

## **Chapitre 6**

### **Patterns of predation by ermine on lemmings in the Canadian Arctic**

Bilodeau, F., Gauthier, G., Lai, S. & Berteaux, D. Ce manuscrit sera soumis pour publication au journal *Écoscience*.

## Résumé

Les prédateurs peuvent parfois réguler leurs proies, spécialement dans les réseaux trophiques simples. Dans les écosystèmes nordiques, il a été suggéré que la prédation par les petits mustélidés pourrait générer les cycles de population de petits mammifères en raison de leur réponse décalée face à l'augmentation de la population de leurs proies. Pourtant, très peu d'information est disponible sur les patrons de prédation des lemmings par les mustélidés dans la toundra. Nous avons travaillé à l'île Bylot dans l'Arctique Canadien où le lemming brun (*Lemmus trimucronatus*) et variable (*Dicrostonyx groenlandicus*) sont présents, ainsi que l'hermine (*Mustela erminea*). Nous avons (1) examiné si l'abondance d'hermine montrait une réponse numérique décalée face aux fluctuations des densités de lemming, (2) estimé les taux de consommation de l'hermine à travers des observations sur le terrain et (3) déterminé les taux de prédation globale de l'hermine sur les lemmings. Nous avons estimé l'abondance d'hermine et les taux de prédation pendant l'été et l'hiver en utilisant une combinaison de relevés de nids d'hiver, d'observations directes aux tanières d'hermine, de télémétrie et d'utilisation de boîtes de trappage. Notre indice hivernal de densité d'hermine suggère une réponse numérique instantanée face aux variations annuelles de densité de lemming. Cependant, la proportion de nids d'hiver de lemming prédatés par l'hermine, ainsi que nos indices estivaux d'abondance d'hermine, suggèrent une réponse décalée d'une année. Ceci suggère que le déclin des densités de lemming survient plus rapidement que celui de l'hermine. La reproduction de l'hermine était plus élevée dans les années de fortes abondances de lemming. Le domaine vital d'une femelle suivie au cours de deux étés était de 6.5 km<sup>2</sup> et 1.6 km<sup>2</sup> et son taux de consommation pendant qu'elle nourrissait ses jeunes était en moyenne 3.95 lemmings/jour/hermine. Ce taux de consommation est plus élevé que ceux prédits à partir des calculs énergétiques et indique que l'hermine tue des proies en surplus. Globalement, nous avons estimé le taux de prédation journalier de l'hermine à environ 1.2 % de la population de lemming durant les étés de fortes abondances de proie. Nous concluons que l'hermine pourrait jouer un rôle clé dans la phase du déclin des lemmings en prélevant une grande proportion de la population de lemming durant l'été de pic d'abondance et en maintenant une pression de prédation élevée au cours de l'hiver suivant.

## Abstract

Predators may sometimes regulate their prey, especially in simple food webs. In northern ecosystems, it has been suggested that predation by small mustelids may generate population cycles in small mammals due to their delayed response to population increase of their prey. However, little is known about the predation pattern of mustelids on lemmings in the tundra. We worked on Bylot Island in the Canadian Arctic where the brown (*Lemmus trimucronatus*) and collared (*Dicrostonyx groenlandicus*) lemmings are present together with the ermine (*Mustela erminea*). We (1) examined if ermine abundance showed a delayed numerical response to fluctuations of lemming densities, (2) estimated the consumption rate of ermine through field observations and (3) assessed the overall predation rate of ermine on lemmings. We assessed ermine abundance and predation rate in summer and winter using a combination of lemming winter nest observations, direct observations at ermine dens, radio-tracking of ermines and use of trapping boxes. Our winter index of ermine density suggested an instantaneous numerical response to annual variations in lemming density. However, proportion of lemming winter nests predated by ermines, as well as our summer indices of ermine abundance, indicated a delayed response of up to one year. This suggests that the decline of lemmings occurred faster than the decline in ermine density. Breeding activity of ermines was highest in years of high lemming abundance. The home range of one female tracked during two summers was 6.5 km<sup>2</sup> and 1.6 km<sup>2</sup> and her consumption rate while provisioning young averaged 3.95 lemmings/day/ermine. This consumption rate is higher than those predicted from energetic calculations and is indicative of surplus killing. Overall, we estimated the daily predation rate of ermine at about 1.2 % of the lemming population during summers of high prey abundance. We conclude that ermines may play a key role in the lemming decline phase, by removing a large proportion of the lemming population during a summer of peak abundance and by maintaining a high predation pressure during the following winter.

## Introduction

Predators may play a key role in simple ecosystems by regulating prey populations (Korpimäki and Krebs 1996, Korpimäki and Norrdahl 1998, Berger et al. 2001). Examples include the control of large ungulate populations by wolves (*Canis lupus*) on Isle Royale and Yellowstone Park, USA (Ripple et al. 2001, Post et al. 1999, Post et al. 2002), and the trophic cascade initiated by the introduction of arctic foxes (*Vulpes lagopus*) in the Aleutian Islands, which preyed on seabirds and induced changes in the vegetation (Croll et al. 2005). In the tundra, which has a simplified food web in comparison to ecosystems located at lower latitudes (Gilg et al. 2003), small mammals are preyed upon by a diverse suite of small to medium-size predators (Krebs et al. 2003, Ims and Fuglei 2005). In such environments, just a few species of rodents typically support a large guild of predators (Legagneux et al. 2012). It has thus been suggested that predation pressure may be a key factor regulating rodent populations, and that predation could control the cyclic dynamic of several species (Korpimäki and Krebs 1996, Reid et al. 1997, Angerbjörn et al. 1999, Hanski et al. 2001, Gilg et al. 2003).

Small mustelids, mainly the ermine (*Mustela erminea*) and least weasel (*M. nivalis*), have been invoked as key predators able to generate a cyclic dynamic in their prey through a delayed response to prey population increase (Korpimäki et al. 1991, Korpimäki and Krebs 1996, Hanski et al. 1993, Heikkilä et al. 1994, Hanski et al. 2001, Gilg et al. 2003, Klemola et al. 2003). Mustelids specialize on rodents and are the only predator that can easily access lemming tunnels under the snow (Bjørnstad et al. 1995, Sittler 1995). The absence of alternative prey combined to the high energetic requirement of mustelids due to their small body size (King and Powell 2007) often lead to high predation rates in winter. Mustelids are also known to have a strong functional response to variations in rodent densities and to show high recruitment rates during years of small mammal abundance (Sundell et al. 2000, King and Powell 2007). These specialist predators are also notorious for surplus killing, presumably an adaptation to survive during periods of low prey abundance (Jędrzejewska and Jędrzejewski 1989). Caching prey could prevent mustelid populations from declining too rapidly during prey population crashes and could contribute to their delayed numerical response.

Mustelids are elusive animals and only anecdotal observations exist on their density and predation rate on arctic small mammals, particularly lemmings (but see Gilg et al. 2006). Direct field observations are rare and most studies trying to assess the impact of mustelid predation on small mammal populations used indirect signs such as predated winter nests (Sittler et al. 1995) or faeces (Gilg et al. 2006). Determining the role of these predators in the population dynamic of lemmings is thus a critical but difficult task as it requires a good understanding of their numerical and functional responses to fluctuations in prey abundance. We examined these questions in a Canadian arctic tundra ecosystem where a single mustelid, the ermine, preys on two lemming species, the brown (*Lemmus trimucronatus*) and collared lemming (*Dicrostonyx groenlandicus*). Our objectives were to (1) determine if ermine abundance showed a delayed numerical response to fluctuations of lemming densities over a 6-year period, (2) estimate the consumption rate of ermines through direct field observations, and (3) assess the potential overall predation rate (i.e. total response) of ermines on lemmings.

## Methods

### Study area

The study was conducted on Bylot Island, Sirmilik National Park, Nunavut Territory in the Qarlikturvik glacial valley (73° 08' N, 80°00' W). The study area (70 km<sup>2</sup>) was composed of lowlands bordered by a large river to the north and uplands with rolling hills to the south. Mesic tundra dominated the landscape and was composed mainly of prostrate shrubs (*Salix* spp., *Cassiope tetragona*, *Dryas integrifolia*), forbs (*Saxifraga* spp., *Potentilla* spp., *Ranunculus* spp., *Pedicularis* spp.), a sparse graminoid cover (*Arctagrostis latifolia*, *Alopecurus alpinus*, *Poa* spp., *Luzula* spp.) and mosses and lichens (Duclos 2002). In the lowlands, tundra polygons, thaw lakes and ponds were common and formed wetlands dominated by sedges (*Carex aquatilis*, *Eriophorum sheuchzeri*), grasses (*Dupontia fisheri*, and *Pleuropogon sabinei*) (Massé et al. 2001) and a uniform moss carpet. Small, intermittent streams running through upland areas were often located at the bottom of small

gullies and were characterized by a thin band of wetland vegetation surrounded by mesic tundra.

In our study area, only two species of rodents are present, the brown and collared lemming, and they represent the only significant herbivore population during winter. Lemming predators can be numerous in summer and include the snowy owl (*Bubo scandiaca*), long-tailed jaeger (*Stercorarius longicaudus*), rough-legged hawk (*Buteo lagopus*), glaucous gull (*Larus hyperboreus*) and arctic fox, in addition to the ermine. Mammals are the only predators that remain in the area during winter. Nesting passerines (*Calcarius* and *Plectrophenax* spp.) and shorebirds (*Calidris* and *Pluvialis* spp.) are potential alternative prey for the ermine and are abundant in the summer.

### **Lemming density**

Lemming populations are characterized by strong, multi-annual cyclic fluctuations of abundance at our study site (Gruyer et al. 2008) and we monitored their summer abundance by live-trapping from 2004 to 2012. We trapped lemmings on two 10.9 ha grids (one in wet and one in mesic tundra) three times during the summer (mid-June, mid-July and mid-August) to obtain mark-recapture estimation of abundance. The trapping grids were laid out in a Cartesian plane of rows and columns, with numbered stakes spaced every 30 m. At each stake, we set out a Longworth trap baited with apples near signs of lemming use or active burrows. We trapped lemmings during 3 consecutive days (4 days in 2004-2007) at each session and traps were checked twice a day, yielding 6 to 8 capture occasions. We considered the lemming population closed within each trapping session. All density estimates were carried out with DENSITY 4.4 (<http://www.otago.ac.nz/density>) using Efford's maximum likelihood estimates (Efford et al. 2004, Borchers and Efford 2008; see Krebs et al. (2011) for parameter settings in our analysis). Summer densities used in our analysis were the averaged values between the two grids during the three trapping sessions.

During winter, lemmings build nests for better insulation against cold temperatures (Casey 1981), and nest counts can provide an index of lemming winter abundance (MacLean et al. 1974, Sittler 1995, Duchesne et al. 2011b). Lemming nest density was estimated annually

from winter 2006-2007 to 2011-2012 by sampling them soon after snow-melt. Winter nests were systematically counted on our two live-trapping grids by walking parallel lines spaced 5 m from each other. To estimate winter nest density in trapping grids, the total number of nests sampled was divided by the trapping area, assuming all nests were detected. Winter nest density was also estimated on transects (75 in 2007, 30 in 2008 and 60 in 2009-2012) randomly located across the study area. Permanent transects were distributed equally in 3 habitats (wetlands, mesic tundra and along stream gullies) and reused every year. Transects were approximately 500 m long and sampling was done using the line transect method (for details see Buckland et al. 2001). Estimates of winter nest density were obtained with the software for distance sampling analysis Distance 6.0 (<http://www.ruwpa.st-and.ac.uk/distance/>, Thomas et al. 2009). Winter nest densities used in our analysis were averaged values across all the transects. Nests were also sampled opportunistically in years of low lemming abundance. The locations of all winter nests were taken using a Global Positioning System (GPS). To examine a delayed response of ermines to lemming winter density, we had to estimate nest densities prior to 2007 (our first year when estimates of ermine abundance were available, see below). We did that by transforming spring lemming densities estimated by live-trapping into lemming nest densities using the following equation (a reciprocal of the equation provided by Krebs et al. (2012);  $R^2 = 0.64$ ):

$$\text{Log}_{10}(\text{nest density}) = 0.0499 + 0.6842 \log_{10}(\text{spring density})$$

The species of lemming using a given nest was identified through the length, form and color of the faeces left inside (MacLean et al. 1974, Duchesne et al. 2011a). Collared lemmings have dark reddish faeces about 4-6 mm long, whereas brown lemmings produce green faeces about 6-10 mm long (Duchesne et al. 2011a).

### **Monitoring of ermine activity**

When ermines prey on lemmings living in winter nests, they sometimes line the nest with the fur of their prey and use the nest themselves, or leave rodent body parts and partially eaten carcasses in the nest (MacLean et al. 1974, Sittler 1995). It is thus possible to obtain an index of ermine activity by counting nests with fur lining.

We obtained an index of winter ermine density by dividing the number of predated lemming nests (i.e. those lined with fur) found on transects and grids by the surface covered by those transects and grids assuming that each fur-lined nest was predated by a different individual (Gilg et al. 2006). The surface covered by a transect was estimated by multiplying its length (500 m) by the effective detection distance estimated by the program Distance 6.0, which varied across habitats and years. We counted aggregation of predated nests as a single event, because an ermine can use several nests and we wished to reduce inflation of ermine density potentially generated by this behaviour. To do so, we calculated the nearest-neighbor distance for each nest using the “spatstat” package in R (Baddeley and Turner 2005). Multiple predated nests found <500 m from each other were counted as a single predation event. We also estimated the proportion of predated winter nests by dividing the ermine density by the density of winter nests. For calculating this proportion, only nests found along transects and in trapping grids were used and predated nests located close to each other were also counted as a single predation event.

Wooden boxes, originally deployed to trap lemmings under the snow (Bilodeau et al. 2013c), were used to monitor ermine winter and summer activity. In 2009, 40 boxes were deployed in habitats preferred by lemmings during winter (mesic tundra and stream gullies) over a 1.0 km<sup>2</sup> area. Lemmings sometimes used the boxes to make winter nests and some ermines used them to store lemming carcasses and to rest. The boxes (hereafter called shelter boxes) were visited soon after snow-melt in late June or early July, and again in mid-August. At each visit, lemming carcasses, winter nests and faeces were collected, and carcasses were identified to the species and counted. This method provided another index of ermine activity during the period 2010-2012.

During summers 2009 to 2012, we searched opportunistically for signs of ermine activity throughout the study area. From 2009-2011, whenever individuals, tracks or fresh scats were observed, we set 5 to 10 Havahart® live-traps baited with tuna and checked them at 6-hour intervals to capture ermines. Captured animals were sexed, weighed to  $\pm 1$  g, anesthetized with isoflurane and marked with 3-g VHF radio-collars (Model Pip-2,



Biotrack Ltd., Dorset, UK). Daily locations of radio-marked animals were obtained for periods ranging from 14 to 32 days. Sometimes, a female and her young were captured. The locations obtained then refer to the family group. Family groups were always associated with dens but they frequently changed denning site (they stayed at a den  $1.9 \pm 0.2$  (SE) days). Locations of ermines and of their dens were taken using a GPS. We estimated home range of radio-marked individuals (or families) using the 100% minimum convex polygon method (Grigione et al. 2002, Herfindal et al. 2005, Nilsen et al. 2008). We calculated the observation-area curve (Odum and Kuenzler 1955) to determine if sufficient locations had been collected to reach an asymptotic value of home range size. This was the case for the 2 families but not for the only male we radio-tracked. Thus, only home range size of families is presented.

We conducted behavioral observations at the den of radio-marked individuals. The observer stood quietly at a vantage point located 5 to 10 m from the den and observed for periods ranging from 10 to 200 minutes between 6h30 AM and 2h00 AM. Typically, the mother went out hunting lemmings or rested at the den, while young played around the den, even sometimes visiting the observer. We concluded that observation distance did not disturb ermines. We performed 26 observations bouts for a total of 1004 minutes of observation in 2010 and 19 bouts (1607 minutes) in 2011. For each observation period, we noted when the female left and returned to the den, and the number and type of prey brought back to the den (all were lemmings). These observations also allowed us to determine the litter size of each family.

The 17 ermine dens that we found, either through radio-tracking or opportunistically, were revisited several times every summer. If an unmarked family was present, observations were also conducted to determine litter size. The combination of radio-marked animals and incidental ermine observations (mostly near dens) allowed us to determine the minimum number of ermines present in the study area each summer.

## Statistical analysis

To fit the numerical responses of ermines, we used a type II response curve following the equation provided by Sundell et al. (2000):

$$Y = a N / (b + N)$$

where  $Y$  could be either the ermine density ( $D$ ) or the proportion of predated winter nests ( $P$ ),  $a$  is the asymptotic ermine density (or proportion of predated winter nest),  $N$  the density of lemming winter nest (or of lemmings in summer) and  $b$  the half-saturation constant. We also fitted a type III response curve following the equation provided by Gilg et al. (2006):

$$Y = a N^2 / (c^2 + N^2)$$

where  $c$  is the density of winter nests (or of lemmings in summer) at the inflexion point of the curve. We also fitted the same equations with lemming winter nest (or summer) density measured at year  $t-1$  or the mean of years  $t-1$  and  $t-2$ , to test if a delayed response fitted the data better based on the  $R^2$ . The `nls` function in program R was used to fit the curves.

We also examined if ermine showed a preference for occupying the nests of a particular lemming species by using a log-linear model, which takes into account the availability of nests each year. All nests, including those found opportunistically were used for this analysis. Analyses were conducted in R 2.13.1 (R Development Core Team 2010).

## Results

### Lemming densities

Summer densities of brown and collared lemmings ranged from 10 to 800 and from 0 to 112 ind/km<sup>2</sup>, respectively, from 2004 to 2012, and their winter nest densities ranged from 10 to 1076 and from 5 to 341 nest/km<sup>2</sup> from 2007 to 2012 (Table 1). Brown lemming density was high in 2004 but had crashed by summer 2005. They peaked again in 2008 but

crashed before winter 2008-2009. They started to increase during winter 2009-2010 and peaked again in summer 2011 but crashed before winter 2011-2012. Collared lemmings followed a somewhat different pattern. Summer densities were relatively low in 2004 and 2005 and even lower in 2006. During winter 2006-2007, they reached high densities but apparently crashed before the summer. Densities increased slightly in 2008 but decreased to very low values before winter 2008-2009. Densities increased in winter 2009-2010 and remained high until winter 2010-2011, but crashed before summer 2011 and remained low in 2012. The seasonal dynamic thus appears to differ between the two species, as brown lemming populations crash in late summer whereas those of collared lemmings crash mostly in late winter or early summer.

### **Ermine response during winter**

The index of winter ermine abundance was generally highest in years of high lemming densities (Table 1). Indeed, an instantaneous response between the ermine abundance index in winter and lemming nest densities gave the best fit (both species, type II:  $R^2 = 0.60$ ,  $F_{2,4} = 18.3$ ,  $P = 0.010$ ; estimated parameters,  $a = 15.1$ ,  $b = 217$ ; brown lemming, type II:  $R^2 = 0.65$ ,  $F_{2,4} = 20.7$ ,  $P = 0.008$ ;  $a = 14.5$ ,  $b = 110$ ; collared lemming, type III:  $R^2 = 0.45$ ,  $F_{2,4} = 12.5$ ,  $P = 0.019$ ;  $a = 12.0$ ,  $c = 31.5$ ; Fig. 1). However, the ermine winter activity index from shelter boxes revealed a different picture as it suggested a delayed response to lemming abundance. In 2009-2010, utilisation of boxes by ermines was very low when lemming density were increasing, slightly higher in 2010-2011 when lemmings peaked, and highest in 2011-2012 when lemmings had crashed (Table 1).

The proportion of winter nests predated by ermines also suggested a delayed impact on lemmings. We found that lemming summer densities at time  $t-1$  yielded the best fit with the proportion of winter nests predated for both species combined and for brown lemmings, although the relationships were not significant (both species, type II:  $R^2 = 0.33$ ,  $F_{2,4} = 3.89$ ,  $P = 0.116$ ; estimated parameters  $a = 0.05$ ,  $c = 50$ ; brown lemming, type II:  $R^2 = 0.32$ ,  $F_{2,4} = 3.80$ ,  $P = 0.119$ ;  $a = 0.06$ ,  $b = 61$ ; Fig. 1). For collared lemmings, none of the relations tested showed a good fit ( $P > 0.18$ ).

Ermines showed a preference for collared lemmings in winter as a much higher proportion of collared lemming nests were predated and used by ermines (annual range: 0.05 to 0.29) compared to brown lemming nests (0 to 0.06;  $\chi^2 = 26.6$ ,  $df = 12$ ,  $P < 0.001$ ; Table 1).

### **Ermine response during summer**

In summer 2009, when lemming densities were very low, only one male ermine was observed. The number of individuals observed increased in 2010 and peaked with lemming density in summer 2011 (Table 1). However, the number of observed individuals remained high in 2012, when lemmings had crashed. Summer use of trapping boxes also revealed evidence of a delayed response. No shelter box was used in 2010 and only one was used in 2011, but in summer 2012 a large proportion of boxes were used as food caches by ermines (Table 1). Ermine families were observed only when summer lemming densities were increasing ( $N = 1$ ) or when they peaked ( $N = 2$ ). The family of 8 that was radio-tagged during the year of increasing lemming abundance had a home range of 6.51 km<sup>2</sup> over the period 7 June to 3 August 2010. The same female was again radio-tagged during the peak lemming year; she had 10 young but this time her home range was 4 times smaller (1.64 km<sup>2</sup>) although she was monitored during a slightly shorter period of time (12 June to 13 July 2011). However, another female was occupying the western part of her 2010 home range.

The few lemming remains found in shelter boxes in 2010 and 2011 appeared to be all brown lemmings. In 2012, 94 % of lemming carcasses stored in winter ( $N = 66$ ) and 67 % of those stored in summer ( $N = 15$ ) were brown lemming. During behavioral observations, all lemmings brought back by the female to the den were brown lemmings in 2010 ( $N = 30$ ) and 98% in 2011 ( $N = 45$ ). The female brought back an average of  $25.6 \pm 7.2$  lemmings/day in 2010 and  $56.2 \pm 12.8$  lemmings/day in 2011, the peak lemming year. In 2010, the per capita consumption rate was estimated at 2.8 lemmings/day (25.6 lemmings/day for a family of 9 ermines) and 5.1 lemmings/day (56.2 lemmings/day for a family of 11 ermines) in 2011. These values are higher than the consumption rate estimated by Gilg et al. (2006) in Greenland (1.9 lemmings/day). The body mass of ermines caught on Bylot Island was  $175.8 \pm 7.9$  g for males ( $n = 10$ ) and  $98.5 \pm 8.5$  g for females ( $n = 2$ ),

which is comparable to those in Greenland (Gilg et al. 2006). If we estimate food requirements to achieve energy balance using the equations provided by Nagy et al. (1999), a 137-g ermine needs to consume only 0.9 lemming/day (assuming a mean lemming mass of 40 g). However, one must consider that the equations are for all mammals in non-breeding state and that mustelids are small predators with a high metabolism (Iversen 1972).

We attempted to determine from our admittedly scant data the predation rate that ermine could impose on lemmings during summers of intermediate (2010) and high lemming abundance (2011). If we assume that (1) all the study area is used by ermines, (2) adult female and male home ranges are contiguous and non-overlapping and (3) adult sex-ratio is 1:1 (King and Powell 2007), we can estimate ermine density in 2010 as  $0.8 \text{ ind/km}^2$   $((9 + 1)/(6.51 * 2))$  and in 2011 as  $2.9 \text{ ind/km}^2$   $((8.5 + 1)/(1.64 * 2))$ . These estimates are somewhat conservative since densities could be almost twice as high if home ranges overlap between sexes (Johnson et al. 2000). Nonetheless, using our first density estimates combined with our observed consumption rates, the proportion of the lemming population consumed daily by the ermine would be 0.5 % in 2010  $((2.8 \text{ lemmings / day} * 0.8 \text{ ermine / km}^2) / 470 \text{ lemmings / km}^2)$  and 1.8 % in 2011  $((5.1 \text{ lemmings / day} * 2.9 \text{ ermine / km}^2) / 800 \text{ lemmings/km}^2)$ .

## **Discussion**

### **Ermine numerical response**

Ermines showed a strong numerical response to variations in lemming density on Bylot Island. However, it is unclear to what extent they displayed a delayed response to variations in lemming density, as reported elsewhere (Hanski et al. 1993, Heikkilä et al. 1994, Hanski et al. 2001, Gilg et al. 2003). Our results are conflicting in that respect. Ermine abundance in winter seemed to display a direct response to lemming density (as judged from winter nests) but summer abundance/activity data seemed to indicate a 1-year delayed response, though we have fewer years of data for this season. The low ermine abundance in summer 2009, after the 2008 lemming peak, is apparently not consistent with the idea of a delayed

response. However, lemming densities were much lower during the 2008 peak and the following winter than in 2011-2012, suggesting that the lemming decline occurred more rapidly in 2008-2009. A hypothesis is that ermines had more difficulty storing lemmings in 2008 than in 2011, which could have increased their mortality during the winter 2008-2009, hence their low density in summer 2009.

The proportion of winter nests predated by ermines was best explained by lemming density during the previous summer. Therefore, these data also suggest a 6 to 12 month delay in the impact of ermines on lemmings. The proportion of predated nests provides an index of how ermine predation rate changes with lemming abundance. Even though ermine density may start to decline as soon as lemmings crash, a greater proportion of lemming nests can still be predated at that time if the decline in ermine density is more gradual during fall/winter than the lemming decline. Thus, although the absolute number of lemmings killed per day may decline, the proportion of the lemming population consumed by the ermine may actually increase. A reason why we did not find a similar relationship with collared lemming winter nests may be that this species does not exhibit large fluctuations in abundance at our study site. We also found that ermine reproductive activity was directly related to lemming density during the current summer. Thus, ermine abundance should be highest during the winter that follows the peak, provided that young can at least partly survive through the winter. The surplus killing and food caching of mustelids reported in other studies (Jędrzejewska and Jędrzejewski 1989, King and Powell 2007) were also observed on Bylot Island (i.e. lemmings stored in shelter boxes), during fall/early winter, when lemmings were still abundant. This could allow ermines to survive the winter following a peak.

Deriving an index of ermine abundance or predation with lemming winter nests has unfortunately some limitations. A first problem is that ermine density can potentially be overestimated because the same individual may use multiple nests. We strived to reduce this potential bias by counting only one individual when aggregations of predated nests were found, but cannot evaluate the validity of this approach. In future studies, collecting ermine hairs in the nests and identifying individuals through genetic analyses could allow

more reliable estimation of the minimum number of individuals present in the study area (Boulanger et al. 2006). A second problem is that a predated winter nest can only provide one data point per winter. Yet, lemming densities can change considerably over the 8-month winter period if the population is in an increasing or decreasing phase. Therefore, similar winter nest densities could be obtained in two years characterized by opposite trends in lemming numbers, although these two years would offer a very different environment for the predator.

Finding an appropriate index of ermine activity or density is challenging. Techniques other than those that we applied exist. For instance, snowtracks have been used (Korpimäki et al. 1991, Klemola et al. 1999) to assess mustelid activity in winter, whereas tracking tunnels were used to assess summer activity (Feige et al. 2012). Yet, these techniques cannot provide robust information on mustelid densities and consumption rates, which are needed to evaluate the role of mustelids in the cyclic dynamic of arctic rodents.

### **Diet and consumption rate**

Data from winter nests indicate that ermines showed a strong selection for collared lemmings in winter. This could reflect their preference for this species or a difference in vulnerability between brown and collared lemmings. However, another possibility is that ermines prefer to occupy collared lemming nests because fur of these lemmings is more insulating (Ferguson and Folk 1970, Batzli et al. 1983, Malcolm and Brooks 1993). This point to another limitation of using winter nests to infer ermine predation rate as ermines likely do not occupy all the nests in which they prey on lemmings.

In contrast, observations made during summer and in shelter boxes do not provide evidence that collared lemmings are preferred by ermines. Almost all lemmings caught by the female that we observed in wetlands were brown, although this may not be surprising because collared lemmings usually prefer mesic tundra over wetlands (MacLean et al. 1974, Batzli et al. 1983). However, virtually all carcasses cached by ermines in the trapping boxes in winter 2011-12 were also brown lemmings even though the abundance of the two species was rather similar based on winter nest densities. Similarly, in summer 2012, the

percentage of brown lemmings cached in trapping boxes (67%) was virtually identical to the percentage of brown in the population based on live-trapping data (69%; calculated from Table 1). Thus, our results do not offer good evidence for selection by ermine of one lemming species over the other.

Our limited observations suggest that the consumption rate of ermines may have been underestimated in the past. Gilg et al. (2006) and Wilson (1999) based their estimates on the daily energetic requirement of ermines, and reported values of 1.92 and 1.35 lemmings/day/ermine, respectively. We found, based on direct behavioural observations conducted during two summers of high lemming abundance, that breeding ermines can have a consumption rate 2.4 times higher, which can even exceed that of a breeding snowy owl pair with chicks (up to 28.5 lemmings/day vs 56.2 lemmings/day for an ermine female with young; Therrien 2012). These values strongly suggest that ermines engage in surplus killing on lemmings when the latter are abundant, as previously reported in several mustelids, including the ermine (Jędrzejewska and Jędrzejewski 1989, King and Powell 2007). This would explain the large discrepancies between our consumption rates and those based on energetic requirements. Unfortunately, we made observations on only one female caring for large litters in two consecutive years, and we cannot exclude the possibility that this individual had unusually high predation rates.

### **The role of the ermine in lemming population dynamics**

The information presented here can provide us with some insights regarding the potential role of ermines in lemming population dynamics. Therrien (2012) demonstrated that predation rate by avian predators on lemmings was high at our study site and that they had the potential to reduce lemming densities during the summer. However, these predators leave the area for the winter. Moreover, avian predators show a strong and immediate response to lemming fluctuations and thus it is unclear if they could generate a cyclic dynamic without a delayed response (Hanski et al. 1993, Stenseth et al. 1996, Stenseth 1999). The ermine has been shown to exhibit a delayed response to fluctuations in lemming density in Greenland (Gilg et al. 2003, 2006) and we did find some evidence of a delayed



response in our data. However, the delay in our system appears shorter (less than 1 year) than what has been reported in Greenland (between 1 and 2 years; Gilg et al. 2006).

According to our estimates, summer daily predation rate of ermine on Bylot Island would be around 1.2% (range: 0.5-1.8%). This is below the maximum potential growth rate of brown lemmings (2.4%; Stenseth and Ims 1993a). However, avian predators and foxes are also present in summer and can also exert heavy predation rates on lemmings (Gilg et al. 2006, Legagneux et al. 2012, Therrien 2012). Combining the total response of all these predators may be sufficient to stop population growth of brown lemmings in peak years and initiate their decline during summer. Although avian predators leave in late summer, ermines and foxes remain and their population should then be at their highest point with the recruitment of young. Their combined effect, along with the cessation of lemming reproduction, could drive further down lemmings before the onset of winter. This would agree with our observation that, for the brown lemming, winter density is always low following a summer peak, suggesting a summer/fall decline. By exhibiting a delay in their population decline (due to food caching during the peak), ermine could depress further lemmings populations during the first winter after the peak and thus deepen and prolong the low phase. Foxes, which are also known to cache lemmings (Careau et al. 2007), could also contribute to the depression of lemming densities because they can still hunt lemmings under the snow, though less efficiently (Bilodeau et al. 2013a) and they can remain on Bylot Island for most of the winter (Berteaux and Lai, unpublished data).

In conclusion, our results suggest that ermines can potentially remove a large proportion of the lemming population during the summer and contribute to their decline in peak lemming years on Bylot Island. Moreover, by maintaining high predation pressure in winter, at least in the winter following the peak, they could play a critical role in lemming population dynamics. However, our results also highlight that ermines alone are unlikely to regulate lemming populations and that the combined effects of other predators, such as birds of prey and possibly also foxes, are probably essential. This suggests that mechanisms controlling the two lemming populations on Bylot Island may be similar to what has been reported in eastern Greenland (Gilg et al. 2003). Nonetheless, more data are needed, in particular about

the functional response of ermines to varying lemming density and on the winter ecology of this predator. The use of shelter boxes as described by Bilodeau et al. (2013c) may be an additional tool to assess ermine activity in summer and winter. Use of automated cameras inside such boxes could be a promising tool to provide more information on lemming consumption rates by ermines.

Table 1. Summer lemming density, density of lemming winter nests and various indices of ermine abundance, activity and predation rate on lemming during the summer and winter from 2005 to 2012.

	2004	2005	2006	2007	2008	2009	2010	2011	2012
Total number of individual lemmings captured in summer	172	55	44	35	188	11	222	312	15
Brown lemming summer density (ind/km <sup>2</sup> )	470 ± 96	26 ± 4	26 ± 5	21 ± 7	345 ± 79	18 <sup>e</sup>	358 ± 46	800 ± 90	10 ± 3
Collared lemming summer density (ind/km <sup>2</sup> )	46 ± 4	46 ± 7	12 ± 3	11 ± 2	36 ± 9	0	112 ± 11	0	5 <sup>e</sup>
Total number of winter nests found <sup>a</sup>	-	-	-	189 (36)	170 (0)	15 (82)	429 (54)	578 (4)	85 (29)
Brown lemming winter nest density (nests/km <sup>2</sup> ) <sup>b</sup>	491 <sup>f</sup>	65 <sup>f</sup>	24 <sup>f</sup>	20 ± 73	1000 ± 360	10 <sup>e</sup>	1076 ± 202	1072 ± 165	75 ± 22
Collared lemming winter nest density (nests/km <sup>2</sup> ) <sup>b</sup>	57 <sup>f</sup>	81 <sup>f</sup>	32 <sup>f</sup>	341 ± 100	108 ± 31	5 <sup>e</sup>	109 ± 31	168 ± 71	57 ± 27
Number of nests predated by ermines <sup>a,c</sup>	-	-	-	6 (3)	10 (0)	1 (9)	5 (0)	6 (0)	4 (3)
Density of lemming winter nests predated by ermine (nests/km <sup>2</sup> )	-	-	-	8.4	19.6	1.6	10.1	10.2	6.4
Proportion of all lemming winter nests predated	-	-	-	0.02	0.02	0.10	0.01	0.01	0.05
Proportion of brown lemming winter nests predated <sup>d</sup>	-	-	-	0.02 (0.01)	0.06	0.00 (0.00)	0.02 (0.02)	0.01 (0.01)	0.00 (0.02)
Proportion of collared lemming winter nests predated <sup>d</sup>	-	-	-	0.06 (0.08)	0.17	0.20 (0.29)	0.04 (0.03)	0.05 (0.05)	0.13 (0.13)
Proportion of shelter boxes used by ermines in winter (N = 40)	-	-	-	-	-	-	0.03	0.10	0.38
Proportion of boxes used by ermines in summer (N = 40)	-	-	-	-	-	-	0	0.03	0.20

Minimum number of adult ermines sighted in summer	-	-	-	-	-	1	2	5	5
Number of known ermine families in the study area	-	-	-	-	-	0	1	2	0
Individual ermine litter size	-	-	-	-	-	-	8	10, 5	-
Ermine home range (km <sup>2</sup> ; N = 1 each year)	-	-	-	-	-	-	6.51	1.64	-

<sup>a</sup> Number of opportunistic nests sampled in parentheses.

<sup>b</sup> Because winter nests are sampled at snow-melt, densities refer to the previous winter.

<sup>c</sup> This excludes nests considered to have been used by the same individual (see methods). N excluded: 2007: 3, 2008: 6, 2009: 0, 2010: 1, 2011: 2 and 2012: 0.

<sup>d</sup> Proportion of predated nests including those found opportunistically in parentheses.

<sup>e</sup> Density estimated by using the minimum number known to be alive divided by the effective trapping area.

<sup>f</sup> Winter nest density obtained with the equation provided by Krebs et al. (2012). See text for details.

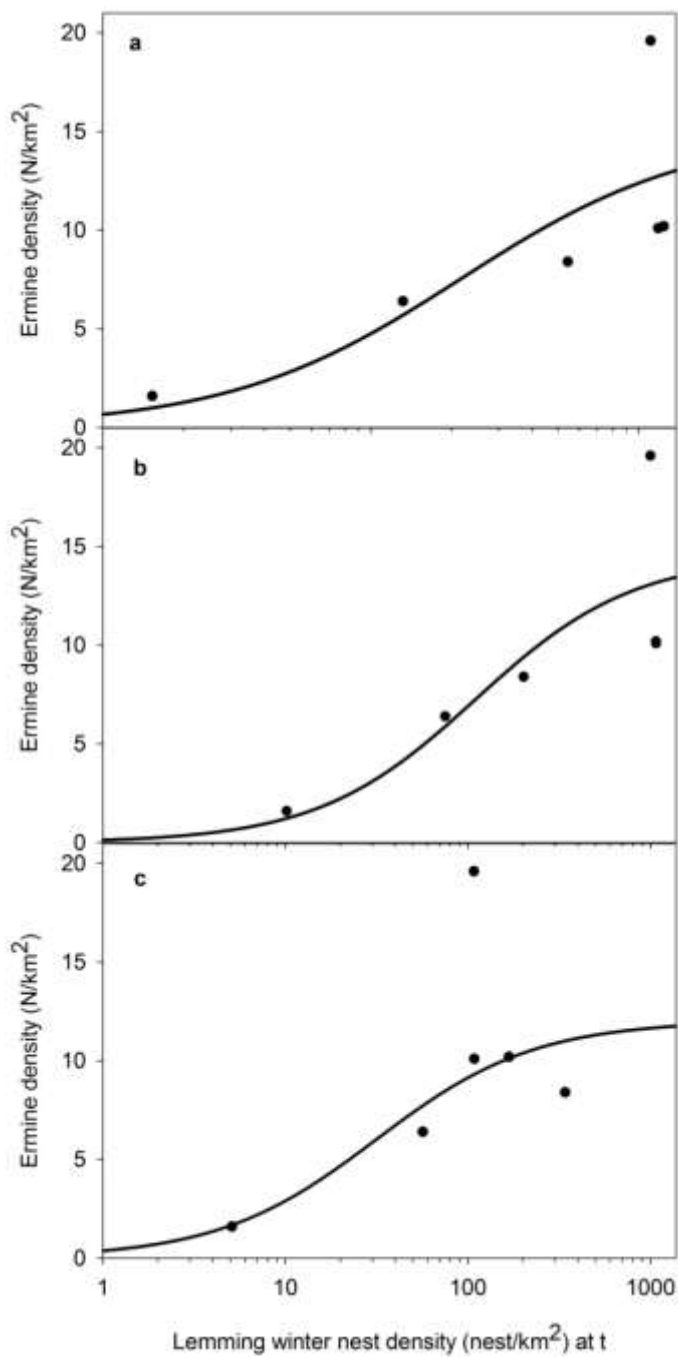


Figure 1. Index of winter ermine abundance (density of lemming winter nests predated and used by ermine) in relation to the density of winter nests of both lemming species (a), brown lemming (b) and collared lemming (c) at time *t*. The lines represent type II asymptotic curves fitted with the data for both species combined and brown lemming and type III sigmoid curve for collared lemming.

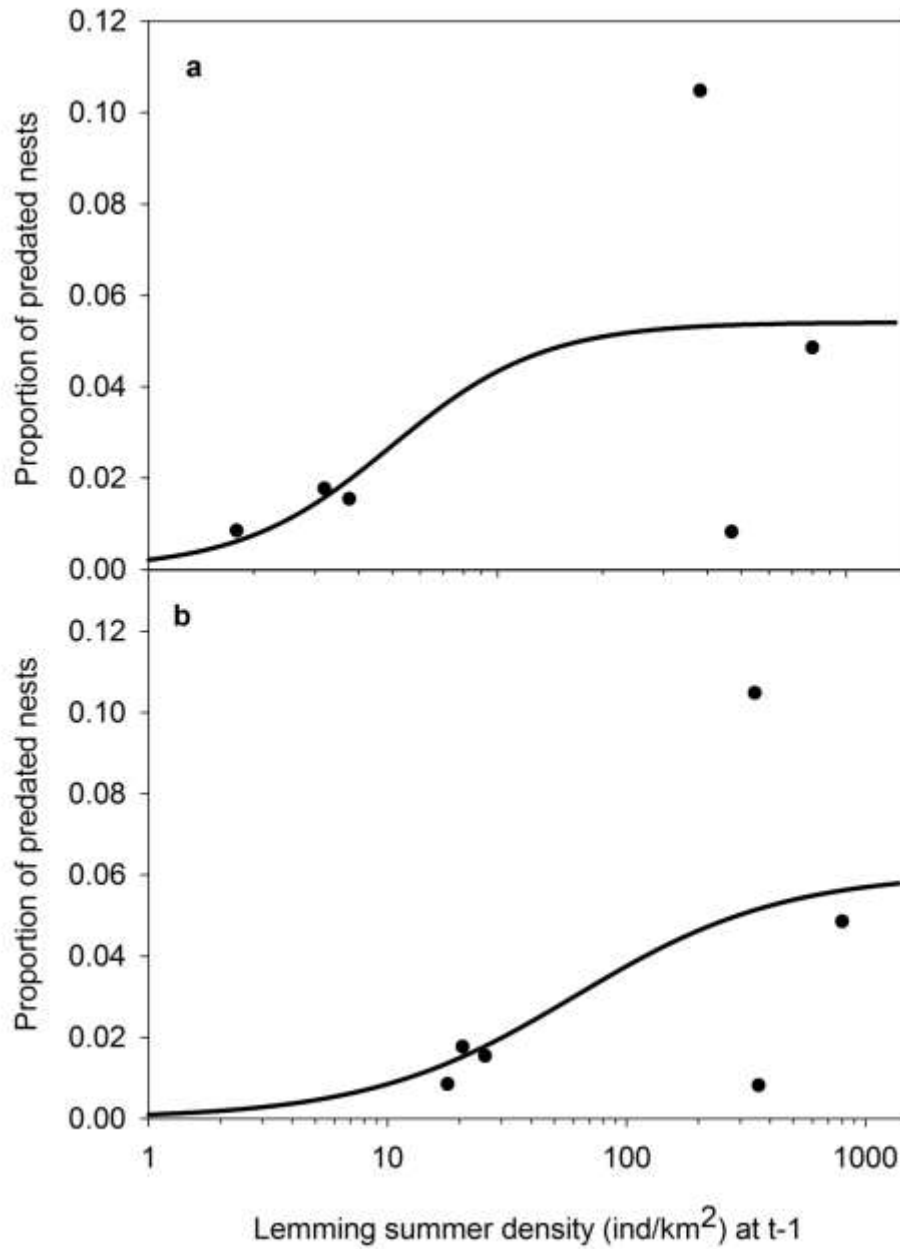


Figure 2. Proportion of predated winter nests by ermine from 2007-2012 in relation with both lemming species (a) and brown lemming (b) summer density at time  $t-1$ . The lines represent type II asymptotic curves fitted with the data.

## Conclusion

Le lemming peut être considéré comme la clé de voute de l'écosystème arctique terrestre (Gauthier et al. 2011, Legagneux et al. 2012). À lui seul, le lemming permet à une vaste guildes de prédateurs de se maintenir (Körpimäki et al. 2005, Gilg et al. 2006, Schmidt et al. 2012) et ce dans un environnement où la production primaire est faible (Gauthier et al. 2004). De plus, ses fluctuations d'abondance vont même influencer la dynamique des autres herbivores et insectivores via les interactions avec les prédateurs (Bêty et al. 2002, McKinnon et al. 2012). Ce n'est donc pas surprenant que les populations de lemming sont étudiées depuis près de cent ans (Elton 1924). Cependant, aucun consensus permettant d'expliquer les causes de la cyclicité de ces populations n'a encore été atteint (Krebs 2011). Jusqu'à très récemment, la majorité des études sur le lemming portaient sur l'écologie estivale en raison des difficultés inhérentes à l'étude des petits mammifères pendant la période hivernale (Aars et Ims 2002), qui représente néanmoins la majorité de l'année dans l'Arctique. Un énorme vide au niveau des connaissances caractérise donc la période hivernale qui apparaît critique dans le maintien des cycles de populations de petits mammifères de la toundra. À travers cette thèse, j'ai abordé différents processus liés à la dynamique de ces populations. J'ai examiné des facteurs qui peuvent moduler le cycle des lemmings en m'intéressant principalement à l'écologie hivernale, mais j'ai aussi examiné certains facteurs qui peuvent aussi le contrôler. Dans le souci d'approfondir nos connaissances sur des sujets peu étudiés et où les connaissances sont plutôt anecdotiques, j'ai examiné dans un premier temps, les effets de la qualité de la neige sur les populations de lemmings. Ensuite j'ai examiné à partir du broutage hivernal si les lemmings pourraient être contrôlés par leur nourriture. Finalement, j'ai examiné les patrons de prédation de l'hermine (*Mustela erminea*), considérée par plusieurs comme étant un prédateur essentiel pour générer la dynamique cyclique des lemmings (Korpimäki et al. 1991, Hanski et al. 1993, Heikkilä et al. 1994, Korpimäki and Krebs 1996, Hanski et al. 2001, Gilg et al. 2003).