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Demography of two lemming species on Bylot Island, Nunavut, Canada

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Abstract Lemmings play a key role in the tundra food web and their widely reported cyclic oscillations in abundance may have a strong effect on other components of the ecosystem. We documented seasonal and annual variations in population density, reproductive activity, survival, and body mass of two sympatric species, the brown (*Lemmus trimucronatus*) and collared lemmings (*Dicrostonyx groenlandicus*), over a 2-year period on Bylot Island, Nunavut, Canada. We live trapped and marked lemmings on two grids throughout the summer and we estimated demographic parameters using three different capture–recapture methods. All three methods are based on robust estimators and they yielded similar population density estimates. The density of brown lemmings declined markedly between the 2 years whereas that of collared lemmings was relatively constant. For brown lemmings, 2004 was a peak year in their cycle and 2005 a decline phase. Density of brown lemmings also decreased during the summer, but not that of collared lemmings. The recruitment of juvenile brown lemmings in the population increased during the summer and was higher in the peak year than in the year after, but no change was detected in collared lemmings. Survival rates of both species tended to be lower during the peak year than in the following year and body mass of brown lemmings was higher in the peak year than in the following year. We conclude that both changes in adult survival and juvenile recruitment occur during the population decline of brown lemmings.

Keywords Capture-mark-recapture · Population dynamic · Population cycle · Population density · Survival · Reproduction · Small mammals

Introduction

Cyclic fluctuations of large amplitude have been reported for a long time in small mammal populations (Elton 1924; Krebs et al. 1973; Stenseth and Ims 1993a). These fluctuations are characterised by a remarkable periodicity (typically 3–5 years) but can be of highly variable amplitude (Framstad et al. 1993b; Stenseth 1999; Angerbjörn et al. 2001). Although cyclic fluctuations are most prevalent in northern species such as lemmings, they can vary in space or time within a given species (Stenseth 1999; Angerbjörn et al. 2001; Ims et al. 2008). Lemmings (genus *Lemmus* and *Dicrostonyx*) are widespread throughout the arctic tundra and, because they are at the base of the animal tundra food web, their population fluctuations have considerable impact on the whole ecosystem (Krebs et al. 2003; Gauthier et al. 2004; Ims and Fuglei 2005). The cause(s) of cyclic fluctuations in lemmings and other small mammals is a lasting enigma and a source of controversy (e.g. Korpimaki et al. 2004; Lambin et al. 2006; Sundell 2006; Gauthier et al. 2009). Although there is a growing consensus that cycles may result from specialised trophic interactions, some argue that they are driven by lack of food (i.e. bottom-up forces, Turchin et al. 2000; Turchin and Batzli 2001; Oksanen et al. 2008) whereas others advocate that predation by specialised

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predators drives the cycles (top-down forces, Reid et al. 1995; Hanski et al. 2001; Gilg et al. 2003; Krebs et al. 2003).

Progress in our understanding of the causes of population cycles in small mammals has been hindered by the fact that many studies have focused only on the dynamic patterns (e.g. occurrence or not of multiannual cycles and their shape; the density paradigm) rather than on the underlying demographic mechanisms (Gilg 2002; Krebs 2002; Gauthier et al. 2009). Population fluctuations are the results of basic demographic processes, such as survival, birth, emigration, and immigration, but we know relatively little about how demographic parameters vary during a cyclic phase (i.e. seasonally) or between phases (i.e. between years) of most lemming populations.

Lemmings mature early, have large litters, breed frequently, and have a short life span (Millar 2001). Early born young mature and reproduce during their first summer and, in some species, reproduction starts during late winter, when snow cover reduces predation risk (Korpimaki et al. 2004). Predation is the main source of lemming mortality (Reid et al. 1995; Wilson et al. 1999; Gilg 2002; Korpimaki et al. 2003, 2004), and can be sufficient to prevent summer population growth and to limit populations. In small mammals, life-history traits such as survival, reproduction and body mass are typically higher during the increase and peak years than during the decline phase, but this may result both from intraspecific density-dependent effects and predation (Wilson et al. 1999; Gilg 2002; Klemola et al. 2002; Norrdahl and Korpimaki 2002; Korpimaki et al. 2004).

Detailed demographic studies of lemming populations in North America are mostly limited to coastal areas of the Western Arctic (e.g. Krebs et al. 1995; Reid et al. 1995; Wilson et al. 1999), with relatively few studies conducted in the Canadian Arctic islands (Fuller et al. 1975; Negus and Berger 1998). Since 1993, we have been monitoring their annual abundance on Bylot Island, Nunavut, in the eastern Canadian High Arctic, and we have found that lemmings exhibited regular 3–4 year cycles of abundance at this site (Gruyer et al. 2008). In this study, we analysed the seasonal demography of the brown (*Lemmus trimucronatus*) and collared lemmings (*Dicrostonyx groenlandicus*) during a year of peak abundance and a year of population decline. Though sympatric, these two species are ecologically separated at the local level (Rodgers and Lewis 1986b; Pitelka and Batzli 1993).

Accurate estimation of densities and demographic parameters of secretive species like lemmings requires methods based on the recapture of marked animals (Williams et al. 2002). Abundance is traditionally estimated using closed population estimators, which can then be converted into density estimates using appropriate information on movements of animals (Williams et al. 2002; Parmenter et al. 2003). However, Efford (2004) recently proposed a new method to estimate density directly from capture–recapture data using spatial detection function (Efford 2004; Efford et al. 2005). Demographic parameters such as survival can be estimated with capture–recapture methods for open populations although the robust design, which combines both open and closed populations methods, may allow for a better estimation of such parameters (Kendall et al. 1997; Williams et al. 2002).

Our first objective was to compare estimates of lemming density obtained with traditional models for closed populations with those obtained with the new Efford's (2004) method. Our second and third objectives were to examine variations in abundance, reproduction, survival, and body mass of two sympatric lemming species within the summer season (second objective) and between different phases of their population cycle (third objective). We predicted that abundance and survival decreased during the summer due to high predation rate, and that reproduction and survival were lower in the decline phase than in the peak phase of the cycle.

Methods

Study area and species

Field work was carried out on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada (73°N, 80°W) in the summers of 2004 and 2005. The landscape in the area is a mixture of wetlands in lowland areas, mesic tundra in both lowlands and hilly areas, and, at higher elevation, xeric tundra (Gauthier et al. 1996). Plant communities of mesic tundra are dominated by shrubs (e.g. *Salix arctica*, *Cassiope tetragona*, and *Vaccinium uliginosum*), grasses (e.g. *Arctagrostis latifolia*, *Alopecurus borealis*, and *Poa arctica*) and forbs (e.g. *Dryas integrifolia*, *Stellaria longipes*, *Oxytropis maydelliana* and *Oxyria digyna*) (Duclos 2002). In wetlands, graminoids such as *Dupontia fisheri, Eriophorum scheuchzeri* and *Carex aquatilis* are the most abundant plants (Gauthier et al. 1996).

The distribution of collared lemmings extends to the northernmost arctic islands whereas that of brown lemmings stops in the mid-arctic (in the eastern Canadian Arctic, Bylot Island is the northern limit of its geographical range; Banfield 1974). Brown lemmings are found primarily in wet meadows of lowland tundra whereas collared lemmings are mostly associated with upland dry heaths (Rodgers and Lewis 1986a). Brown lemmings eat graminoids during the summer and a mixture of graminoids and mosses in winter whereas collared lemmings feed on dicotyledons such as evergreen shrubs, herbs and forbs year round (Batzli and Jung 1980; Rodgers and Lewis 1986a). Demography also tends to differ between the two species. Generally, population fluctuations are of greater magnitude in the brown than in the collared lemmings and the breeding season of collared lemmings generally starts earlier than that of the brown (Pitelka and Batzli 1993, Negus and Berger 1998). The most important predators of lemmings at our site are arctic foxes (*Vulpes lagopus*), ermines (*Mustela erminea*) and several species of bird of prey (Gauthier et al. 2004).

Trapping protocol

We trapped lemmings on two grids of 7.3 ha (270 × 270 m) located 1,800 m apart, one in wet meadow habitat (wet grid) and one in mesic habitat (mesic grid). Trapping stations were at grid intersections every 30 m, for a total of 100 per grid. Within 15 m of each station, we set a Longworth® live-trap at a suitable trapping site such as active burrows or runways showing signs of recent use when possible. Trap positions were noted to the nearest meter. Traps were left on site throughout the summer (but removed in winter) and were blocked open between trapping sessions. During trapping sessions, traps were constantly provided with clean and dry bedding material (fibre fill) and baited with apple quarters (Wilson et al. 1999). Apple baits usually do not affect body mass of trapped small mammals (Unangst and Wunder 2002).

We marked animals by injecting an electronic PIT tag (12 × 2 mm; 70 mg; Gibbons and Andrews 2004) under the skin in the back of the neck. These tags were read with a 1002 AVID® mini tracker reader (http://www.avidcanada.com). Every time an animal was captured, we noted the date, time, trapping station, species, sex, and reproductive condition (females only). We weighed animals with a spring scale (±0.5 g). Females were considered reproductive when they were lactating.

Our trapping schedule followed the robust design of Kendall et al. (1997), which requires two sampling periods. Primary periods were separated by ~14-day intervals without trapping. We had three primary periods in 2004 and four in 2005 (the first period is missing in 2004 because we arrived too late at the site). In 2005, the first period started as soon as snow melt allowed trapping. Each primary period had secondary sampling periods that consisted of five (in 2004) or four (in 2005) consecutive days of trapping. Even though traps were checked twice a day (or more often during adverse weather conditions), data were pooled on a daily basis (i.e. an individual captured twice on the same day counted for a single recapture on that day). Due to manpower limitation, each grid was trapped sequentially rather than simultaneously (Table 1).

Table 1 Calendar of lemming live trapping using the robust design (see "Methods") on two grids on Bylot Island, Nunavut, 2004–2005

Year	Primary period	Dates of secondary periods	
		Mesic tundra grid	Wet meadow grid
2004	II	2–7 July	8–13 July
	III	22–27 July	27 July–1 August
	IV	11–16 August	16–21 August
2005	I	22–26 June	17–21 June
	II	10–14 July	5–9 July
	III	29 July–2 August	24–28 July
	IV	17–21 August	12–16 August

Age determination

We categorised each individual captured as juvenile if its body mass was <33 g (brown lemming) or <40 g (collared lemming) (Framstad et al. 1993a). Because eye lens mass grows continuously through life, we used this variable to estimate age more precisely (Ostbye and Semb-Johansson 1970; Mallory et al. 1981; Hansson 1983; Erlinge et al. 1999). We determined eye lens mass in brown lemmings from a sample of individuals that died accidentally or were obtained from a concurrent study using snap traps (insufficient dead collared lemmings were available for such determination). We removed the eye lens of freshly dead individuals, fixed it in a formalin solution (4%) for 1 week, and then transferred it to 70% alcohol. In the laboratory, lenses were dried and weighed to the nearest 0.0001 g, and age was determined using the equation $\ln(a) = 2.1 \ln(m) + 2.7$ where a represents the age (in days) and m the combined dry mass (in mg) of both eye lenses (Erlinge et al. 1999). This allowed us to determine the relationship between whole body mass (M in g) and estimated age (a) amongst our sample of dead individuals. This relationship ($a = 0.26M^{1.75}$, $R^2 = 0.81$, $n = 16$, $P < 0.0001$) was then used to estimate the age of all live lemmings based on body mass at first capture. We used this estimated age to determine the season of birth of all captured individuals (Ostbye and Semb-Johansson 1970; Erlinge et al. 1999).

Analyses of trapping data

The estimation of abundance with closed capture models assumes that there is no birth, death, or migration so that the population size is constant over the trapping period. The assumption that the population is closed is usually valid for data collected over a relatively short period of time (a few days). Estimation of abundance, however, is sensitive to variations in probability of capture and thus we used the models of Otis et al. (1978) to test for these sources of variation. The four basic models considered are

M_t, which allows capture probabilities to vary by time, M_b, which allows behavioural responses to capture (i.e. trap happiness or trap shyness), M_h, which allows heterogeneous capture probabilities, and M_0 without any variation. Various combinations of these three sources of variation in capture probabilities were also considered. We selected the most appropriate model for our data with the Akaike's information criterion (AIC; Burnham and Anderson 1998). We used the software CAPTURE (Otis et al. 1978) to adjust these models separately to each 4 or 5-day trapping session.

The robust design model combines the Cormack–Jolly–Seber (CJS) model for open populations with models for closed populations (Kendall and Nichols 1995; Kendall et al. 1997). Closed population models are applied to secondary sampling periods whereas open ones are applied to primary periods. We used the robust design model implemented in program MARK 4.2 (White and Burnham 1999). Closed population models in the robust design are similar to those in CAPTURE except that the heterogeneity model is a simplified one. The CJS model in the robust design allows the estimation of the probability of survival (ϕ_i) between all primary periods *i*, as well as the probability of emigration from the trapping grid area (γ_i'') and the probability of staying away from the trapping area given that the animal has already left (γ_i') (Kendall et al. 1997). Reduced models constraining parameters in either closed population or CJS models (e.g. models assuming no emigration, $\gamma'' = \gamma' = 0$) can be implemented. The most appropriate model for the data was also selected based on the AIC. In presence of uncertainty in model selection, we averaged parameter estimates across various models taking into account the model weights (Burnham and Anderson 1998). If an animal died in a trap, his capture history was censored (i.e. it was used until time of death).

Trapping data on each grid usually consisted of individuals from the two species, both sexes, and juveniles and adults. However, data were sometimes too sparse to test for all these effects on capture probabilities, ϕ and γ, and thus some categories (e.g. sexes in 2005) were pooled. When age, sex or species (spp) effects were included in open models, they were indicated by subscripts. In the case of closed capture models (*M*), these effects appeared in superscripts and always applied to the probability of capture. For instance, model $M_{tb}^{spp*age}$ indicates that probability of capture changed over time, differed between newly marked individuals and previously marked ones (i.e. behavioural effect, *b*), and differed between species and age classes. Population size (*N*) was estimated for each species and age class separately, though sexes were pooled due to data sparseness.

As goodness-of-fit tests specific to the robust design do not exist, we only tested the fit of the CJS model to the data between primary periods in each year and grid using the program U-CARE (Choquet et al. 2005).

Density estimation

Because population density can be more easily compared amongst study sites than raw abundance, we converted our abundance estimates into density estimates (*D*), defined as the number of animals (*N*) per unit area (*A*), $D = N/A$. However, since trapped individuals can have most of their home range outside the trapping grid, we need to determine the spatial extent of the trappable population, i.e. the effective sampling area. The size of this area is usually derived by adding a boundary strip of width *W* around the trapping grid. We estimated *W* as half of the mean maximum distance moved by individuals trapped twice or more, excluding 0 values (i.e. individuals always recaptured in the same trap) as recommended by Williams et al. (2002). The mean maximum distance moved by animals within grids did not differ between years, juveniles and adults and sexes ($P > 0.05$; Gruyer 2007). We therefore use the overall mean for density calculations (brown lemming 81.8 ± 7.7 m, collared lemming 104.7 ± 7.6 m). We calculated standard error of estimates using the delta method (Williams et al. 2002).

The method recently developed by Efford (2004) allows a direct estimation of density by fitting a simple spatial model to the animal trapping data without the requirement of determining an effective trapping area using arbitrary criteria. It uses simulations and inverse predictions to estimate jointly *D* and two parameters of individual capture probability, magnitude (g_0) and spatial scale (σ), from the information contained in the estimated abundance, the mean capture probability and the distance moved between successive captures (see Efford 2004; Efford et al. 2005 for details). For these estimations, we used the program DENSITY 3.2 (Efford et al. 2004) and we selected the best model for our data with the AIC.

For each trapping session (i.e. primary sampling periods), we thus obtained three density estimates (sometimes less due to sparse data) using different methods (CAPTURE, the MARK robust design, and DENSITY). We used the reduced major axis regression (Sokal and Rohlf 1995) to compare these independent estimates because both were measured with errors. We estimated confidence intervals of parameters by bootstrapping and randomization tests.

Other data analyses

We compared the proportion of lactating females amongst all captured females, the proportion of juveniles amongst all captured individuals (two indices of reproductive activity) and the distribution of birth dates between years and time periods with contingency tables (χ^2 tests). When sample size was too small, we pooled data from adjacent time periods. We compared mean adult body mass of each species between years with t tests. Finally, we examined the effects of species, age and sex on movements (i.e. the maximum distance moved by individuals trapped twice or more) using factorial ANOVA.

Results

Model selection and comparison of methods

We captured 126 brown lemmings and 23 collared lemmings in 2004, and 28 and 26 in 2005, respectively. Open-population models fitted well the data for both the wet and mesic grids in 2004 ($\chi^2 = 2.60$, $df = 3$, $P = 0.46$ and $\chi^2 = 17.3$, $df = 13$, $P = 0.18$, respectively) but the test was not possible in 2005 due to sparse data.

In CAPTURE, the preferred models in 2004 differed between periods. On the wet grid, model M_t was preferred at period I and model M_b at periods II and III, whereas in the mesic grid, model M_0 was preferred at period I and model M_b at periods II and III, with a species effect at periods I and II. In 2005, the preferred model was model M_0 at all time periods, though with an age effect on capture probability at period II and a species effect on the wet grid at period IV. Preferred models for closed populations in MARK included both time variation and behavioural trap response (model M_tb) on the capture probability in 2004 and no variation in 2005 (model M_0) when sample sizes were much smaller (Table 2). No effect of age or species on capture probability was detected. Preferred models in DENSITY were the same as those in CAPTURE in 92% of the cases.

Despite differences in the models selected, closed population density estimates obtained in CAPTURE or in MARK were very similar [mean difference −0.06 ± 0.02 (SE) $n = 31$]. The slope of the relationship between pairs of estimates differed slightly from 1.0 [1.09 (95% CI: 1.02, 1.27)] but the intercept did not differ from 0 [0.003 (95% CI: −0.07, 0.04); Fig. 1], indicating that CAPTURE estimates were slightly higher than those of MARK at large population size. Density estimates obtained with DENSITY were also well correlated with those obtained with either CAPTURE or MARK. The slopes of the relationships between DENSITY and CAPTURE or MARK estimates did not differ from 1.0 [1.09 (95% CI: 0.89, 1.46); and 1.18 (95% CI: 0.92, 1.80), respectively], and intercepts did not differ from 0 [−0.04 (95% CI: −0.26, 0.08); and −0.03 (95% CI: −0.39, 0.12)]. The mean difference between DENSITY and CAPTURE or MARK estimates was 0.05 ± 0.08 (SE) and 0.12 ± 0.10 $n = 19$, respectively, indicating that DENSITY gave similar population density estimates.

Table 2 Model selection in MARK for the robust design applied to the live-trapping data of brown and collared lemming on two trapping grids on Bylot Island, Nunavut, 2004 and 2005

Grid (year)	Model		Δ AICc	ω AICc	np	Deviance
Wet meadow grid (2004)	M_{tb}	$\Phi^\mathrm{m}\ \Phi^\mathrm{f,\ juv}\ \gamma = 0$	0.00	0.67	20	121.97
	M_tb	$\Phi^\mathrm{m}\ \Phi^\mathrm{f}\ \Phi^\mathrm{juv}\ \gamma = 0$	2.12	0.23	21	121.70
	M_tb	$\Phi\ \gamma = 0$	4.33	0.08	19	128.67
Wet meadow grid (2005)	M_0	$\Phi\ \gamma$	0.00	0.31	3	94.05
	M_0	$\Phi\ \gamma = 0$	0.67	0.23	2	97.01
	M_0	$\Phi^\mathrm{age}\ \gamma$	1.72	0.13	4	93.38
	M_0	$\Phi^\mathrm{age}\ \gamma = 0$	2.03	0.11	3	96.09
	M_0	$\Phi^\mathrm{spp}\ \gamma$	2.31	0.10	4	93.96
	M_0	$\Phi^\mathrm{age}\ \gamma = 0$	2.88	0.07	3	96.93
Mesic tundra grid (2004)	M_tb	$\Phi\ \gamma = 0$	0.00	0.91	10	207.42
	M_tb	$\Phi^{\mathrm{spp}*\mathrm{age}}\ \gamma = 0$	5.26	0.07	13	205.72
Mesic tundra grid (2005)	M_0	$\Phi\ \gamma$	0.00	0.37	6	115.93
	M_0^age	$\Phi^\mathrm{age}\ \gamma$	0.98	0.23	8	111.63
	M_0^age	$\Phi\ \gamma$	1.31	0.19	7	114.65
	M_0^spp	$\Phi\ \gamma$	2.48	0.10	7	115.82

For each model, we present the ΔAIC statistic (differences in AIC between the current and the best model), the AIC weights (ω), the number of estimated parameters (np) and the deviance. For closed population models (M), effects apply only to the probability of capture

Model notation: ϕ survival, γ emigration, t time, b behavioural effect, 0 no effect, *spp* species effect, *m* male, *f* female, *juv* juvenile, *ad* adults, * interaction

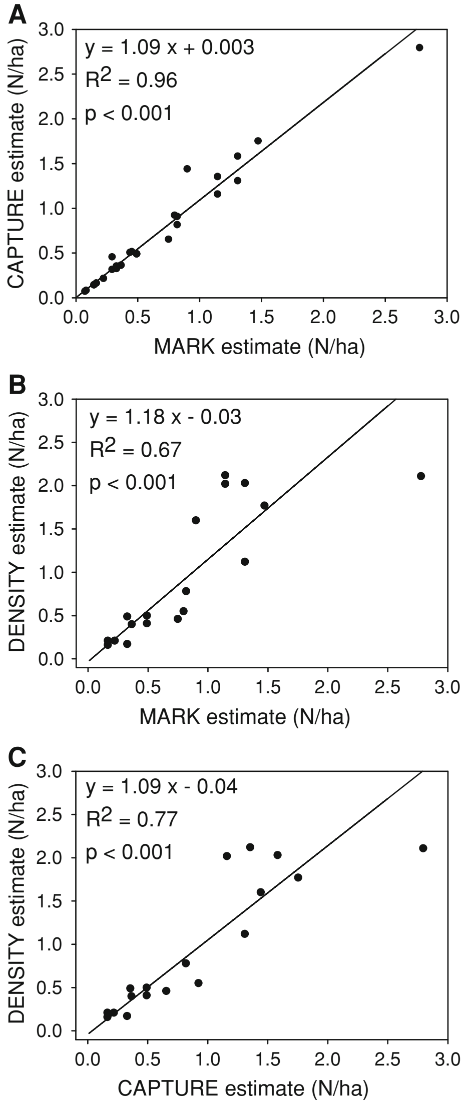

Fig. 1 Relationship between density estimates (N/ha) obtained by various methods: closed population in CAPTURE versus closed population in the robust design in MARK (**a**), DENSITY versus closed population in the robust design in MARK (**b**), DENSITY versus closed population in CAPTURE (**c**). Each data point is an independent estimate for a unique combination of trapping grid, sampling period, species and age group. The regression line and associated parameters are the reduced major axis regression

For the presentation of results, we used density estimates obtained with CAPTURE, except in 13% of the cases where the CAPTURE algorithm did not converge properly and failed to provide an estimate (we then used estimates from MARK).

Population density

Density of brown lemmings was much higher in 2004 than in 2005 (Fig. 2). In the wet grid, mean brown lemming densities were 1.20 adults/ha and 1.53 juveniles/ha in 2004 compared to 0.20 and 0.11, respectively, in 2005. In the mesic grid, densities were 0.99 adult/ha and 1.14 juveniles/ha in 2004 compared to 0.50 and 0.06 in 2005. Density of collared lemmings varied much less between years (Fig. 2). On the wet meadow grid, only one collared lemming was trapped in 2004 whereas densities were 0.07 adult/ha and 0.16 juvenile/ha in 2005. On the mesic grid, collared lemming densities were 0.34 adult/ha and 0.36 juvenile/ha in 2004 compared to 0.17 and 0.26, respectively, in 2005.

In both years, density of adult brown lemmings generally declined throughout the summer (Fig. 2). The only exception was in the mesic grid in 2005 where density increased at the last sampling occasion (late July to mid-August). In 2004, density of juveniles in the wet grid increased during the summer, a trend opposite to adults. In the mesic grid, juvenile density initially decreased but then stabilized or increased slightly in late summer. Juvenile density remained very low on both grids in 2005. For collared lemmings, adult density did not show clear trends throughout the summer in either year (Fig. 2). On both grids, density of juveniles tended to be higher shortly after snow-melt and in late summer than in mid-summer.

Reproductive activity

In brown lemmings, the proportion of lactating females tended to be higher in early than in late summer ($\chi^2 = 3.57$, $df = 1$, $P = 0.06$ Fig. 3), and higher in 2005 than 2004 ($\chi^2 = 3.94$, $df = 1$, $P = 0.05$). No significant effects were found in collared lemmings due to small sample sizes but proportion of lactating females tended to be highest in late summer and higher in 2005 than 2004. The proportion of juvenile brown lemmings in the population increased throughout the summer ($\chi^2 = 31.6$, $df = 3$, $P < 0.001$) and was higher in 2004 (0.54) than in 2005 (0.29) ($\chi^2 = 24.0$, $df = 1$, $P < 0.001$). In collared lemmings, the proportion of juveniles was high in late summer and variable earlier ($\chi^2 = 20.5$, $df = 3$, $p < 0.001$), and similar between the 2 years ($\chi^2 = 0.64$, $df = 1$, $P = 0.42$) (Fig. 3).

The distribution of inferred birth dates of brown lemmings captured in summer 2004 showed a progressive pattern over time, with the highest number of individuals being born in the current summer and the lowest in the previous summer (Fig. 4). This pattern is expected because the longer the time interval since birth, the lower the proportion of individuals surviving. Nonetheless, a surprisingly large number of individuals were estimated to be born during the previous winter. This pattern was drastically different in 2005 since, amongst individuals captured that summer, a higher proportion was born in the previous winter or spring than in the current summer compared to

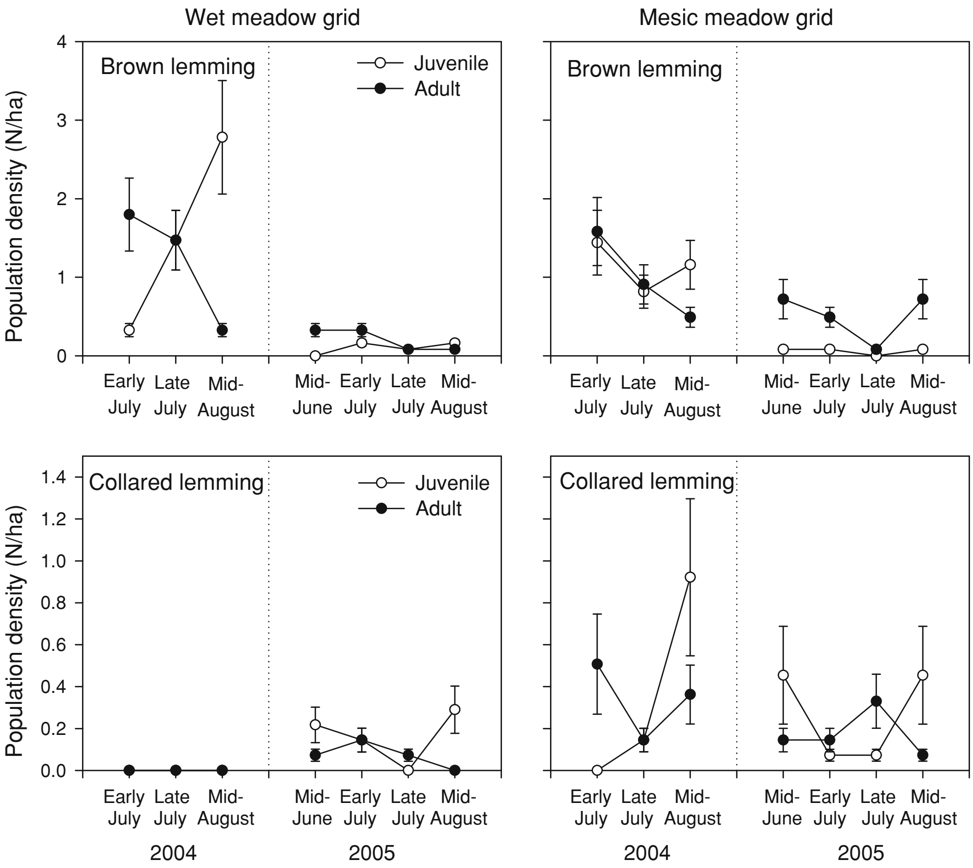

Fig. 2 Population density estimates (±SE) of juvenile and adult brown and collared lemmings in different periods of the summer in two trapping grids (wet meadow and mesic tundra) on Bylot Island, Nunavut, 2004 and 2005. The *dotted vertical line* separates years. Number of individuals caught: brown lemmings, wet grid: 84 (2004) and 12 (2005); mesic grid: 58 (2004) and 16 (2005); collared lemmings, wet grid: 1 (2004) and 13 (2005); mesic grid: 26 (2004) and 14 (2005)

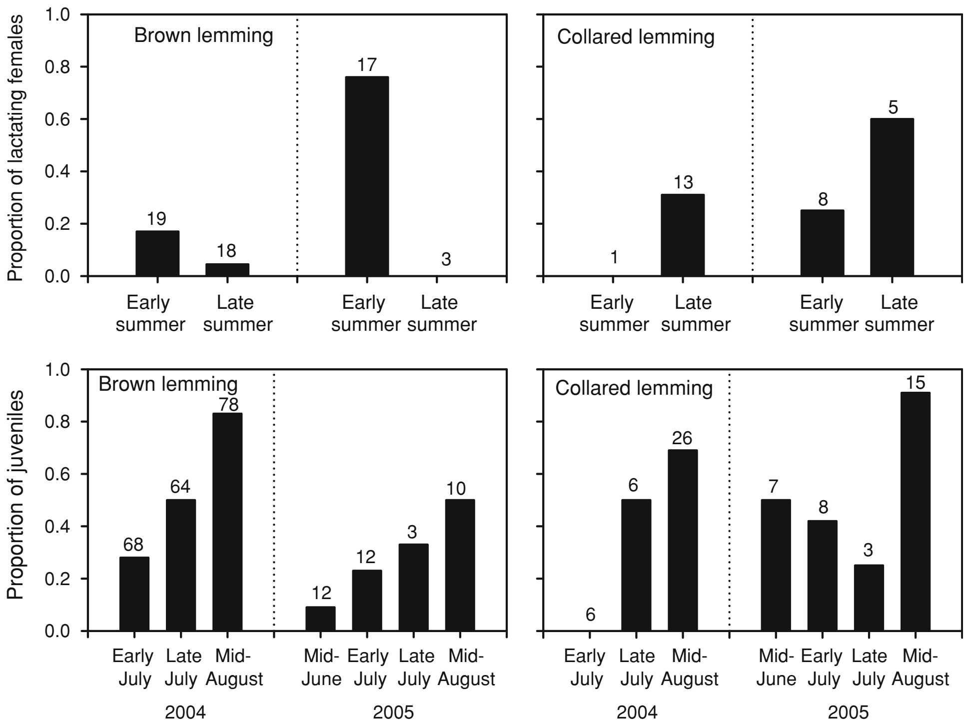

Fig. 3 Proportion of lactating females amongst adult females and proportion of juveniles amongst all individuals trapped in brown and collared lemmings at different periods of the summer on Bylot Island, Nunavut, 2004 and 2005 (wet meadow and mesic tundra grids pooled). *Numbers above bars* indicate sample size. The *dotted vertical line* separates years. *Early summer* mid-June and early July sampling periods, *Late summer* late July and Mid-August sampling periods

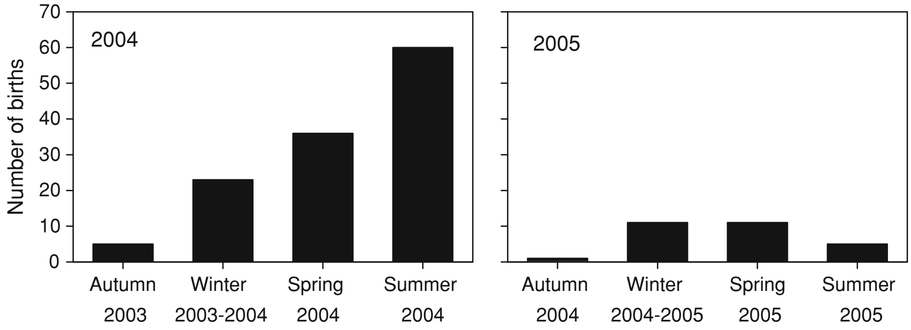

Fig. 4 Distribution of inferred birth season of brown lemmings captured during summers 2004 and 2005 on Bylot Island, Nunavut, based on a relationship between body mass at capture and age determined with eye lens on a sample of dead individuals (see "Methods")

2004 (interaction year × time period: $\chi^2 = 8.68$, $df = 3$, $P = 0.03$).

Survival rate

Preferred models for open populations in MARK had no time, species, age, or sex effects on survival, except for the wet grid in 2004 (Table 2). In the latter case, survival rate of adult male brown lemmings was lower than the one of adult females and juveniles (Fig. 5). In the wet grid, the survival rate of male brown lemmings was lower in 2004 than in 2005 but slightly higher for females and juveniles. However, in the mesic grid, the survival rate was much higher in 2005 than in 2004. When the two species were present in the same grid, their survival rate was similar.

Body mass

The body mass of adult brown lemmings decreased by 12% between 2004 and 2005 [48.5 ± 1.3 (SE) vs. 42.9 ± 2.3; $t = 2.08$, $df = 80$, $P < 0.05$]. However, there was no difference between years in average mass of adult collared lemmings (54.7 ± 2.8 g in 2004 vs. 52.0 ± 2.8 in 2005; $t = 0.68$, $df = 20$, $P = 0.50$).

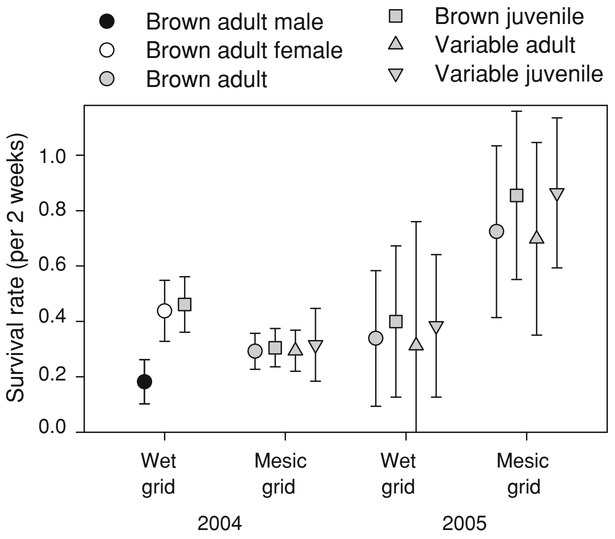

Fig. 5 MARK estimates (±SE) of survival rate (per 2 weeks) of brown and collared lemmings on two trapping grids (wet meadow and mesic tundra) on Bylot Island, Nunavut, 2004 and 2005

Discussion

Comparison of methods used to estimate density

The estimation of population density with capture–recapture data is prone to several biases (Parmenter et al. 2003). In our study, we compared three different methods of density estimation: closed capture estimates implemented in CAPTURE and the MARK robust design, and Efford's DENSITY method. The similarity in the density estimates between CAPTURE and MARK is not surprising as both used the same basic models for estimating abundance (Kendall et al. 1997). However, CAPTURE is slightly more flexible because, unlike MARK, it allows selection of different models for each trapping session, which may explain some of the differences observed between the two methods. In 2005, the models selected were the simplest ones (model M_0) and did not include any temporal or behavioural effects on capture probabilities, presumably because sample size was too small to detect such effects.

Density estimates obtained with Efford's DENSITY method were similar to those obtained with closed population models. DENSITY has the advantage of not requiring the estimation of a somewhat arbitrary effective trapping area (Efford 2004), which critically depends on the width of the boundary strip area. In our calculations, we used half the mean maximum distance moved by individuals trapped twice or more, as traditionally used (Williams et al. 2002). Parmenter et al. (2003) suggested that not halving this value may provide a better estimate of the boundary strip area. When following the latter recommendation, density estimates obtained with DENSITY were then 32–53% higher than those obtained with closed population models. We found that DENSITY required larger sample sizes and for several of our datasets it failed to converge on an estimate when CAPTURE or MARK did. Although our estimates based on traditional closed capture methods may be biased by the size of the effective trapping area used, they have the advantage of being readily comparable to other studies using similar methods. Our analysis nonetheless suggests that DENSITY provides an interesting alternative to previous ones and should deserve consideration in future studies when sample sizes are sufficiently large.

Temporal and spatial variations in abundance

The density of brown lemmings differed markedly between the two years (on average 6.2 times higher in 2004 than in 2005) whereas the density of collared lemmings was lower and similar between the 2 years (1.6 times higher in 2004 than in 2005 on the mesic grid). In 2005 the brown lemming population had declined to densities similar to those of collared lemmings. These changes in density between the 2 years are corroborated by long-term snap-trap data collected at our site (Gruyer et al. 2008) which indicated that 2004 was a year of peak abundance and 2005 a year of decline. It further showed that brown lemmings are more abundant than collared lemmings and they exhibit stronger oscillations, a pattern similar to the one reported by Krebs (1964) at Baker Lake, Nunavut, Canada. However, this pattern may not be ubiquitous because at other sites in Nunavut, collared lemmings are apparently more abundant than brown lemmings (Igloolik Island, Rodgers and Lewis 1986b; Walker Bay, Kent Peninsula, Wilson et al. 1999).

The pattern of abundance of each species in each grid is consistent with their known habitat and food preferences. Brown lemmings prefer wet meadows dominated by graminoids and mosses, whereas collared lemmings use mainly mesic tundra dominated by shrubs (Batzli and Jung 1980; Rodgers and Lewis 1986a, b; Pitelka and Batzli 1993). However, these basic patterns of habitat use may be modified by changes in the availability of preferred foods and by intra- and inter-specific interactions. Indeed, the brown lemming is apparently a superior competitor than the collared lemming and direct and indirect competition may occur in the use of runways and burrows in years when brown lemmings are very abundant (Wilson et al. 1999; Morris et al. 2000; Predavec and Krebs 2000). This could explain why in 2004, when brown lemmings were very abundant in wet meadows, their preferred habitat, collared lemmings were almost totally absent from this habitat but were present in mesic tundra. The decline in abundance of brown lemmings in 2005 may have allowed collared to move into areas normally used by browns, and thus explain their presence in both habitats that year (Rodgers and Lewis 1986a). Therefore, competitive interactions may be important in explaining patterns of habitat use by these two species. However, this conclusion remains tentative because we only sampled one grid in each habitat, and thus we lack spatial replicates.

Comparing lemming densities across studies is difficult because trapping and analytical methods often differ and many studies only report indices of abundance. Nonetheless, our density estimates (average annual density, brown: 0.45–2.43 ind/ha, collared: 0.43–0.47) appear low for both species. For instance, in northern Greenland the density of collared lemmings in good habitats ranged from <0.1 ind/ha to 11 ind/ha (Gilg 2002). Similarly, densities at Kent Peninsula, Nunavut, ranged from 0.1 to 16 ind/ha (Blackburn et al. 1998; Wilson et al. 1999). However, at Pearce Point, NWT, collared lemmings densities remained constantly low (<3 ind/ha; Krebs et al. 1995; Reid et al. 1995). In Atkasook (Alaska) where the two species are sympatric, densities averaged 0.3–1.4 ind/ha for each species, reaching a low of 0.1 ind/ha for collared lemmings and a high of 2.2 ind/ha for brown lemmings (Batzli and Jung 1980), a pattern similar to our study. However, densities of brown lemmings ranging from <1 to >100 ind/ha have been reported at Barrow, Alaska (Pitelka 1973). In the eastern Canadian Arctic, Bylot Island is the northern limit of the geographical range of brown lemmings (Banfield 1974), which may partly explain our observed low densities.

Summer declines in lemming densities are common and suggest that mortality (mostly due to predation) exceeds recruitment during the summer (Wilson et al. 1999; Gilg 2002; Korpimaki et al. 2004; Gilg et al. 2006). The absence of protective snow cover and the high abundance of predators (such as migratory bird of prey) may explain a higher predation rate in summer than in winter. We observed a decline in abundance of brown lemmings throughout the summer, in accordance with our initial prediction, but not of collared lemmings. This could occur if the effect of predation differs on the two species. Angerbjörn et al. (1999) showed that arctic foxes, a major lemming predator, had a type II functional response for *Lemmus* but a type III response for *Dicrostonyx*. He therefore suggested that foxes had the capacity to deepen and prolong the crash phase of *Lemmus*, thereby increasing the amplitude of their cycles, while at the same time they could dampen oscillations of *Dicrostonyx*.

Variations in demographic traits

The higher proportion of individuals estimated to be born during the summer and of juveniles captured in 2004 compared to 2005 suggest that recruitment of juvenile brown lemmings was higher during the peak than the decline year. Poor recruitment and high predation rates are often reported to be the proximate causes of the summer declines in lemmings (Gilg 2002). A reduction in recruitment of young can be due to a fall in reproductive activity (Erlinge et al. 2000) and/or a reduced early survival of juveniles (i.e. before they can be caught; Krebs 1964). Because the proportion of lactating females tended to be higher during the decline year of 2005 than during the peak year of 2004, reduced early survival of juveniles may be the main reason for a lower recruitment in 2005. In contrast, reproductive parameters of collared lemmings did not change between the 2 years. The apparent constant reproductive activity fits with the low variation in abundance observed between 2004 and 2005. Collared lemmings are well known for reproducing under the snow in late winter (Krebs et al. 1995; Millar 2001), which could explain the relatively high proportion of juveniles observed in early summer, soon after snow-melt. The estimated age of brown lemmings captured during summer nonetheless shows that many of them were also born the previous winter, suggesting a significant winter reproductive activity in that species as well. More recent data based on examination of brown lemming winter nests at our study site also confirmed the occurrence of winter reproduction in this species (Duchesne 2009). The low proportion of juvenile brown lemmings captured in early summer is not incompatible with the previous conclusion because flooding of wetlands, their preferred habitat, during snow-melt would presumably interrupt their breeding activity in spring (Rodgers and Lewis 1986b). The increasing proportion of juveniles recruiting in the population over the summer suggests that after snow-melt reproductive activity either resumed (in brown lemmings) or increased (collared lemming). The high proportion of collared lemming females still lactating in late summer in comparison to browns further suggests that the reproduction of the former species may extend later in summer (Negus and Berger 1998).

Our survival analyses have low power due to small sample sizes. The strongest effect was a lower survival of adult male brown lemmings compared to adult females and juveniles in the wet grid in 2004, when sample sizes were largest. The high activity level exhibited by males while searching for reproductive females in summer may lead to a greater exposure to predators (Banks et al. 1975; Stenseth and Ims 1993b; Predavec and Krebs 2000).

We did not detect any change in survival rate over the summer as we had predicted. However, survival rate of lemmings on the mesic grid were lower during the peak year (2004) than in the following year when density had declined, and also for male brown lemmings in the wet grid. This contrasts with some previous results showing that survival rates of small mammals are higher in the increasing and peak phases than in the decline phase (Krebs 1964; Wilson et al. 1999). It is possible that the lemming population peaked earlier in spring or even in late winter under the snow (i.e. before we started trapping) and thus that they entered into the declining phase during summer 2004. The strong decline of adult brown lemmings during the summer 2004 is consistent with this hypothesis. Although we lack comparative data during the increasing phase, it is possible that a low adult survival at high density is one of the factors initiating the subsequent population decline. Finally, one has to remember that even though open-population models control for the probability of detection, they do not control for permanent emigration, which is confounded with mortality, and hence we can only estimate an apparent survival rate.

The decrease in body mass observed in brown lemmings between 2004 and 2005 may indicate a shift in individual quality, which apparently did not occur in collared lemmings. Again, this pattern is consistent with the change of abundance that we observed between years in the two species. In strongly fluctuating populations, individuals reach maximum size during peak abundance, apparently because animals born into rapidly expanding populations have high growth rates (Krebs et al. 1973; Framstad et al. 1993a; Chitty 1996). Conversely, animals born during declining populations grow more slowly, and usually fail to reach large sizes (Mallory et al. 1981; Framstad et al. 1993a; Norrdahl et al. 2004).

Conclusion

Our study revealed annual and seasonal differences in demographic parameters of lemmings. Our results suggest that a low adult survival rate when populations are still high may be one of the demographic factors initiating the population decline. Even though adult survival had increased during the declining phase, juvenile recruitment had decreased considerably by then, possibly due to a reduced early juvenile survival rather than a reduced reproductive activity. Abundance of adults declined during the summer whereas recruitment of juveniles into the population increased. Finally, fluctuations in demographic parameters were generally more pronounced in brown than in collared lemmings.

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