Life in the fast lane: learning from the rare multi-year recaptures of brown lemmings in the High Arctic

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| Complete List of Authors: | Fauteux, Dominique; Universite Laval Faculte des sciences et de genie, Biologie; Gauthier, Gilles; Universite Laval Faculte des sciences et de genie, Biologie et Centre d'études nordiques Slevan-Tremblay, Guillaume; Universite Laval Faculte des sciences et de genie, Biologie et Centre d'études nordiques Berteaux, Dominique; Université du Québec à Rimouski , Canada Research Chair on Northern Biodiversity and Centre for Northern Studies |
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Life in the fast lane: learning from the rare multi-year recaptures of brown lemmings in the High Arctic

Running head: Multi-year recaptures of brown lemmings

Dominique Fauteux\textsuperscript{a,*}, Gilles Gauthier\textsuperscript{a}, Guillaume Slevan-Tremblay\textsuperscript{a}, Dominique Berteaux\textsuperscript{b}

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\textsuperscript{a} Department of Biology and Centre d’études nordiques, Université Laval, 1045 Avenue de la Médecine, Québec, QC, Canada G1V 0A6.

\textsuperscript{b} Canada Research Chair on Northern Biodiversity and Centre d’études nordiques, Université du Québec à Rimouski, 300 Allée des Ursulines, Rimouski, QC, Canada G5L 3A1.

*Corresponding author: dominique.fauteux.1@ulaval.ca
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 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.

Keywords

Small mammals, life expectancy, life history, winter survival, long-term monitoring.
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 due to 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 may survive the 10-month long winter. Other studies reported overwinter survival probabilities ranging from ~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. Since 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 to 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 x 12) each separated by 30 m. In 2007, a third grid was deployed in mesic tundra and consisted of ~100 stations (10 x 10 or 8 x 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 12h 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, Kentucky). 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 between 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 (26g), 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 8 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 non-significant
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 since
<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, as 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 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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Table 1. Number of individual brown lemmings marked and released each year from 2004 to 2015 and number recaptured the following year. 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.

| 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                  | $8^{\dagger}$     |

$^{\dagger}$ Including a lemming recaptured for a second year in a row.