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Life in the fast lane: learning from the rare multiyear recaptures of brown lemmings in the High Arctic

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Abstract: Inter-annual recaptures of Arctic lemmings are extremely rare because their life expectancy is very short, typically less than one year. On Bylot Island, Nunavut, Canada, we live-trapped in summer, marked and released brown lemmings (*Lemmus trimucronatus*, Kerr 1792) between 2004 and 2016 and we performed a large-scale, before-after control-impact experiment from 2014 to 2016 to study the effects of predator reduction on their population dynamics. Although inter-annual recaptures of marked lemmings were rare, our long-term study and predator reduction allowed us to capture 21 (1.4%; $n = 1523$) individuals over two consecutive years and one over three consecutive years. The inter-annual recapture rate was much higher in the predator-reduction grid (5.7%; $n = 193$) than in the other grids (0.7%; $n = 425$) during the experiment. Average distance moved between inter-annual recaptures was small (74 m). Our data thus demonstrate that lemmings are physiologically capable of living up to 24 months in the High Arctic, that predation is a major factor affecting lemming survival, including over winter, and that they show high site fidelity among years.

Key words: small mammals, life expectancy, life history, winter survival, long-term monitoring.

Résumé : Les recaptures inter-annuelles des lemmings arctiques sont extrêmement rares car leur espérance de vie est très courte, typiquement inférieure à un an. Sur l'île Bylot, Nunavut, Canada, nous avons piégé des lemmings bruns (Lemmus trimucronatus, Kerr 1792) en été, les avons marqués puis relâchés entre 2004 et 2016. De plus, nous avons mené une expérience de comparaison avant-après à grande échelle de 2014 à 2016 afin d'étudier les effets de la réduction des prédateurs sur leur dynamique de population. Bien que les recaptures inter-annuelles de lemmings marqués soient rares, notre suivi à long terme et l'expérience de réduction des prédateurs nous ont permis de capturer 21 individus (1,4 %; $n = 1523$) pendant deux années consécutives et un individu pendant trois années consécutives. Le taux de recapture interannuelle était beaucoup plus élevé dans la grille de réduction des prédateurs (5,7 %; $n = 193$) que dans les autres grilles (0,7 %; $n = 425$) pendant l'expérience. La distance moyenne parcourue entre les recaptures interannuelles était faible (74 m). Nos données montrent donc que les lemmings sont physiologiquement capables de vivre jusqu'à 24 mois dans le haut Arctique, que la prédation est un facteur majeur

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réduisant leur survie, y compris en hiver, et qu'ils montrent une fidélité au site élevée d'une année à l'autre.

Mots-clés : petits mammifères, espérance de vie, cycle biologique, survie en hiver, surveillance à long terme.

Introduction

Lemmings are the most widespread rodents in the Arctic and have often been identified as keystone species of the tundra (Gauthier et al. 2011; Krebs 2011). Their dramatic variations in abundance have an impact not only on predators but also on other prey (Bêty et al. 2002; McKinnon et al. 2014; Therrien et al. 2014). In some regions, lemmings are also important grazers that can have a significant impact on plant productivity (Johnson et al. 2011; Olofsson et al. 2014).

Robust research on lemming demography is challenging because it requires live capture and recapture of individuals. Several capture–recapture studies have considerably improved our understanding of the summer demography of lemmings and showed that summer survival is low and highly dependent on predation intensity (Gilg et al. 2003; Fauteux et al. 2016). However, our knowledge of their winter demography (particularly overwinter survival but also seasonal movements) remains very limited because of the impossibility of trapping lemmings under the snow during the long Arctic winter. There is no published overwinter survival rate value for any lemming species, but Krebs (1964) suggested that ≤10% of brown lemmings (*Lemmus trimucronatus*, Kerr 1792) may survive the 10-month long winter. Other studies reported overwinter survival probabilities ranging from approximately 0 to 0.25 for tundra voles (*Microtus oeconomus*) in the low Arctic (Aars and Ims 2002; Korslund and Steen 2006).

Because of their multiple annual generations, winter reproductive activity (MacLean et al. 1974; Millar 2001), and low survival rates (Fauteux et al. 2015), lemmings marked in summer are rarely recaptured the following year. Yet, such recaptures, when they occur, have the potential to reveal extremely useful information on (1) the physiological limit of lemmings in terms of life expectancy under the harsh arctic conditions, (2) the factors affecting their overwinter survival, and (3) their inter-annual site fidelity and factors affecting it. We captured, marked, and recaptured brown lemmings during 13 years in the Canadian High Arctic and performed a large-scale, before-after control-impact experiment to study effects of predation on their population dynamics (Fauteux et al. 2016). This setting provided a unique opportunity to obtain some inter-annual recaptures of lemmings and gain some new insights on their biology. Because the predator-reduction grid generally showed higher lemming densities in both summer and winter (Fauteux et al. 2016), we expected that lemmings should survive better and make shorter inter-annual movements in this grid compared with outside during winter.

Material and methods

Between 2004 and 2016, brown lemmings were live-trapped at three sites, two located in mesic tundra and one in wet tundra on Bylot Island, Nunavut, Canada (73°N, 80°W; see Fauteux et al. 2015 for details on the study area). Two grids set in 2004 (one in each habitat) were made of 144 stations (12 × 12) each separated by 30 m. In 2007, a third grid was deployed in mesic tundra and consisted of ~100 stations (10 × 10 or 8 × 12 depending on year). This grid was used from 2009 to 2011 for a snow fence experiment evaluating the effect of snow depth on lemming winter demography (Bilodeau et al. 2013), after which fences were removed. From 2012 to 2013, we created an 8.6 ha fenced area covered by an anti-avian predator net at the same site. This provided us with a predator-reduction grid from 2014 to 2016. One longworth trap was deployed at each station on each grid.

From 2004 to 2007, lemmings were trapped on all grids over five consecutive days (traps were checked at 12 h intervals) four times during the summer (mid-June, early-July and late-July, and mid-August). Starting in 2008, lemmings were trapped over three consecutive days three times during the summer (mid-June, mid-July, and mid-August). Captured lemmings were marked with a PIT-tag (most often; AVID®; Avid Identification Systems, Inc., Norco, CA, USA) or an ear-tag (National Band & Tag Company, Newport, KY, USA). Before marking, lemmings were checked for presence of tags to detect recaptures. Field manipulations were approved by the Animal Welfare Committee of Université Laval and by Parks Canada.

Results

The number of lemmings captured fluctuated considerably among years (Table 1) because of the cyclic dynamics of their populations (Gruyer et al. 2008; Fauteux et al. 2015). From 2004 to 2015, we marked 1544 brown lemmings during the summer. Only 21 of them were recaptured the following year (Table 1), including one female in the predator-reduction grid that was marked on the 18 July 2014, recaptured in summer 2015, and last recaptured on the 19 August 2016, 764 days after the first capture. Based on its mass at initial capture (26 g), this female was considered a juvenile close to maturity (Fauteux et al. 2015), and thus, we can estimate its minimal life expectancy at ~800 days.

The inter-annual recapture rate was almost eight times higher in the predator-reduction grid (5.7%; $n = 193$) than in the control grids (0.8%; $n = 1330$), a highly significant difference ($\chi^2 = 28.5$; $P < 0.001$). Restricting the analysis to 2014–2016, when the predator-reduction grid was effective, yielded the same result (5.7% recapture rate in the predator-reduction grid vs. 0.7% in the control, $n = 425$; $\chi^2 = 14.0$; $P < 0.001$).

The distance moved by individuals between the last capture in a given year and the first capture in the subsequent year averaged 74 m (±13 SE; $n = 19$; min–max = 0–242 m). Individuals recaptured in the predator reduction grid had a nonsignificant tendency to move less on average over winter (51 m ± 15 SE) than those in the control grids (94 m ± 19; $t_{(17)} = 1.92$; $P = 0.07$).

Discussion

These results confirm that life expectancy of brown lemmings is very short because <1% of lemmings marked in a given summer were recaptured the following summer in our control grids. This was not caused by trap-shy lemmings because on average 60% of marked individuals were recaptured at least once during the same summer. However, it is important to remember that the raw recapture rates presented here are not a measure of absolute survival rate because probabilities of survival and recapture, the latter being conditional on having survived, are confounded (Lebreton et al. 1992).

Very little information exists on lemming life expectancy. Krebs (1964) suggested that up to 5%–10% of brown lemmings survived the 10-month long winter at Baker Lake, Canada, but this was based on calculated estimations rather than direct observations of recaptured animals. Our results confirm that most individuals do not survive over the winter and must be replaced by younger generations to maintain the population. Nonetheless, the recapture of some individuals one year after they have been marked, and in one case two years later, indicates that lemmings are physiologically capable of surviving for relatively long periods over the winter. Thus, a shift in the age-structure of lemming populations caused by an increasing proportion of older individuals in periods of high survival is possible because this is likely the case in our predator-reduction grid (see below). Such shift has been proposed as an explanation for variations in average body mass of individuals captured among

Table 1. Number of individual brown lemmings marked and released each year from 2004 to 2015 and number recaptured the following year.

Year	Grids	Marked and released	Recaptured year + 1
2004	Controls	90	1
2005	Controls	17	0
2006	Controls	24	0
2007	Controls	22	0
2008	Controls	186	0
2009	Controls	15	0
2010	Controls	209	6
2011	Controls	336	0
2012	Controls	6	0
2013	Controls	0	0
2014	Controls	256	2
	Predator reduction	120	3
2015	Controls	169	1
	Predator reduction	73	8[a]

Note: Lemmings were first captured in June, July, or August of year *t* and were recaptured mainly in June, but also in July or August of year *t* + 1. For 2014–2015, data are shown separately for the predator-reduction grid and the control grids.

[a] Including a lemming recaptured for a second year in a row.

phases of their population cycles (Wilson et al. 1999), although alternative explanations may exist if lemmings reach a plateau in weight early in life.

The very large difference in inter-annual recapture rate between our predator-reduction and control grids suggests that predation is a major factor affecting overwinter survival of brown lemmings. This is in good agreement with studies showing that predation is the main factor affecting summer survival of lemmings in the High Arctic and that it may be the main driver of their population dynamics over multiple seasons (Wilson et al. 1999; Gilg et al. 2003; Fauteux et al. 2016). Predation is stronger in summer than winter because avian predators (i.e., mainly snowy owls, *Bubo scandiacus*; long-tailed jaegers, *Stercorarius longicaudus*; rough-legged hawks, *Buteo lagopus*) migrate north to reproduce in addition to mammalian predators (i.e., arctic fox, *Vulpes lagopus*; ermine, *Mustela erminea*), which are present year-round (Legagneux et al. 2012; Therrien et al. 2014). Even though the small number of recaptures did not allow us to estimate true survival rate using robust capture–recapture methods, the raw recapture rate suggests a much higher overwintering survival rate of brown lemmings when predation was experimentally reduced. Therefore, even though the predator guild is reduced, predation by foxes and ermines, and possibly some avian predators before their departure in autumn appears sufficient to strongly affect lemming winter survival. Fauteux et al. (2015) showed that reproductive rate was a strong driver of population change of brown lemmings during winter, but were unable to assess the role of predation during that season. The results of this study, therefore, support the hypothesis that predation is an important factor affecting lemming population dynamics throughout the year, including during winter.

The 74 m average distance moved by lemmings between inter-annual capture sites is larger than the distance moved between monthly captures during the summer [26 m ± 2 (SE), Fauteux et al. 2016], but nonetheless suggests long-term site fidelity. We acknowledge that these are minimum estimates given that long-distance dispersers, if any, were unlikely to be recaptured. Maximum known distance moved by brown lemmings is 1.1 km for an adult male (Krebs 1964) and studies conducted on collared lemmings (*Dicrostonyx groenlandicus*) reported distances of up to 800 m (Reid et al. 1995; Wilson et al. 1999). During winter, lemmings are known to seek moderately steep sites with a rugged micro-topography conducive to deep snow accumulation (Duchesne et al. 2011). This habitat is common in our study area, including on our trapping grids. The small inter-annual distance moved suggests that individuals can find such suitable wintering sites close to their summer range. This is further confirmed by the high density of winter nests found in our trapping grids in years of high lemming abundance (Fauteux et al. 2016). Site familiarity may be beneficial, as individuals gain knowledge of good feeding patches and efficient predator refugia, such as burrows.

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