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Top-down limitation of lemmings revealed by experimental reduction of predators

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Abstract. It is generally recognized that delayed density-dependence is responsible for cyclic population dynamics. However, it is still uncertain whether a single factor can explain why some rodent populations fluctuate according to a 3–4 yr periodicity. There is increasing evidence that predation may play a role in lemming population cycles, although this effect may vary seasonally. To address this issue, we conducted an experiment where we built a large exclosure (9 ha) to protect brown lemmings (*Lemmus trimucronatus*) from avian and terrestrial predators. We tested the hypothesis that predation is a limiting factor for lemmings by measuring the demographic consequences of a predator reduction during the growth and peak phases of the cycle. We assessed summer (capture-mark-recapture methods) and winter (winter nest sampling) lemming demography on two grids located on Bylot Island, Nunavut, Canada from 2008 to 2015. The predator exclosure became fully effective in July 2013, allowing us to compare demography between the control and experimental grids before and during the treatment. Lemming abundance, survival and proportion of juveniles were similar between the two grids before the treatment. During the predator-reduction period, summer densities were on average 1.9× higher inside the experimental grid than the control and this effect was greatest for adult females and juveniles (densities 2.4× and 3.4× higher, respectively). Summer survival was 1.6× higher on the experimental grid than the control whereas body mass and proportion of juveniles were also slightly higher. Winter nest densities remained high inside the predator reduction grid following high summer abundance, but declined on the control grid. These results confirm that predation limits lemming population growth during the summer due to its negative impact on survival. However, it is possible that in winter, predation may interact with other factors affecting reproduction and ultimately population cycles.

Key words: capture-mark-recapture; population cycle; population regulation; predator–prey interactions; seasonality; trophic interactions.

Introduction

Cyclic populations are known since the pioneer work of Charles Elton in rodents (1924) but factors responsible for such dynamics have remained elusive in many instances (Sinclair and Krebs 2002, Krebs 2013, Barraquand et al. 2014). Collapsing cycles in several boreal and arctic environments and taxa have been suggested to be a consequence of climate change (Ims et al. 2008, Gilg et al. 2009, Cornulier et al. 2013), which emphasizes the critical need to identify the mechanisms driving these cycles.

Several hypotheses have been proposed to explain why some populations of small rodents fluctuate according to a 3–5 yr periodicity (Stenseth 1999). It is generally recognized that delayed density-dependence is required to force populations into decline once the potential for growth is overcome by opposing forces (Royama 1992). These forces can be both extrinsic (Krebs 2013) and intrinsic (e.g., maternal effects; Inchausti and Ginzburg 2009). Predation and food availability are two leading hypotheses to explain vole and lemming cycles (Krebs 2011, Prevedello et al. 2013). Other hypotheses such as parasites (Forbes et al. 2014) and intrinsic factors like stress (Boonstra and Boag 1992) have also been proposed but even if they may negatively affect population growth, there is still no evidence that they can be solely responsible for population cycles in small mammals.

Single factor hypotheses, however, have often failed to fully explain cyclic dynamics (Boonstra et al. 1998, Huitu et al. 2003, Gauthier et al. 2009, Krebs 2013), which has spurred new interest into the phase or seasonal dependency of population growth processes (Barraquand et al. 2014). For instance, population growth may be mainly limited by mortality during periods of high predation rate while it may be limited by reproduction (i.e., resource availability) during periods of low predation rate such as when individuals are protected from predators by the snow (Fauteux et al. 2015). Predation and food availability may thus both play a role as the strength of trophic interactions can vary through time at a single site (Sinclair

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et al. 2000). In this context, field experiments are critical to identify the causal relationships between hypothesised factors and population growth.

There is increasing evidence that predation may be a key factor in the cyclic dynamics of lemmings in Arctic Canada and Greenland (Reid et al. 1995, Gilg et al. 2003, Therrien et al. 2014, Fauteux et al. 2015). Manipulating predation in the field, however, is a daunting task and previous studies have reported multiple potential problems such as mechanical failures of fences (e.g., predators going through fences, Reid et al. 1995) or indirect manipulation of non-target factors (e.g., fence-effect, Ostfeld 1994). Another caveat of several predator manipulation experiments is the paucity of empirical evidence that predators were effectively excluded from protected areas or the potential attraction of predators to the neighborhood of the exclusion area (Salo et al. 2010). The lack of replication has also been presented as a limitation for large-scale predator manipulation experiments. However, as the number of experimental studies increases in the literature, meta-analyses can successfully identify general patterns (Salo et al. 2010, Prevedello et al. 2013). Manipulative field experiments remain the most powerful method to test clearly defined hypotheses, even when they involve the manipulation of a single factor due to logistic constraints (Krebs 2011).

On Bylot Island, Nunavut, Canada, brown lemmings (*Lemmus trimucronatus*) show large amplitude fluctuations in abundance (up to 100-fold) according to a 3–4 yr periodicity (Fauteux et al. 2015). Because previous studies at this site suggested that food availability was not limiting for lemmings (Legagneux et al. 2012, Bilodeau et al. 2014), our manipulation focused on predation. Our study is the first to assess experimentally the effects of predation on brown lemming population dynamics in the High Arctic. Moreover, our long-term dataset included pre-experiment trapping surveys spanning several years, thereby providing a rare opportunity to compare our treatment effect with the pre-treatment situation at the same site, in addition to comparison with a control site (Smith 2013). Our main goal was to determine the demographic consequences of a reduction in predator abundance on brown lemmings in both summer and winter during the growth and peak phases of the cycle. We hypothesized that predation is a limiting factor that reduces the realized growth rate of lemming populations. We tested the following predictions: (1) population densities and survival will be higher in our predator reduction grid compared to the control; (2) the proportion of juveniles captured will also be higher in the predator reduction grid due to a higher survival of juveniles; and (3) average body mass of adults will be higher in the predator reduction grid due to a longer life expectancy resulting from a reduced mortality rate. Population densities were assessed during both summer and winter but survival and proportion of juveniles could not be assessed during winter due to the difficulties of trapping lemmings under the harsh High Arctic winter conditions.

Methods

Study area

Our study was conducted on Bylot Island, Nunavut, Canada (73°08′ N; 80°00′ W) in the Qarlikturvik valley. The valley is surrounded by gentle slopes and hills mostly covered by mesic tundra vegetation while the bottom of the valley consists of a mosaic of wet habitat (i.e., tundra polygons, ponds and lakes) and mesic tundra. The mesic tundra is dominated by prostrate shrubs (*Salix* spp., *Cassiope tetragona*) with a sparse cover of grasses (*Arctagrostis latifolia, Alopecurus alpinus*), forbs (*Saxifraga* spp., *Ranunculus* spp.) and some mosses (such a *Polytrichum swartzii*) (Bilodeau et al. 2014). In contrast, sedges (*Eriophorum* spp., *Carex aquatilis*), grasses (*Dupontia fisheri*) and brown mosses (such as *Limprichtia cossonii* and *Campylium stellatum*) dominate in the wet tundra. In the mesic tundra, numerous small streams running down the slopes form small gullies, which are conducive to the formation of snow banks and are heavily used by lemmings in winter (Duchesne et al. 2011*b*). Snow covers the ground from October to mid-June and the average annual temperature is −15°C with a warming trend in recent decades (Gauthier et al. 2013).

Both brown and collared lemmings (*Dicrostonyx groenlandicus*) are present in our study area but we focused only on the former species because it is the most abundant and the only one clearly showing large, cyclical fluctuations in abundance. Lemming predators consist mainly of the ermine (*Mustela erminea*), arctic fox (*Vulpes lagopus*), snowy owl (*Bubo scandiacus*), rough-legged hawk (*Buteo lagopus*), long-tailed jaegers (*Stercorarius longicaudus*) and glaucous gull (*Larus hyperboreus*). All of these species are major predators of lemmings in the Canadian Arctic (Bilodeau 2013, Therrien et al. 2014, Gauthier et al. 2015, Ruffino et al. 2015).

Experimental design

We used a Before–After Control-Impact design (Smith 2013), with the control and experimental trapping grids set in relatively homogenous patches of mesic tundra. The two grids were 600 m apart, a distance much larger than the average 15–30 m movements of individuals within each grid (see *Results*). The control grid (11 ha) was set up in 2004 and consisted of 12 × 12 trapping stations every 30 m. The experimental grid was set up in 2007 and originally consisted of 10 × 10 stations (7.3 ha), also every 30 m, but changed in 2012 to 8 × 12 stations (6.9 ha) to better fit inside the predator exclosure (see more details herein). From 2008 to 2011, the experimental grid was used for a snow fencing experiment but snow enhancement had no effect on summer density or other demographic parameters (Bilodeau et al. 2013). Each station consisted of a single Longworth trap and trapping grids were surveyed in mid-June, mid-July, and mid-August (primary occasions). Primary occasions

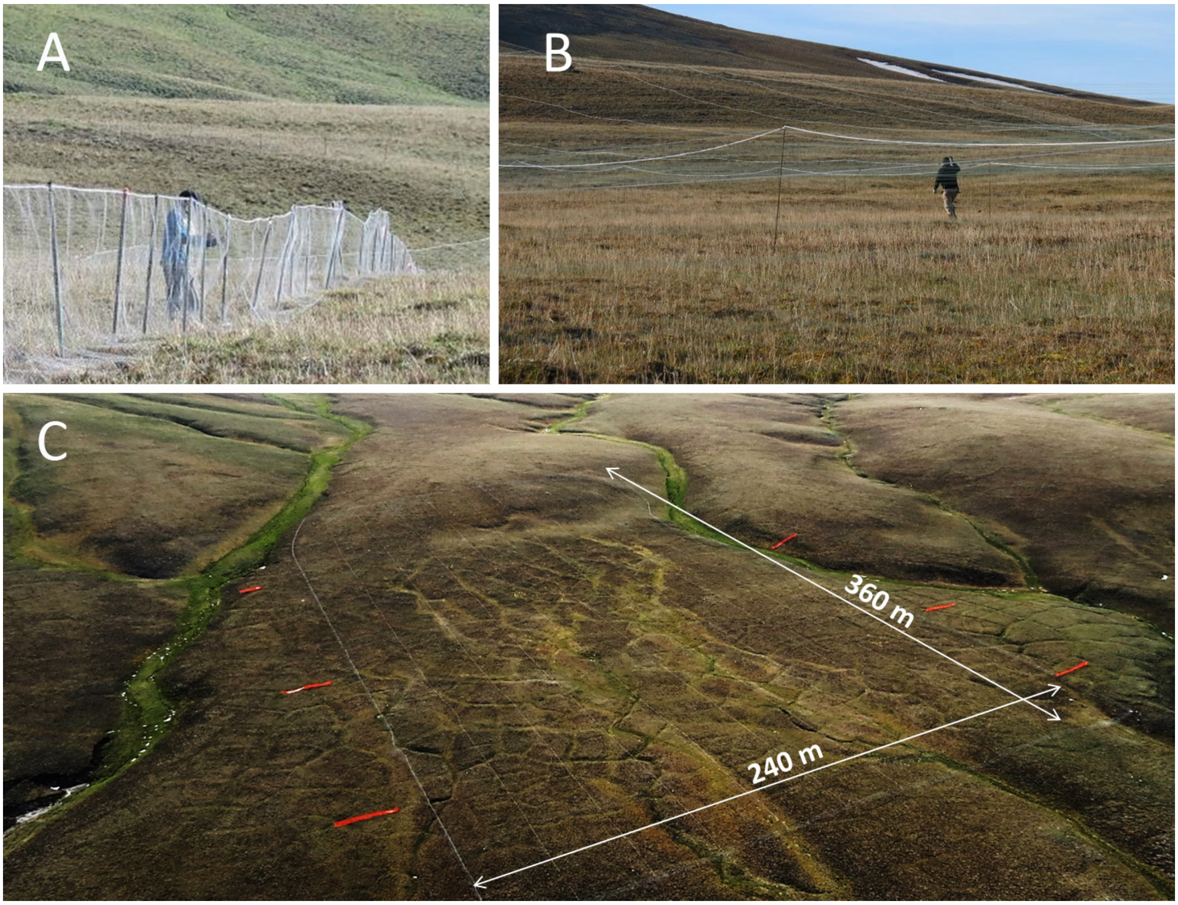

Fig. 1. Predator exclosure used to reduce predation pressure on brown lemmings. The fence around the perimeter was made of chicken wire (1-inch mesh) 1.4 m high (2.0 m high when crossing snow drift areas) attached to T-shaped steel bars in order to prevent foxes from entering the protected area (A). The fence had a 60-cm long outward extension on the ground to prevent foxes from digging under the fence. To exclude avian predators, we built a "roof" made of criss-crossing nylon fishing line 0.5 m apart in order to completely cover the 8.6 ha area (B). The roof was supported by steel rods and nylon cords spaced out every 20 m. The aerial photograph (C) shows the total area covered by the fence (8.6 ha).

consisted of three consecutive days of trapping and grids were visited twice per day. Trapping was conducted sequentially on both grids. Each captured lemming was identified to species, sexed, weighed, and tagged with a passive integrated transponder (PIT) or a uniquely numbered ear-tag (see Fauteux et al. 2015 for details). For the purpose of the current study, we focused on the 2008–2015 period, when live trapping data were collected on both trapping grids.

We started the construction of a fence delimiting an area slightly larger than the experimental trapping grid, approximately 240 × 360 m (8.6 ha; see Fig. 1 for details), in July 2012. In order to prevent foxes from entering the protected area, the perimeter was made of chicken wire (1-inch mesh) 1.4 m high (2.0 m high when crossing snow drift areas) attached to T-shaped steel bars. This mesh size allowed movements of lemmings in and out of the grid. To exclude avian predators, we built a "roof" made of criss-crossing nylon fishing line 0.5 m apart in order to completely cover the 8.6 ha area. The roof was completed in July 2013. Both the fence and the roof sustained well weather conditions although some minor repairs (e.g., bent rods, broken fishing lines, loose nylon cords) were made every summer. Similar experimental designs were successfully used in previous studies in the Canadian tundra and proved effective against all predators except small mustelids (Reid et al. 1995, Wilson et al. 1999).

Estimation of demographic parameters

We estimated four demographic parameters of lemmings during the summer: density (D), survival (S), proportion of juveniles (J), and body mass (M). In addition, movements (σ) were also estimated within spatially-explicit capture-recapture (SECR) analyses for densities (see herein). Parameters were estimated for each trapping grid at monthly occasions except survival which was estimated for two time intervals (June-July, July-August). When sample size allowed, we separated lemmings into three groups to estimate those parameters: adult males, adult females, and juveniles (disregarding the sex). However, σ, S, J, and M were not analyzed when sample size was too low (<5 ind., which happened in the low phase of the cycle; Appendix S1: Table S1). Because interannual recapture of marked lemmings is extremely rare (Fauteux et al. 2015), we calculated parameters separately for each year.

Monthly lemming densities and movements were estimated annually for each trapping grid by combining monthly occasions into a single model with SECR models using the package "secr" implemented in the R software (Borchers and Efford 2008, Efford 2015). When lemmings were in very low abundance (<5 lemmings captured per month per grid), we used the known minimum number alive divided by the average effective sampling area of the respective trapping grids determined with SECR models in other years. We report densities as the number of individuals per ha. Statistical details are presented in Appendix S2. Survival was estimated with the RMark package implemented in R (Laake et al. 2013). Our sampling corresponded to Pollock's robust design and we used the Huggins parameterisation to minimise the number of parameters per model (Williams et al. 2002). More details on survival estimation are presented in Appendix S3.

We determined the proportion of juveniles (J) among all individual captured at each occasion. Females <28 g and males <30 g were considered juveniles (Fauteux et al. 2015). The average body mass was calculated for adults of both sexes separately.

Nests built by lemmings under the snow during the cold season can be used to obtain an estimate of winter densities (D^W) (Duchesne et al. 2011*a*, Krebs et al. 2012). Winter nest densities were obtained by searching thoroughly trapping grids with several persons walking side by side along parallel lines set 10 m apart. Winter nests are easily detected on the Arctic tundra (Krebs et al. 2012), so we assumed that observers had a 100% probability of detecting nests located within 5 m of their walking path. For each nest found, the species using it was recorded based on the size, shape and color of faeces (Duchesne et al. 2011*a*, Soininen et al. 2015*a, b*). Nest density was calculated as the total number of nests occupied by brown lemmings divided by the size of the searched grid. The presence of a snow fence on our experimental grid from 2008 to 2011 affected winter nest density but the effect was mostly concentrated within 10 m from the snow fences (Bilodeau et al. 2013). Results from our analyses did not differ if we included or not winter nests located within 10 m from the snow fence, hence we present the results including all winter nests.

Predator activity

We conducted observations of predator activity at trapping grids every 2-3 d during the summers (June-August) of 2014 and 2015. No observations were conducted in 2013 due to the complete absence of lemmings and the scarcity of predators (no long-tailed jaeger, rough-legged hawk, or snowy owl nest was found in our study area; Gauthier et al. 2014). Observations were done during predetermined periods of time (~1 h) one grid at a time from lookout points that offered good visibility. Presence of predators was also noted opportunistically when walking the grids during trapping sessions or during other activities (time spent doing these activities were considered as observation periods). All mammalian predators passing nearby or inside the trapping grids were noted as well as their behavior: hunting, digging, running, or vocalizing. Similarly, avian predators and their behavior were noted as flying above the grids, vocalizing, hovering (e.g., jaegers), or perching. The number of predators seen divided by the total length of observation periods yielded the frequency of observations by species. In early July 2015, we placed seven artificial bird nests made of 4 quail eggs inside the experimental grid while 40 were placed outside the exclosure (<5 km) as part of a long-term monitoring of predation risk in the area (McKinnon et al. 2014). Nests were monitored daily for the first 3 days and weekly thereafter. Field manipulations were approved by the Animal Welfare Committee of Université Laval (2014-061) and Parks Canada (SIR-2013-13953).

Statistical analyses

Our long-term dataset allowed us to compare the experimental and control grids before (2008–2012) and during (2013–2015) the treatment but with no replicate during the predator reduction experiment (we return to this topic in the Discussion). Quantitative comparisons of densities, movements, and survival estimates obtained with the capture-recapture data were conducted using 90% and 95% confidence intervals (CI). Estimates with overlapping 90% CI between the control and experimental grids were considered statistically similar while non-overlapping 95% CI were considered statistically different. Overlapping 95% but nonoverlapping 90% CI were considered marginally different.

We analyzed the effects of the period (before and during predator reduction) and trapping grids on J using a generalised linear mixed model with a binomial distribution and on M using a linear mixed model (LMM) with a Gaussian distribution. An interaction between both variables was included in all models to consider that predator reduction on the experimental grid started in 2013 and month nested in year were used as random variables to consider potential temporal variation. We also used a LMM with a Gaussian distribution to compare D^W between trapping grids and periods in interaction using year as a random variable. We used the coefficient of determination (R^2) of Nakagawa and Schielzeth (2013) to estimate the variance explained by the mixed-effects models with and without the random variables.

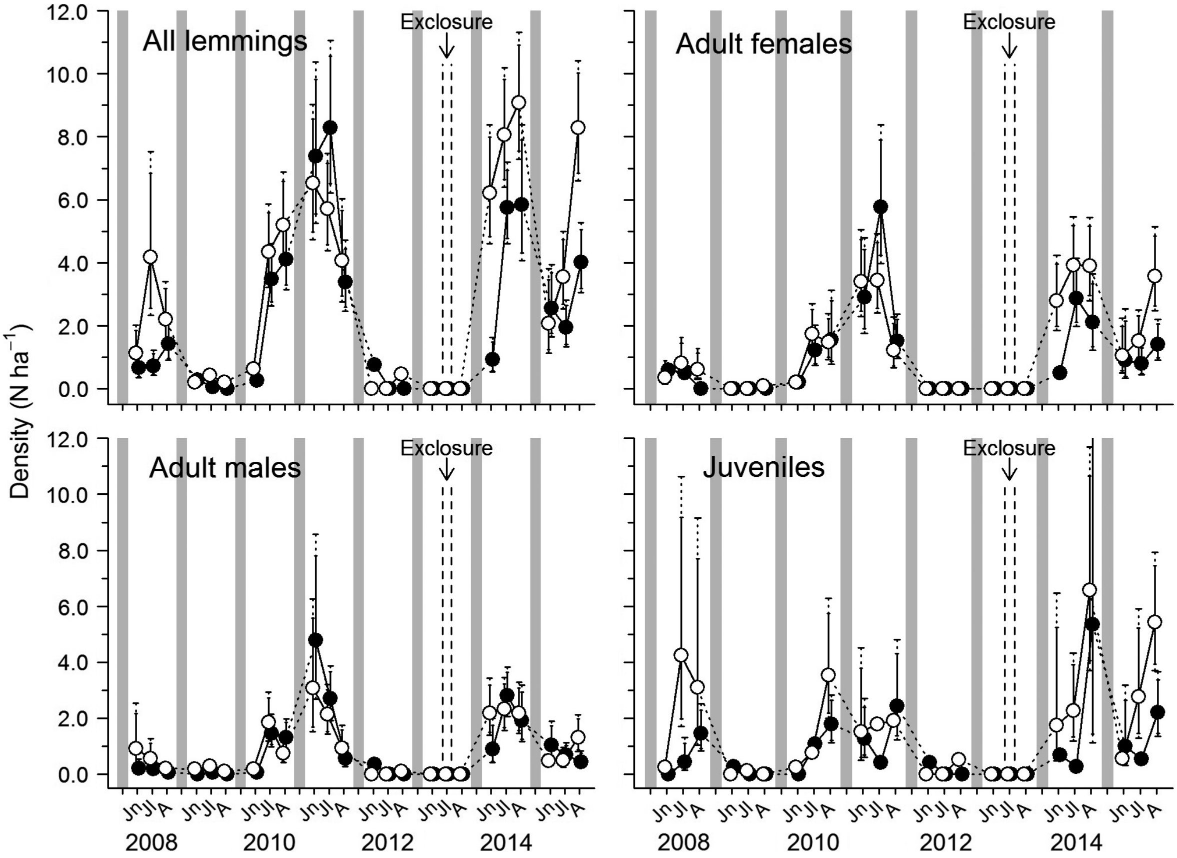

FIG. 2. Temporal fluctuations of brown lemming densities (total and separated in adult males, adult females and juveniles) in the control (black circles) and experimental trapping grid (open circles) with their 90% (solid line) and 95% (dotted line) confidence intervals. Gray bars correspond to the winter period. The vertical dashed double-line separates the pretreatment from the treatment (predator exclusion) period. Jn = June, Jl = July, A = August.

RESULTS

Before the predator exclosure became effective in 2013, we had three years of high abundance (2008, 2010, and 2011) and two years of low abundance (2009 and 2012; Fig. 2). The low phase persisted in 2013 as no brown lemming was captured that year. Populations built up during the winter 2013–2014, as shown by the high winter nest density (Fig. 3). Populations peaked in summers 2014 before declining in 2015 (Fig. 2).

Demographic response

During 2014 and 2015, densities of brown lemmings were higher in the predator-reduction grid compared to the control grid at all times, with slightly overlapping to nonoverlapping 95% CI, except in June 2015 (Fig. 2). The difference was especially marked in July 2014 and July-August 2015 for juveniles, and June 2014 and August 2015 for adult females (densities were >2.4× higher on the predator-reduction grid). Densities of adult males, however, were similar between the 2 grids at most occasions. During the two previous peaks (2008 and 2010–2011) before establishment of the predator exclosure, we found no consistent differences in densities between the two grids as densities were slightly higher (no 95% CI overlap) in the experimental grid compared to the control grid at only 1 out of 15 occasions (July 2008, Fig. 2).

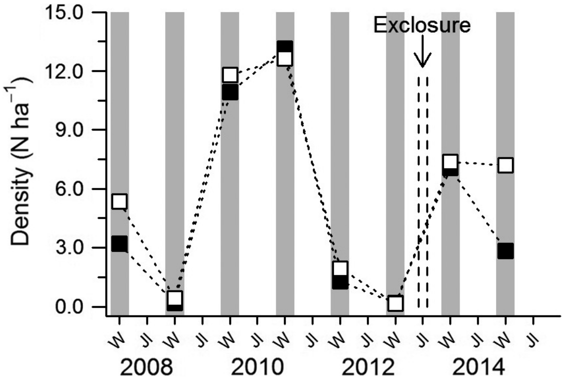

FIG. 3. Temporal fluctuations of winter nest densities of brown lemmings for the control (black squares) and the experimental grid (open squares). The vertical dashed double-line separates the pretreatment from the treatment (predator exclusion) period. Gray bars correspond to the winter period. Jl = July, W = winter.

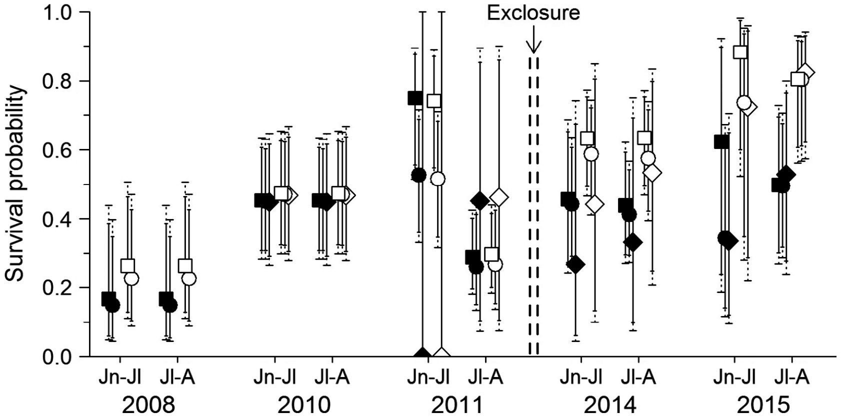

FIG. 4. Monthly survival estimates of adult female (squares), adult male (circles), and juvenile (diamonds) brown lemmings with their 90% (solid line) and 95% (dotted line) confidence intervals. Black symbols = control grid; open symbols = experimental grid. The vertical dashed double-line separates the pre-treatment from the treatment (predator exclusion) period (≥2013). Jn = June, Jl = July, A = August.

There were no systematic differences in distances moved by lemmings between the predator-reduction grid and the control either before or after the treatment, although males generally had longer movements than females or juveniles (Appendix S2: Figure S1). Similar inconsistent differences were observed during the pre-experimental period.

In 2014 and 2015, survival of adult females and males were 1.4× and 1.6× higher inside the predator exclosure than outside, although all 90% CI overlapped slightly (Fig. 4). Similarly, survival of juveniles was 1.6× and 1.8× higher inside the predator exclosure compared to the control grid in 2014 and 2015, respectively, but all 90% CI overlapped. Model selection, however, provided strong support for a grid effect on survival in both years (Appendix S3: Table S2). Prior to the predator exclosure, survival was similar between both trapping grids (Fig. 4) and model selection provided weak (2008) or no (2010 and 2011) evidence for a grid effect (Appendix S3: Table S2). Survival generally did not differ between periods or lemming groups except in 2011, when adult female survival was lower in July-August compared to June-July.

The proportion of juveniles was similar in the 2 grids before the treatment period (control: J = 0.23 ± 0.06, experimental: J = 0.23 ± 0.07), but was lower in the control (J = 0.16 ± 0.06) compared to the experimental grid (J = 0.25 ± 0.08) during predator reduction (significant interaction grid*period; Table 1, Fig. 5).

Adult body mass differed between the 2 grids and the 95% CI of the interaction with period almost excluded 0 (Table 1). Adult lemmings were generally heavier inside the exclosure (M_{exp} = 52.2 ± 2.5 g) than in the control grid (M_{con} = 46.8 ± 2.6 g) during the predator-reduction period, whereas body mass was more similar between the 2 grids (M_{exp} = 51.3 ± 2.2 g v.s. M_{co} = 49.0 ± 2.2 g) before that period.

TABLE 1. Slope parameters (β) and their 95% confidence intervals (CI) for the effects of trapping grid (control vs. experimental) and time period (before and after predator reduction) on lemming demographic parameters. We report both marginal R^2_g (fixed-effects only) and conditional R^2_c (with random effects). Month nested in year were used as the random factors for J and M while only year was used for D^W. Number of parameters (K) and observations (n) are also reported.

			95% CI					
Demographic parameter	Explanatory variables	β	(low)	(high)	K	n	R^2_g	R^2_c
J	Grid	−0.05	−0.44	0.33	6	1,308	0.01	0.23
	Period	−0.47	−1.64	0.72				
	Grid*period	0.63	0.07	1.20				
M	Grid	2.30	0.05	4.43	7	984	0.02	0.15
	Period	−2.17	−8.27	4.02				
	Grid*period	3.12	−0.05	6.39				
D^W	Grid	0.35	−0.07	0.78	6	16	0.04	0.97
	Period	−0.50	−3.25	2.25				
	Grid*period	−0.11	−0.80	0.59				

J = proportion of juveniles; M = body mass of adults; D^W = density of winter nests.

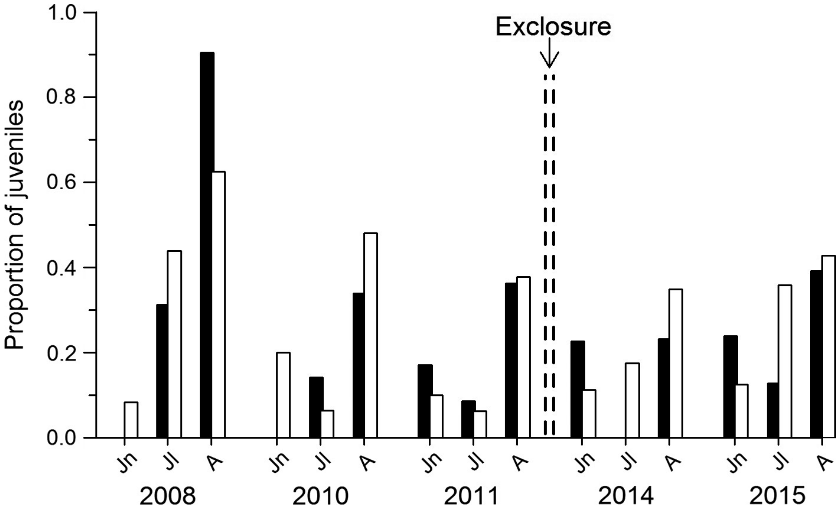

FIG. 5. Proportion of juveniles among captured individuals on the control (black bars) and experimental (white bars) trapping grids. The vertical dashed double-line separates the pretreatment from the treatment (predator exclusion) period (≥2013). Jn = June, Jl = July, A = August.

Winter nest densities (B^W) were not statistically different between the experimental and control grids or the periods although the 95% CI of the grid effect nearly excluded 0 (Table 1). We note a trend for higher nest density on the experimental grid in winter 2008 (a year when the snow fence was present) and especially in 2015 during the predator-reduction experiment (Fig. 3).

Predator activity

During behavioral observations, predators were observed on 22 occasions (n = 127 h of observations) above and near the predator-reduction grid and on 44 occasions (n = 143 h) for the control grid. All predator species were seen more often at the control than at the experimental grid except parasitic jaegers (Table 2). Among the 161 long-tailed jaegers observed (commonest predator), most were just passing by in flight or vocalizing from a short distance (<200 m). We observed jaegers attempting to catch lemmings three times in the control grid, and two were successful. Four snowy owls were seen flying above the control grid and a single one sitting <100 m from the experimental grid in 2014. An arctic fox was observed inside the control grid five times during July-August 2014. Fecal deposits found before snow-melt were the only evidence that foxes entered inside the exclosure during winter 2014. In 2015, arctic fox digging under the anti-predator fence was found soon after snow melt and small holes were dug inside the exclosure, apparently to catch lemmings. It is unclear when a fox breached the fence (i.e., spring or fall) but potential entry points were blocked in June 2015 and the fence was reinforced. In 2015, all artificial bird nests placed within the predator exclosure remained intact after 48 d (n = 7) whereas all 40 nests placed outside the exclosure were depredated within 72 h. In 2014, none of the winter nests sampled had signs of predation by ermine (n = 120) and in 2015 a single nest on the control grid (n = 78) had signs of predation.

TABLE 2. Number of individuals per 100 h of observation for each predator species moving, vocalizing, or attacking prey near the experimental grid or near and in the control grid.

	2014		2015	
Species	Experimental grid (n = 89 h)	Control grid (n = 80 h)	Experimental grid (n = 38 h)	Control grid (n = 63 h)
Arctic fox	0.0	6.3	2.6	4.8
Snowy owl	1.1	5.0	0.0	0.0
Common raven	3.4	12.5	0.0	21.0
Glaucous gull	2.2	6.3	5.3	7.9
Long-tailed jaeger	16.9	100.3	57.9	61.9
Parasitic jaeger	0.0	2.5	13.2	3.2
Total	23.6	132.9	79.0	98.8

TABLE 3. Comparison of results obtained by studies using large predator exclosures to study lemming demography in the Canadian Arctic. Empty cell indicates no information available. Reid et al. (1995) and Wilson et al. (1999): collared lemming. Our study: brown lemming.

Parameter	Group	Reid et al. 1995	Wilson et al. 1999	This study
Density	Adult females	++*	++*	+ +
	Adult males			0
	Juveniles			+ +
Survival	Adult females	++*	+†	+
	Adult males			+
	Juveniles		+	+
Prop. of juveniles/Recruitment		+ +		++
Body mass	Adult females		+ +	+†
	Adult males		+ +	
	Juveniles		+	
Movements/Dispersal	Adult females		0	0
	Adult males		0	0
	Juveniles		0	0

+ +, − − = statistical support for a positive (or negative) effect of predator exclusion. +, − = evidence suggests a weak positive (or negative) effect of predator exclusion. 0 = no effect of predator exclusion. * = sex and age not differentiated. † = sex of adults not differentiated.

DISCUSSION

Predation was sufficient to limit population size

In accordance with our first prediction, brown lemming densities were generally higher in the experimental than in the control grid during the peak and initial phase of the decline (2014–2015). Indeed, the average densities of adult females and juveniles were 2.4× and 3.4× more abundant inside the experimental than in the control grid, respectively. In contrast, comparisons of densities between the experimental and control grids did not reveal any consistent pattern during the preexperimental period (2008–2012). Therefore, the higher density of brown lemmings in the predator-reduction grid supports the limitation by predation hypothesis (Krebs 2011). Interestingly, predator reduction had a negligible effect on adult males as their average density in the experimental grid was only 1.4× higher than in the control during the experiment.

Previous predator-removal experiments conducted in the low Arctic of Canada reported positive numerical responses of collared lemmings similar to ours (Table 3). In Scandinavia, predator removal experiments also yielded positive effects on vole densities (Korpimaki and Norrdahl 1998, Klemola et al. 2000, Huitu et al. 2003). The density ratios of all lemmings between the experimental and control grids were higher in our study compared to what Salo et al. (2010) reported in their meta-analysis (1.9× vs. 1.7×). This is consistent with suggestions that in the High Arctic, predation may have a stronger impact on prey populations than in other areas (Gilg et al. 2003). The simple trophic system of the High Arctic tundra and the strong and immediate numerical response of several raptors during the summer may explain why predation had such a strong impact on lemming population growth (Gilg et al. 2006, Therrien et al. 2014). Predator reduction led to a large increase in lemming survival during the summer in our experiment. This shows that summer population growth is mainly limited by mortality caused by predators, a pattern already inferred in this system based on correlative evidence (Fauteux et al. 2015) and confirms that predation was sufficient to limit population size. Habitat is unlikely to be a confounding factor in our experiment because trapping grids were both located in mesic tundra with similar plant communities and biomass. Furthermore, lemming demographic parameters did not differ between the control and experimental grids prior to the start of the experiment. Previous studies at our study site also found little impact of lemming grazing on plant biomass, even in peak years (Bilodeau et al. 2014).

The higher body mass observed in the experimental grid compared to the control during the period of predator reduction may be related to the higher survival of lemmings observed in that grid as we hypothesized. Indeed, a higher proportion of lemmings may have reached older age classes and hence a higher body mass, thereby increasing average body mass in the population (Wilson et al. 1999). It is also possible that the absence of predators inside the experimental grid may have reduced the predation risk perceived by lemmings and thus increased the time spent feeding (Dupuch et al. 2014), thereby leading to higher body mass.

It is surprising that the difference in lemming density observed in August 2014 between the predator-reduction and control grids had vanished at snow-melt in 2015. At our study site, population declines usually occur in fall, likely due to high predation during this period (Fauteux et al. 2015). This is supported by the trend for a higher nest density inside the experimental grid compared to the control during winter 2014–2015. The breach of our exclosure by a fox during winter 2014–2015 may explain why the June 2015 density was not higher in the experimental grid compared to the control. We also note that the proportion of winter nests with signs of reproduction was unusually low on both grids that year (0.07, Fauteux et al. unpubl. data) compared to 2014 and previous winters of high abundance (0.20–0.34; Fauteux et al. 2015). Poorer snow conditions in 2015 compared to 2014 may have contributed to that (Domine et al. 2016).

Predator abundance at the study site was generally lower in 2015 compared to 2014 except for foxes which were more abundant. In 2015, snowy owls were absent, most long-tailed jaeger nests failed early, and we did not observe any active ermine den in either year (Gauthier et al. 2016). Considering that these predators can have a major impact in summer (they can eat up to 5 lemmings per day per individual depending on the species; Gilg et al. 2003, Bilodeau 2013, Therrien et al. 2014), this may explain why lemming populations were able to grow during summer 2015 even though the population had declined by that spring. This is supported by a trend for higher survival of lemmings between July–August 2015 compared to the same period in 2014. Nonetheless, we note that population growth was much more pronounced in the experimental grid than in the control as a consequence of a higher survival rate in the former area. By the end of 2015, lemming populations had not yet crashed in our study area, possibly because ermines, a key predator (Gilg et al. 2003), were still low. Ermine populations often respond with a delay to lemming abundance, as we observed in 2012 (i.e., high ermine populations coincident with the crash of lemmings; Bilodeau 2013).

The proportion of juveniles was slightly higher in the experimental grid compared to the control during the predator-reduction period. This could be due to a higher fecundity of females or a better survival of juveniles after birth. However, female fecundity was apparently not affected by the reduction of predators and remained high on both grids (Fauteux et al. unpubl. data). Other predator removal experiments in lemmings and voles also reported no density-dependent effects on female reproductive activity (Reid et al. 1995, Wilson et al. 1999, Klemola et al. 2000). In contrast, juvenile density increased more inside the predator exclosure than on the control in 2015, which supports the hypothesis that the higher proportion of juveniles in the experimental grid was a consequence of a higher juvenile survival in absence of predators.

Scope and caveats of the experiment

The most serious problem encountered was the entry of foxes inside the predator exclosure between late summer 2014 and spring 2015. This is a common risk faced by large-scale predator manipulation experiments because fences are prone to damage (Reid et al. 1995, Wilson et al. 1999). Although we do not know when this event occurred exactly, the high density of lemming nests inside our exclosure in winter 2014–15 suggests that it may have happened at snow melt and that it had a small impact overall (see above). Our predator observations and artificial nests depredations suggest that our exclosure successfully excluded all predators at least during the summer, and that predator attraction was not a relevant confound.

Our anti-predator fence was permeable to lemmings, which was confirmed by the observation of runways that had been carved in the vegetation under the fence. This prevented the so-called fence effect (Ostfeld 1994) by allowing natural movements and dispersal of individual lemmings. We found that adult males moved longer distances between trapping events than did females and juveniles. The search for females to mate may be responsible for these long movements but aggressiveness among males may also have led some to look for unoccupied areas (Krebs 1964, Predavec and Krebs 2000). Longer movements by males may drive them more often outside of the exclosure, exposing them to higher mortality risk (Reid et al. 1995, Wilson et al. 1999). This could also explain why we found a weak effect of our manipulation on male density. Dispersal of individuals and especially young outside our exclosure may also explain why total densities did not reach abnormally high levels compared to the pre-experimental period.

Other common criticisms of predator removal experiments are their small spatial scale and lack of replicates (Sundell 2006). We used an exclosure (9 ha) that was much larger than the average home range of lemmings (0.4–0.9 ha; Banks et al. 1975) in order to have a large enough population in our experimental grid. This, however, was done at the expense of experimental replication. Absence of spatial replicates in our study was partly compensated by the multiple years of measurement, including a 5-yr long pre-experiment survey (2008–2012). This allowed us to confirm that demographic parameters were similar between the two grids prior to our manipulation, a critical information in any before-after control-impact study (Smith 2013). We must also recognize that our study did not cover the full decline and low phases of the lemming cycle, although we believe that results presented herein provide compelling evidence in support of our hypotheses.

Lastly, we can compare our results to similar experiments that were conducted on a different lemming species (collared lemming) in the Canadian low Arctic (Table 3). Our study and those of Reid et al. (1995) and Wilson et al. (1999) all reported increases in density, survival, proportion of juveniles and body mass of lemmings when predators were excluded. The remarkable consistency in results obtained across experimental, studies repeated in different environments provides robust empirical evidence in favor of the predation hypothesis and allows stronger inferences of general ecological patterns driving population dynamics (Salo et al. 2010, Prevedello et al. 2013).

CONCLUSION

Top-down control by predators has often been identified as one of the most plausible forces driving small mammal population cycles because of its potential to generate delayed density-dependent effects (Hanski et al. 1993, Korpimaki and Krebs 1996, Krebs 2013). In this study, we found that brown lemmings reached much higher densities in absence of predation due to a high survival rate. Therefore, our field experiment confirms that predation can limit their population size, as previously reported for another lemming species in the Canadian low Arctic (Reid et al. 1995, Wilson et al. 1999). It suggests that predation plays a key role in the population dynamics of lemmings, as previously found in boreal voles (Norrdahl and Korpimäki 1995, Huitu et al. 2003), and supports the hypothesis that small arctic herbivores are primarily controlled by top-down forces (Legagneux et al. 2012). Nonetheless, our predator-reduction experiment did not cover all phases of the lemming cycle and future work should examine how predation affects the demography during the low-phase of the cycle, which remains one of the most puzzling phases at the moment (Boonstra et al. 1998). We also do not know if predation can have carry-over effects over multiple seasons.

In contrast with the summer period, our understanding of small mammal population dynamics during winter is still limited (Krebs 2011). Recent work suggests that varying reproductive rate is the main driver of winter population growth rates of lemmings (Fauteux et al. 2015). In winter, poor snow conditions may interact with extrinsic biotic factors (e.g., reduced food availability when plants are encased in ice) or intrinsic factors (e.g., carry-over effects of stress caused by high predator density) and have a detrimental effect on reproduction. Therefore, the role of predation and its interactions with other factors in winter in affecting population cycles of arctic lemmings remain unclear. Camera traps have recently been proposed as a promising method to monitor lemming activity in winter (Soininen et al. 2015*b*) and such methodological innovations will be necessary to fully understand lemming cycles.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.1570/suppinfo

DATA AVAILABILITY

All data used in this manuscript are available at the NordicanaD website: http://www.cen.ulaval.ca/nordicanad/en_index.aspx (DOI: 10.5885/45400AW-9891BD76704C4CE2).

SUPPLEMENTARY MATERIAL

APPENDIX S1. SAMPLE SIZE.

TABLE S1. Number of individual lemmings captured at each time period on each grid annually (recaptures are ignored).

Year	Month	Experimental grid			Control grid		
		Adult males	Adult females	Juveniles	Adult males	Adult females	Juveniles
2008	June	7	4	1	4	6	0
	July	6	8	11	5	5	2
	August	2	7	15	1	0	19
2009	June	2	0	0	0	0	2
	July	3	0	1	1	0	0
	August	1	1	0	0	0	0
2010	June	2	2	1	1	2	0
	July	23	20	3	31	17	8
	August	12	16	26	24	15	20

2011	June	15	27	12	28	24	7
	July	23	33	7	38	52	3
	August	10	12	17	7	18	12
2012	June	0	0	0	6	0	3
	July	0	0	0	0	0	0
	August	1	0	2	0	0	0
2013	June	0	0	0	0	0	0
	July	0	0	0	0	0	0
	August	0	0	0	0	0	0
2014	June	22	25	6	12	5	5
	July	27	35	13	46	34	2
	August	22	32	30	22	21	15
2015	June	6	9	3	13	7	7
	July	9	16	14	16	11	4
	August	17	32	39	10	20	22

SUPPLEMENTARY MATERIAL

APPENDIX S2. SPATIALLY-EXPLICIT CAPTURE-RECAPTURE MODELS FOR DENSITIES.

To facilitate statistical convergence of SECR models with multiple primary occasions and lemming groups (adult females, adult males or juveniles), the 3 groups were considered as if they were 3 separate sessions (only groups with ≥5 individuals captured during each primary occasion were included). This approach allows complex parameterisation of the detection and movement probabilities and the use of a conditional likelihood where lemming densities and their respective 95% confidence intervals are derived *a posteriori* from the models (Borchers and Efford 2008). This also reduces the number of parameters to estimate in each model and speeds up greatly computing time. In addition to group effects, we also examined for possible trap-dependence on detection probabilities (i.e. trap happiness/shyness; Appendix S2: Table S1). These same effects were applied to capture data from both grids in the same analysis but separate estimates were obtained for each grid. We used the halfnormal distribution for the detection function and a buffer width of 100 m, as suggested by Krebs *et al.* (2011) for tundra rodents. The most parsimonious models were selected based on the second-order Akaike's criterion (AICc; Williams *et al.* 2002).

During years of very low abundance (<5 individuals) and/or when recaptures were too low (<2), we used the minimum number alive divided by the average effective sampling area (ESA) estimated by the SECR models (control grid 2008-2015: $ESA_{\text{adult males}}$ = 16.89 ha, $ESA_{\text{adult females}}$ = 10.00 ha, $ESA_{\text{juveniles}}$ = 7.35 ha; experimental grid 2008-2011: $ESA_{\text{adult males}}$ = 10.22 ha, $ESA_{\text{adult females}}$ = 10.48 ha, $ESA_{\text{juveniles}}$ = 3.92 ha;

experimental grid 2012-2015: $ESA_{\text{adult males}}$ = 12.59 ha, $ESA_{\text{adult females}}$ = 9.28 ha, $ESA_{\text{juveniles}}$ = 5.37 ha).

Model selection issued from the SECR analysis is presented in Table S2 of Appendix S2. Trap-happiness was detected in 2008, 2010, 2014, and 2015 while no trap-dependence was found in 2011. Movements were generally lower for recaptured individuals in 2008, 2010 and 2014, but not in 2011 and 2015. Variations in distances moved by lemmings between trapping grids were inconsistent but adult males generally showed longer movements compared to adult females and juveniles (Appendix S2: Fig. S1). During the predator exclusion period, males had shorter movements (no overlap of 95% CI) in the experimental grid than in the control in June and July 2014 and females in August 2014 but the opposite effect occurred in August 2014 for males.

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Table S1. Spatially-explicit capture-recapture candidate models used for estimating brown lemming densities and movements based on the conditional likelihood (see text).

Model	Detection	Movements
M1	primary*group	primary*group
M2	primary*group+*b*	primary*group
M3	primary*group+*b*	primary*group+*b*

group = adult males, adult females and juveniles (both sexes pooled); primary = primary occasions (months); *b* = trap-dependence; * = interaction; + = additive.

Table S2. Top models ranked according to AICc used to evaluate lemming densities during high abundance years. Densities were estimated with the top-ranked model. We used the halfnormal distribution and a buffer width of 100 m for all five models. The number of parameters (*K*) varied between years because some could not be estimated due to low sample size (≤5 individuals).

Year	Rank	Detection	Movements	*K*	ΔAICc	w_i
2008	1	primary*group+*b*	primary*group+*b*	28	0.00	1.00
	2	primary*group+*b*	primary*group	27	21.83	0.00
	3	primary*group	primary*group	26	21.95	0.00
2010	1	primary*group+*b*	primary*group+*b*	26	0.00	1.00
	2	primary*group+*b*	primary*group	25	10.84	0.00
	3	primary*group	primary*group	24	15.53	0.00
2011	1	primary*group+*b*	primary*group	37	0.00	0.49
	2	primary*group	primary*group	36	0.40	0.40
	3	primary*group+*b*	primary*group+*b*	38	3.04	0.11
2014	1	primary*group+*b*	primary*group+*b*	32	0.00	0.84
	2	primary*group+*b*	primary*group	31	3.26	0.16
	3	primary*group	primary*group	30	11.32	0.00
2015	1	primary*group+*b*	primary*group+*b*	38	0.00	0.64
	2	primary*group+*b*	primary*group	37	0.77	0.30
	3	primary*group	primary*group	36	1.17	0.25

group = adult males, adult females and juveniles (both sexes pooled); primary = primary occasions (months); *b* = trap-dependence; * = interaction; + = additive.

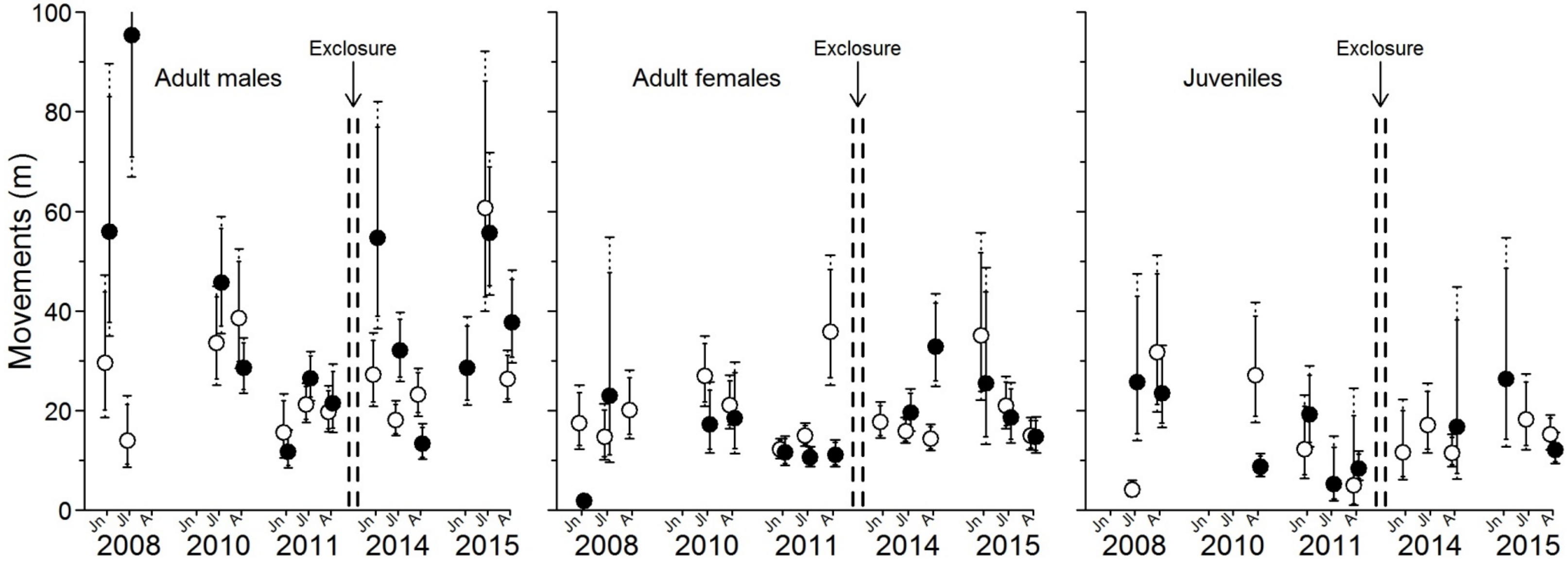

Fig. S1. Mean distance moved between capture sites and their 90% (solid line) and 95% (dotted line) confidence intervals for brown lemmings inside the control (black circles) and experimental grid (open circles). Movements were estimated from the distance separating traps in which individuals were recaptured within primary occasions. Absence of data points at some occasions is due to low sample size or absence of captures. The vertical dashed double-line separates the pre-treatment from the treatment (predator exclusion) period (≥2013). Jn = June, Jl = July, A = August.

SUPPLEMENTARY MATERIAL

APPENDIX S3. METHODS AND MODEL SELECTION FOR SURVIVAL PROBABILITIES.

Methods

We developed up to 112 candidate models to test whether survival was related to predation reduction (grid effect), age, sex, and time (Appendix S3: Table S1). We tested statistical interactions between grids and some other parameters because we thought that the effect of predator reduction could vary over the summer or among age/sex groups. We also tested for the presence/absence of random migration. Several candidate models were created to determine whether detection probabilities varied according to primary occasions, age/sex or were influenced by a trap-response (i.e., trap-shyness/happiness). A high number of candidate models were used to consider that complex models could perform well for years with large sample sizes while simpler models could perform better for years with low sample sizes. The statistical support of each model was assessed with AICc. We used model-averaged parameter values across models with ΔAICc < 4.

Model selection

Ranking of models are presented in Table S2 of Appendix S3. Survival probabilities were affected by different factors among years according to the top models (ΔAICc < 4). In 2008, models with a trapping grid effect on survival had slightly less statistical support ($\Sigma w_i = 0.44$) than those without this effect ($\Sigma w_i = 0.53$) and there was little support for a group effect ($\Sigma w_i =$ 23). Migration was absent ($\Sigma w_i = 0.81$). Probabilities of detection primarily varied among lemming groups ($\Sigma w_i = 0.59$) but also among capture occasions ($\Sigma w_i = 0.53$). Lemmings showed a negative trap-dependence (Σw_i = 1.00) indicating lower capture probability after the first capture.

In 2010, models where survival was the same on both grids received the most support (Σw_i = 0.74) compared to those where it differed (Σw_i = 0.26), and there was little evidence of a group effect (Σw_i = 0.06). Similar to 2008, absence of migration received the highest support (Σw_i = 0.78). Detection probabilities varied among groups (Σw_i = 1.00), often in interaction with primary periods (Σw_i = 0.91), and was affected by trap-shyness (Σw_i = 1.00).

The 2011, survival probabilities did not vary between grids (Σw_i = 0.86) but varied among lemming groups in interaction with time (Σw_i = 1.00). The most parsimonious models indicate that there was no migration (Σw_i = 0.59). Detection probabilities varied between primary occasions (Σw_i = 1.00) but, in contrast with the two previous years, no trap-dependence effect was found (Σw_i = 0.70).

In 2014, the most parsimonious models provide a high support for variation in survival probabilities among trapping grids (Σw_i = 0.88). Migration was absent (Σw_i = 0.88). Probabilities of detection varied primarily among lemmings groups (Σw_i = 1.0) and was also affected by a trap-dependence effect (Σw_i = 1.0) but this time trap happiness was detected.

In 2015, there was again strong support for a grid effect on survival probabilities (Σw_i = 0.96). High statistical support was found for an absence of migration (Σw_i = 0.79). Probabilities of detection varied according to both groups and primary occasions in interaction with each other (Σw_i = 1.00) and trap-dependence was absent (Σw_i = 0.77).

Table S1. List of variables used to build candidate models for estimating survival probabilities of brown lemmings. All possible combinations were made between the variables to obtain the most parsimonious model. We used Pollock's robust design and the Huggins parameterisation.

Model	Survival	Migration	Detection
[M1, M112]	constant;	absent;	constant;
	grid;	random	constant+*b*;
	group;		group;
	group*grid;		group+*b*;
	grid**t*;		primary;
	group**t*;		primary+*b*;
	grid**t*+group**t*		primary*group;
			primary*group+*b*

grid = experimental vs. control grid; group = adult males, adult females and juveniles (both sexes pooled); *t* = time period (June-July and July-August); *b* = trap-dependence; primary = primary occasions; * = interaction; + = additive.

Table S2. Top models ranked according to AICc used to evaluate survival probabilities of lemmings during high abundance years prior (2008, 2010 and 2011) and after (2014 and 2015) the predator exclosure experiment. Models with ΔAICc < 4 were used for model-averaged estimates of survival (presented in Fig. 4).

Year	Rank	Survival	Migration	Detection	*K*	ΔAICc	w_i
				First capture			
2008	1	grid	absent	primary*group+*b*	9	0.00	0.15
	2	constant	absent	primary*group+*b*	8	0.05	0.14
	3	grid	absent	constant+*b*	4	0.70	0.10
	4	constant	absent	constant+*b*	3	0.93	0.09
	5	group	absent	primary*group+*b*	9	1.61	0.07
	6	group	absent	constant+*b*	4	1.98	0.06
	7	grid	random	primary*group+*b*	10	2.42	0.04
	8	constant	random	primary*group+*b*	9	2.42	0.04
	9	grid	absent	group+*b*	5	2.62	0.04
	10	constant	absent	group+*b*	4	2.81	0.04
	11	grid	random	constant+*b*	5	2.90	0.03
	12	group*grid	absent	constant+*b*	6	2.93	0.03
	13	group*grid	absent	primary*group+*b*	11	3.06	0.03
	14	constant	random	constant+*b*	4	3.08	0.03
	15	grid	absent	primary+*b*	6	3.57	0.02
	16	constant	absent	primary+*b*	5	3.71	0.02
	17	group	absent	group+*b*	5	3.92	0.02

	18	group	random	primary*group+_b_	10	4.04	0.02
2010	1	constant	absent	primary*group+_b_	11	0.00	0.44
	2	grid	absent	primary*group+_b_	12	1.66	0.19
	3	constant	random	primary*group+_b_	12	2.14	0.15
	4	constant	absent	group+_b_	5	3.31	0.09
	5	grid	random	primary*group+_b_	13	3.81	0.07
	6	group	absent	primary*group+_b_	13	4.07	0.06
2011	1	group*_t_	absent	primary*group	15	0.00	0.33
	2	group*_t_	random	primary*group	16	0.42	0.26
	3	group*_t_	absent	primary*group+_b_	16	1.28	0.17
	4	group*_t_	random	primary*group+_b_	17	2.32	0.10
	5	grid*_t_+group*_t_	absent	primary*group	17	3.45	0.06
	6	grid*_t_+group*_t_	random	primary*group	18	3.87	0.05
	7	grid*_t_+group*_t_	absent	primary*group+_b_	18	4.73	0.03
2014	1	grid	absent	primary*group+_b_	12	0.00	0.20
	2	grid	absent	group+_b_	6	0.11	0.19
	3	group*grid	absent	primary*group+_b_	16	1.24	0.11
	4	grid	random	primary*group+_b_	13	2.07	0.07
	5	grid	absent	group+_b_	7	2.14	0.07
	6	grid*_t_+group*_t_	absent	primary*group+_b_	18	2.49	0.06
	7	grid*_t_+group*_t_	absent	group+_b_	12	2.95	0.05
	8	group*grid	random	primary*group+_b_	17	3.33	0.04
	9	group*_t_	absent	primary*group+_b_	16	3.51	0.03

	10	group	absent	primary*group+*b*	13	3.61	0.03
	11	group*grid	random	group+*b*	11	3.68	0.03
	12	grid**t*	absent	primary*group+*b*	14	3.89	0.03
	13	grid**t*	absent	group+*b*	8	3.90	0.03
	14	group	absent	group+*b*	7	3.98	0.03
	15	group**t*	absent	group+*b*	10	3.99	0.03
	16	constant	absent	primary*group+*b*	11	4.35	0.02
2015	1	grid	absent	primary*group	11	0.00	0.28
	2	grid**t*+group**t*	absent	primary*group	17	0.48	0.22
	3	grid	absent	primary*group+*b*	12	1.83	0.11
	4	grid	random	primary*group	12	2.10	0.10
	5	grid**t*+group**t*	absent	primary*group+*b*	18	2.40	0.08
	6	grid**t*+group**t*	random	primary*group	18	2.63	0.07
	7	grid**t*	absent	primary*group	13	2.94	0.06
	8	grid	random	primary*group+*b*	13	3.94	0.04
	9	group**t*	absent	primary*group	15	4.10	0.04

grid = experimental vs. control grid; groups = adult males, adult females and juveniles (both sexes pooled); *t* = time period (June-July and July-August); *b* = trap-dependence; primary = primary occasions; * = interaction; + = additive.