereby increasing mortality. This could also force individuals to move more in search of drier grounds, thereby increasing their vulnerability to predators (Shelford 1943).

CONCLUSION

Our study presents for the first time a detailed analysis of the seasonal (summer and winter) demography of a lemming species over multiple cycles. We show that mortality, likely due to predation, drives summer population growth and is the major factor causing fall population crashes during peak years in brown lemmings. High winter reproduction appears to be the main driver of the increase phase of the population cycle, but it is still unclear why reproduction does not increase immediately after the decline (i.e. the low phase remains unexplained). A neuroendocrinological response through maternal effects is a candidate factor, though a limited access to food in years of poor snow condition is another one. Additional experimental manipulations will be required to fully decipher the causal effects of predation or food on these demographic parameters (Huitu *et al.* 2003; Krebs 2011). Our results support a multifactorial hypothesis to explain lemming population growth and decline phases where changes in survival and reproduction may be caused by both biotic (i.e. direct and possibly also indirect effects of predators) and abiotic (i.e. snow cover and rainfall) factors. The general decline of snow cover observed in the Canadian Arctic (Derksen & Brown 2012) may be of particular concern for lemming populations because it may extend their period of vulnerability to predators during the snow-free period while reducing their potential for population growth under the snow.

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Data accessibility

All data used in this manuscript are available at the NordicanaD website: http://dx.doi.org/10.5885/45400AW-9891BD76704C4CE2 (Gauthier 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Sample size.

Appendix S2. Methods and model selection for the estimation of survival probabilities.

Appendix S3. Body mass criteria used to determine maturity.