Fluctuations in lemming populations in north Yukon, Canada, 2007–2010

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Abstract: We estimated population density of brown lemmings (*Lemmus sibiricus* (Kerr, 1792)), Greenland collared lemmings (*Dicrostonyx groenlandicus* (Traill, 1823)), and tundra voles (*Microtus oeconomus* (Pallas, 1776)) on Herschel Island from 2007 to 2010 by mark–recapture on three live-trapping areas. Limited data were also available from Komakuk Beach on the north Yukon coast. In contrast to most previous studies, brown and collared lemmings were partly out of phase. Brown lemmings on Herschel reached peak density in 2007–2008 and were low in 2009–2010, while collared lemmings were at peak density in 2007–2008 and again in 2010. Large adult male body size was characteristic of peak populations. Brown lemmings increased dramatically in the peak summer of 2008 and collared lemmings increased rapidly when winter breeding under the snow was successful in 2009–2010. By contrast, at Komakuk Beach, we could see no clear signs of fluctuations in these three species. Winter snow conditions may be too severe for population persistence on the coastal plain along the north coast of the Yukon. Further work is needed to unravel why peak lemming densities are so variable among sites and why lemming fluctuations are so pronounced on the arctic coastal plain of Alaska and virtually absent on the coastal plain of the north Yukon.

Résumé : Nous avons estimé la densité de populations de lemmings de Sibérie (*Lemmus sibiricus* (Kerr, 1792)), de lemmings à collier du Groenland (*Dicrostonyx groenlandicus* (Traill, 1823)) et de campagnols nordiques (*Microtus oeconomus* (Pallas, 1776)) sur l'île Herschel de 2007 à 2010 par marquage-recapture dans trois aires de piégeage vivant. Nous avons aussi des données provenant de Komakuk Beach sur la côte nord du Yukon. Contrairement à la plupart des observations antérieures, les lemmings de Sibérie et les lemmings à collier sont partiellement déphasés. Sur l'île Herschel, les lemmings de Sibérie ont atteint leur densité maximale en 2007–2008 et avaient une densité basse en 2009–2010, alors que les lemmings à collier affichaient une forte densité en 2007–2008 et de nouveau en 2010. Les populations de densité élevée se caractérisent par la forte taille corporelle des mâles adultes. Les lemmings de Sibérie ont augmenté de densité de façon spectaculaire durant l'été de pointe de 2008 et les lemmings à collier ont crû rapidement en nombre avec le succès de la reproduction sous la neige en 2009–2010. En revanche, aucun signe net de fluctuations n'est apparent chez ces trois espèces à Komakuk Beach. Il se peut que les conditions de neige en hiver soient trop sévères pour la persistance des populations sur la plaine côtière le long de la côte nord du Yukon. Des recherches supplémentaires sont requises pour expliquer pourquoi les densités maximales de lemmings sont tellement variables entre les sites et pourquoi les fluctuations de lemmings sont si marquées sur la plaine côtière arctique de l'Alaska et pratiquement absentes de la plaine côtière du nord du Yukon.

[Traduit par la Rédaction]

Introduction

Small mammals in tundra ecosystems are famous for their cyclic fluctuations. From Scandinavia (Angerbjörn et al. 2001) to Greenland (Gilg et al. 2003), and northern Canada (Gruyer et al. 2008), there are descriptions of similar cyclic fluctuations that suggest common explanations for a circumpolar arctic pattern of population change. But the number of detailed studies of lemming demography for the vast tundra regions are fewer than one would like. In particular we have limited data on spatial and temporal synchrony in fluctuations in two lemming species (brown lemming (*Lemmus sibiricus* (Kerr, 1792)) and Greenland collared lemming (*Dicrostonyx groenlandicus* (Traill, 1823); henceforth, collared lemmings)) and tundra voles (*Microtus oeconomus*

(Pallas, 1776)) where they overlap (Kokorev and Kuksov 2002; Krebs et al. 2002).

The International Polar Year (http://www.ipy-api.gc.ca; accessed 9 March 2011) brought attention to the arctic regions and as a consequence of this we were able to implement an ambitious plan to monitor community dynamics at Herschel Island in the western Canadian Arctic and Bylot Island in the eastern Arctic with fluctuations in lemming populations being a key component. We report here on a small part of the IPY project "Arctic WOLVES" (wildlife observations linking vulnerable ecosystems) from the western Canadian Arctic. Our overall purpose was to quantify the key elements of the food chain for tundra areas, and we worked at two north Yukon sites (Herschel Island and Komakuk Beach). Our major experimental project involved increasing snow

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depths on tundra areas, and the results of this experiment will be presented in a separate paper.

From the background of previous lemming research (Krebs 1964), we present four hypotheses that we try to test with data from Herschel Island and Komakuk Beach:

1. Interspecific synchrony is universal in the two lemming species when they occur in the same region.
2. Peak populations of lemmings and voles are characterized by adults of larger than mean body size.
3. Population growth in lemmings occurs mainly during the winter snow season, and overall summer population change is usually near zero or negative.
4. The two lemming species are habitat-segregated, with brown lemmings in wet habitats and collared lemmings in dry areas.

Materials and methods

The main study area was on Herschel Island (69°34′N, 138°54.1′W) off the north Yukon coast, with a secondary site on the mainland at Komakuk Beach (69°35′N, 140°11.2′W). Herschel Island is a treeless, 112 km^2 postglacial island 1 km off the Yukon arctic coast (Fig. 1). It is dominated by two vegetation types. Much of the higher ground is covered by a tussock tundra community composed of tussock cottongrass (*Eriophorum vaginatum* L.), tealeaf willow (*Salix pulchra* Cham.), and an assortment of forbs, mosses, and lichens. On the previously disturbed or younger surfaces, which compose approximately half of the island, common plant species are entireleaf mountain-avens (*Dryas integrifolia* Vahl), arctic bluegrass (*Poa arctica* R. Br.), arctic willow (*Salix arctica* Pallas), arctic lupine (*Lupinus arcticus* S. Wats.), other forbs, lichen, and mosses. Along the coast, the alluvial fans are dominated by Richardson's willow (*Salix richardsonii* Hook.) and arctic willow, interspersed with sedge and grass meadows. Moss is abundant.

Komakuk Beach is a mainland site, and within 2 km of the coast, there are three major habitats that we sampled: *Eriophorum*–moss tussock, sedge or cottongrass meadow, and low-centred heath polygons. The tussock habitat is dominated by tussock cottongrass and a variety of mosses (notably genus *Aulacomnium* Schwaegr.). There is extensive cover of cloudberry (*Rubus chamaemorus* L.), arctic willow, and lingonberry (*Vaccinium vitis-idaea* L). Forbs and grasses are uncommon. The sedge or cottongrass meadow changes along a gradient of water flow from wet and sloping to wet and flat. The more sloping sites are dominated by a thick growth of water sedge (*Carex aquatilis* Wahlenb.), with frequent clumps of tealeaf willow, narrowleaf cottonsedge (*Eriophorum angustifolium* Honck.), rock sedge (*Carex saxatilis* L.), and creeping sedge (*Carex chordorrhiza* Ehrh. ex L. f.). On flatter sites, white cottongrass (*Eriophorum scheuchzeri* Hoppe) is dominant, with a variety of mosses. The heath polygons combine elements of each of the other two habitats. The major contrast is that the vegetation of Herschel Island is largely upland dry tundra, whereas that of Komakuk Beach is largely coastal plain, wet tundra. In Walker's classification of circumpolar arctic vegetation (CAVM Team 2003), Herschel ranks as erect dwarf – shrub tundra (in the moist to dry tundra types), and Komakuk as non-tussock sedge, dwarf shrub,

and moss tundra (in the moist graminoid tundras). Both sites are in the low Arctic from a circumpolar perspective.
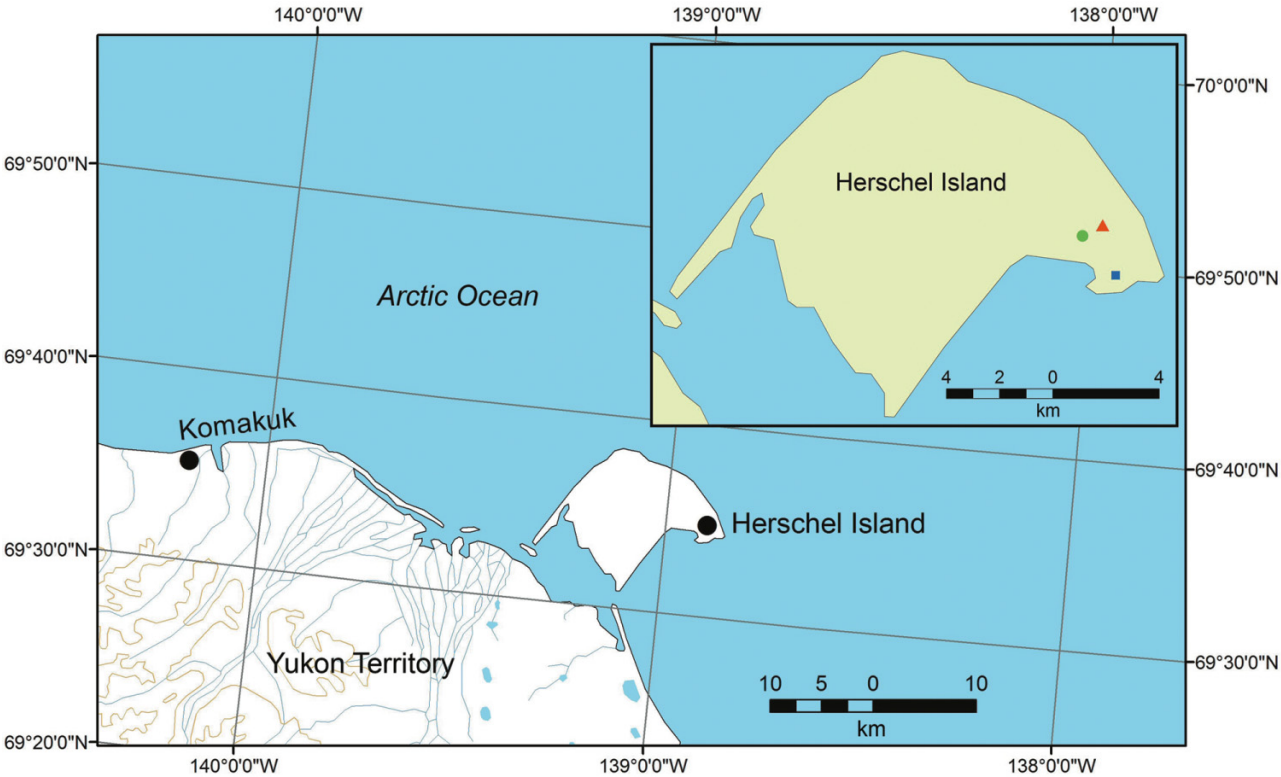
The major lemming predators that breed on Herschel Island are the arctic fox (*Vulpes lagopus* (L., 1758)), the red fox (*Vulpes vulpes* (L., 1758)), the least weasel (*Mustela nivalis* L., 1766), the Snowy Owl (*Bubo scandiacus* (L., 1758)), the Rough-legged Hawk (*Buteo lagopus* (Pontoppidan, 1763)), and the Long-tailed Jaeger (*Stercorarius longicaudus* Vieillot, 1819).

We trapped brown and collared lemmings and tundra voles on Herschel Island and at Komakuk Beach during the summer from 2006 to 2010. Only a preliminary trapping could be carried out in summer 2006 and the major work began in summer 2007. Two control grids and one experimental live-trapping grid were established on Herschel Island (Fig. 1) and we report here on only the control areas. The upland 9 ha live-trapping grid (named Ridgetop) had 256 stations 20 m apart in a 16 × 16 array with 128 Longworth traps in alternate rows (i.e., A1, B2, A3). A smaller 1.8 ha grid (named Pauline Cove) in a 10 × 10 array with 15 m spacing was set up on an alluvial fan near the coast. The larger grid size was designed to fulfil the recommendation of Bondrup-Nielsen (1983) that grids be approximately 16× the mean home range of the species being studied. The smaller grid was used on the fan because the habitat patch was limited in size, and because rodents were clearly at much higher densities in this habitat. All rodents were trapped in Longworth live traps. Traps were prebaited with apple for 3–6 days before livetrapping. Traps were left in place and locked open all year. When set, traps were checked every 4–6 h, and in most cases a trapping session involved 5–6 checks over 2–3 days, with 1–4 trapping sessions each summer. Traps were occasionally closed down in inclement weather. Our approach was to have an excess of traps to prevent trap competition and to space the intertrap distance on the trapping grids in such a way as to catch a high proportion of the animals present. The mean probability of capturing an individual in each of the 5–6 trapping checks was high so that recaptures were frequent within one trapping session. Individuals caught were ear tagged with numbered fingerling fish tags, sexed, weighed, and immediately released at the point of capture.

We used Efford's maximum likelihood (ML) spatial model (Borchers and Efford 2008) to estimate density when more than four individuals were captured in a trapping session. When fewer than four animals were present, none of the methods of estimation can be solved and we reverted to the minimum number known to be alive (MNA) as the best estimate of population size and estimated the effective trapping area to be about 13 ha for the large grid and 3.5 ha for the smaller grid.

All density calculations were carried out in DENSITY version 4.4 (http://www.otago.ac.nz/density; accessed 9 March 2011). The detection function was assumed to be half normal. The buffer width (the spatial model analogue of the boundary strip) for tundra rodents was set to 100 m, approximately 3–4 × σ. It was rare to get individual movements above these distances, and the estimates of density were robust to increasing the buffer width beyond these limits. The spacing for the integration mesh for the maximum likelihood estimator was set to 64 × 64 points on the trapping grids. We

Fig. 1. Location of the two study areas off the north coast of the Yukon. The live-trapping grids on Herschel Island are indicated as follows: Pauline Cove grid (blue square); Ridgetop grid (orange triangle); Fence grid (green circle). Fence grid is an experimental area to be discussed in a separate paper.

used the Jackknife estimator in DENSITY to estimate population size. We used full likelihood to fit all models and each trapping session was treated as an independent sample for estimation. The within-session models of spatially explicit capture recapture (SECR) were the "dot" models as defined in Efford (2009). In general, we took the default values for all the computations in DENSITY, except for the buffer width.

Finite rates of population growth were calculated between each pair of density estimates starting and ending each summer or winter as $(N_{t+1}/N_t) - 1$, and corrected to a standard 30 day rate. Since in early summer there was often population decline, followed by increase in late summer, we estimated an overall seasonal rate of population change (using the first summer population estimate and the last summer estimate) to summarize the overall trend of density change. Similarly, we used the last summer estimate of year t and the first spring estimate of year $t + 1$ to obtain the winter rate of change in density.

All statistical analyses were done in NCSS (Number Crunching Statistical System, Kay, Utah, USA; http://www.ncss.com; accessed 9 March 2011). All livetrapping of rodents was carried out in accord with the animal care principles of the American Society of Mammalogists and all our protocols were approved by the University of British Columbia Animal Care Committee.

Results

Ridgetop grid is typical of the vegetation of most of Herschel Island, and the density changes for the brown lemming

for this grid are shown in Fig. 2a. The maximum density of brown lemmings on this area was about 6 per ha, a relatively low value. By contrast, Pauline Cove grid (2.5 km distant) is on an atypical outwash plain with a dominance of willow, grass, and moss, and this type of habitat occupies <1% of Herschel Island. Density changes for the brown lemming on Pauline Cove grid are shown in Fig. 2b. The maximum density of brown lemmings on this area was 59 per ha, 10 times the equivalent value for the Ridgetop grid. The density plots for brown lemmings show a clear population peak in summer 2008 on Pauline Cove grid, but a less clear peak on Ridgetop grid in late 2007 and summer 2008. The decline phase was clearly in 2009 and a low persisted through the spring of 2010 for the brown lemming on Herschel.
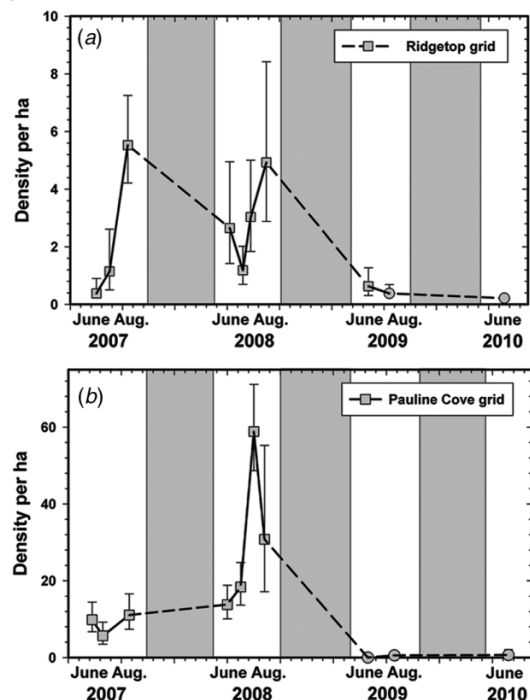
The collared lemming showed a slightly different fluctuation pattern (Fig. 3). On Ridgetop grid, a peak occurred in late summer 2007 at a density of about 6 per ha and again in 2010 with a spring density around 4 per ha (MNA of 44 individuals). Collared lemmings on Herschel were in the decline and low phase in summers 2008 and 2009 with the low density around 1–2 per ha. The population changes of the brown and collared lemmings on Ridgetop grid in 2007 and 2008 are similar, while brown lemmings on Pauline Cove differed in having a pronounced peak in 2008. The Pauline Cove grid was good habitat for brown lemmings and not very suitable habitat for collared lemmings (Morris et al. 2000). Only a few collared lemmings were caught there in 2009 ($n = 4$) and 2010 ($n = 5$).

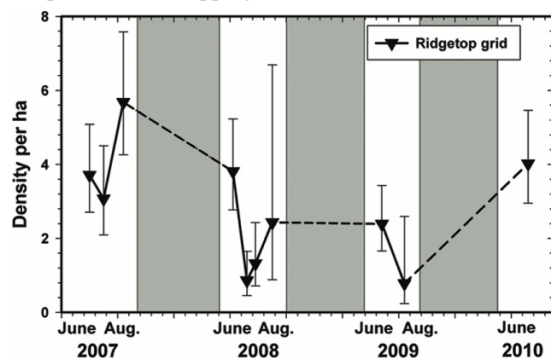At Komakuk Beach, there were virtually no collared lemmings caught, and the habitat is more suitable for brown

Fig. 2. Changes in the density of the brown lemming (*Lemmus sibiricus*) on Herschel Island. (*a*) A 9 ha Ridgetop grid; (*b*) a 3.5 ha Pauline Cove grid. The 95% confidence limits are shown. Winter months are shaded. Density estimates from Efford's maximum likelihood estimator are shown as squares, while estimates from minimum known alive are shown as circles. Each symbol represents one trapping session. Note the differences in scale.

Fig. 3. Changes in the density of the Greenland collared lemming (*Dicrostonyx groenlandicus*) on Herschel Island in the 9 ha Ridgetop grid. The 95% confidence limits are shown. All density estimates are from Efford's maximum likelihood estimator. Each symbol represents one trapping session. Winter months are shaded.

Fig. 4. Changes in the density of the brown lemming (*Lemmus sibiricus*) (black symbols) and the tundra vole (*Microtus oeconomus*) (grey symbols) at Komakuk Beach on two 9 ha grids. The 95% confidence limits are shown. Density estimates from Efford's maximum likelihood estimator are shown as squares and estimates from minimum known alive are shown as circles. The estimate for brown lemmings in August 2006 is very unreliable owing to weather problems. Each symbol represents one trapping session. Winter months are shaded.

and no strong fluctuations at Komakuk Beach. If we were to interpret the anomalous data for brown lemmings as a high density in 2006, then we would have expected another peak of brown lemmings in 2009 or 2010, neither of which was observed. This lends tentative support to the view that brown lemmings were at low density and did not fluctuate at Komakuk during the time interval of our study.

Table 1 gives the descriptive statistics for the three rodent species at the Herschel Island and Komakuk Beach tundra sites. Collared and brown lemmings are both relatively rare at Komakuk compared with Herschel, and tundra vole is nearly identical at low densities on both sites. We had no clear indication that tundra voles showed strong population fluctuations on Herschel Island or at Komakuk, but rather followed a pattern of summer increase and overwinter decline at relatively low densities. Tundra voles on Herschel Island have a very patchy distribution and appears to be most common in the grassy coastal areas around the human settlement at Pauline Cove.

We conclude from the empirical analysis of density changes that brown and collared lemmings fluctuate and may sometimes be out of phase with each other on Herschel Island. Neither lemming species seems to show strong fluctuations at Komakuk Beach. Tundra voles seem to persist at low densities in all years at both Herschel and Komakuk and showed only small fluctuations in density.

One of the characteristic features of fluctuating rodent populations has been a shift in body mass distributions so that adults in the peak summer are 10%–20% larger than they are at other stages of the fluctuation (Chitty and Chitty 1962; Krebs 1964). Figure 5 gives the body mass distributions for male collared lemmings from Herschel Island. Only males were used in this analysis of body mass, as female mass is confounded with pregnancy. The pattern is clear— larger collared lemming males occur in what we have judged to be the peak density springs of 2007 and 2010. Omitting the juveniles from the body mass data so that we deal only with adult male spring body mass, we found a highly signifi-

lemmings and tundra voles. Figure 4 shows the density changes observed at Komakuk. In August 2006, livetrapping was severely hampered by storms and the estimate for brown lemmings must be considered unreliable (confidence limits 2–42 per ha). If we ignore this anomalous point, the Komakuk data support the simplest model of constant low densities of brown lemmings and tundra voles at mean densities each year of 2–3 animals per ha for each of the two species. We were able to visit Komakuk in June 2010 for 1 h to count winter nests and we found virtually no sign of rodents, so again this year seemed to fit into the pattern of low densities

Table 1. Descriptive data for the brown lemming (*Lemmus sibiricus*), Greenland collared lemming (*Dicrostonyx groenlandicus*), and tundra vole (*Microtus oeconomus*) of Herschel Island and Komakuk Beach from 2007 to 2010.
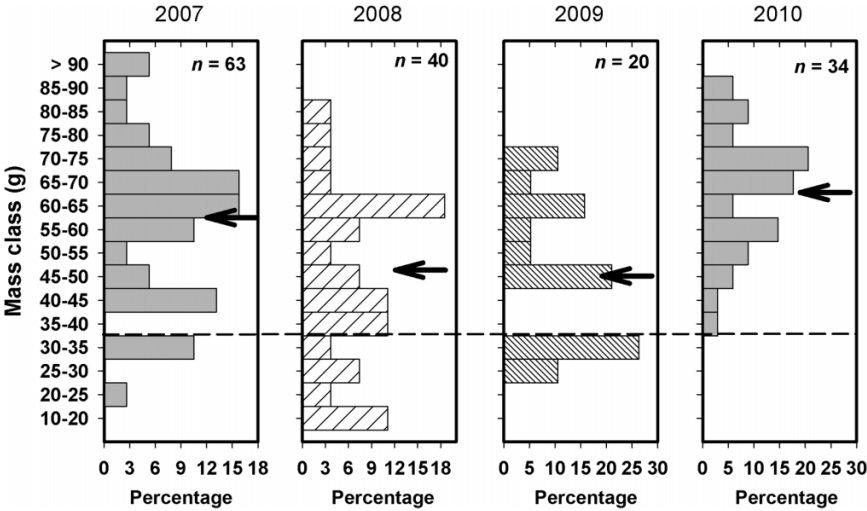
	Herschel Island				Komakuk Beach			
Species	No. of trapping sessions	Mean density per ha	Range of densities per ha	Mean (1 SE) probability of capture	No. of trapping sessions	Mean density per ha	Range of densities per ha	Mean probability of capture
Brown lemming	35	5.27	0.00–58.85	0.21±0.03	14	1.24[a]	0.04–4.87	0.19±0.04
Greenland collared lemming	35	1.80	0.00–7.26	0.23±0.03	14	0.03	0.00–0.33	—
Tundra vole	35	0.69	0.00–5.66[b]	0.29±0.03	14	1.95	0.08–4.15	0.29±0.03

Note: All density estimates were from Efford's maximum likelihood estimator or minimum number known to be alive (see Materials and methods). Probability of capture is estimated from closed-population models in program CAPTURE and is the probability per trap check within a trapping session. A trapping session is defined as 2–3 days of livetrapping on one grid.

[a]Omitting the August 2006 estimate that is unreliable (see Fig. 4).
[b]Virtually all the tundra voles on Herschel Island were caught on the Pauline Cove grid and almost none on the upland grids.

Fig. 5. Body mass distributions for male Greenland collared lemmings (*Dicrostonyx groenlandicus*) in the springs (June) of 2007–2010. Those below the broken horizontal line were born under the snow in spring, based on the dorsal stripe indicating juvenile pelage. The arrows indicate the mean adult body mass.

cant year effect ($F_{[3,133]} = 3.94$, $p < 0.01$), consistent with the density data given above and with the generalization of large male adults in peak springs.

Body mass distributions of brown lemmings from Herschel Island are shown in Fig. 6. Very few individuals were caught in the low-density spring of 2010, but the pattern for remaining years is clear—large male adults in the spring of both 2007 and 2008 and smaller adults in 2009. We tested these adult male mass differences with ANOVA and found they were highly significant ($F_{[2,58]} = 4.87$, $p = 0.01$). A Tukey–Kramer's test indicated that the 2007 and 2009 data were significantly different, while the 2008 data were intermediate. The main difference between 2007 and 2008 is the existence of juveniles born under the snow in March and April in 2008. From the body mass distributions, we could judge the brown lemmings to be at the peak of their fluctuation in both 2007 and 2008.

Table 2 gives the finite rates of increase in population density for both species of lemmings over summer and winter periods. During the summer of 2007, all species on all grids were increasing in density. In 2008, brown lemmings were increasing rapidly in summer on both grids, whereas collared lemmings were declining rapidly. Collared lemmings continued to decline in the summer of 2009. Winter rates of change
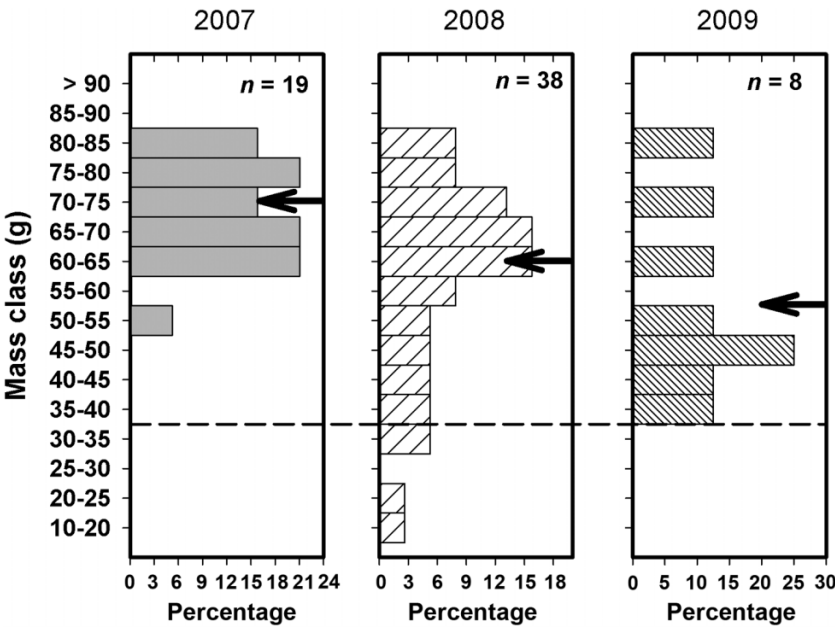
were highly variable. Brown lemmings on both grids declined rapidly during the winter of 2008–2009, whereas collared lemmings were stable in density. During the winter of 2009–2010, brown lemmings on Ridgetop grid declined, whereas collared lemmings on the same grid increased rapidly in density. These patterns of change illustrate the lack of population synchrony in the two lemming species on Herschel. We conclude that on Herschel Island, brown lemmings decline in winter and increase in summer, whereas collared lemmings may increase in winter or summer and more often than not decline in summer.

The two lemming species were strongly habitat segregated on Herschel Island, as illustrated in Fig. 7 for the data from summer 2008. When brown lemmings became very scarce in 2009 and 2010, collared lemmings expanded their habitat niche into areas formerly occupied by brown lemmings. For example, on Pauline Cove grid, collared lemmings were absent in 2007 and 2008 but occupied this area at a density of 1 per ha in spring 2009 and spring 2010.

A syndrome of reproductive changes tends to accompany the population fluctuations of lemmings (Krebs 1964; Erlinge et al. 2000). In general, we would expect high reproductive output when populations are increasing and lower output in peak and declining populations. Because we were livetrapping,

Fig. 6. Body mass distributions for male brown lemmings (*Lemmus sibiricus*) in the springs (June) of 2007–2009 for Herschel Island. The broken horizontal line separates lemmings that are presumed to have been born under the snow in spring. The arrows indicate the mean adult body mass. There were too few brown lemmings in spring 2010 to estimate the body mass distribution.

Table 2. Finite rates of population increase or decline per 30 days for brown (*Lemmus sibiricus*) and Greenland collared (*Dicrostonyx groenlandicus*) lemmings on Herschel Island over three summers and winters.

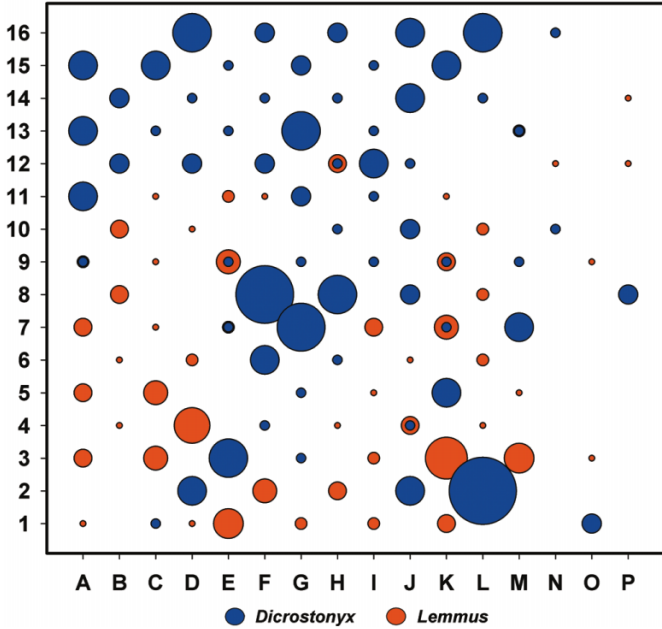|	Brown lemmings				Greenland collared lemmings	
	Pauline Cove grid	Percent change	Ridgetop grid	Percent change	Ridgetop grid	Percent change
Summer						
2007	Stable to slight increase	+4	Increase	+150	Increase	+16
2008	Increase	+29	Increase	+21	Decline	−13
2009	Increase	+19	Decline	−23	Decline	−44
Winter						
2007–2008	Stable or slight increase	+3	Decline	−8	Stable to slight decline	−4
2008–2009	Crash	−47	Crash	−20	Stable	0
2009–2010	Stable	+1	Decline	−5	Increase	+17

we have only limited data to quantify reproductive changes. The results for the two lemmings are not in line with the simple expectation of reproductive output that accompany population changes. In summer 2007, fewer adult female brown lemmings were recorded as lactating than in summer 2008 (45% vs. 55%) (Fig. 8). Winter breeding, as evidenced by the capture of juveniles in spring, was responsible for the limited population growth over the winter of 2007–2008 on Pauline Cove grid but was not sufficient to compensate for losses over winter on Ridgetop grid in 2007–2008. The pattern of change in reproductive output for the collared lemming is even less clear because of the ability of this lemming to breed every spring under the snow so that small juveniles are present at the start of every summer. Reproduction in collared lemmings was curtailed in the late summer of 2007 and began slowly in June 2008 (Fig. 9). More adult females were lactating in summer 2008 (41%) than in summer 2007 (30%), a pattern similar to that in the brown lemming. More detailed necropsy data would be required to pin down these reproductive changes more precisely. In general, reproduction was sufficiently strong in mid- and late-summer to produce summer increases in population density, particularly in 2008, but the population trends shown in Figs. 2a, 2b, and 3 do not follow these reproductive differences. In both lemming species for 2007 and 2008, the higher summer lactation rates were associated with lower rates of population growth, suggesting that mortality rates may be more important than reproduction in determining the rate of population change.

Discussion

In almost all cases where both brown and collared lemmings occupy the same general area, the two species fluctuate in phase. This pattern has been described by Macpherson and Manning (1959), Krebs (1964), Macpherson (1966), Krebs et al. (2002), and Gruyer et al. (2008). But synchrony between the two lemming species is perhaps not absolute, and on Herschel Island, we have an example of the two species being 1 year out of phase during our study. However, the

Fig. 7. Bubble plot of frequency of capture of Greenland collared (*Dicrostonyx groenlandicus*) and brown (*Lemmus sibiricus*) lemmings on Ridgetop grid in summer 2008. There was very little spatial overlap in the two lemming species.

two lemming species appeared to decline in synchrony between 1985 and 1986 on Herschel Island (Slough and Ward 1987).[1] Based on late-July, relative abundance snaptrapping indices (catch per 100 trap-nights) at the same sites where we trapped, brown lemmings declined on the Pauline Cove fan from 1.18 (1985) to 0.18 (1986), and collared lemmings on the upland tundra declined from 2.82 to 0.51, but brown lemmings were not found on the upland tundra in either year. So, synchrony, or lack of synchrony, may not be a fixed phenomenon in any one region. The key question is what facilitates synchrony between species. The conventional explanation for synchrony is shared predators (Korpimäki et al. 2005). The alternative mechanism for small-mammal synchrony is winter weather (Krebs et al. 2002). The key question when we observe asynchrony is whether it is due to predators that impact the dynamics of one species of prey differently than another, or whether it is due to differential impacts of weather events (snow accumulation, duration, and icing) on the species involved. The weather hypothesis logically requires that each species respond in a different demographic or behavioural fashion to the same winter conditions. Although all major lemming predators in north Yukon (i.e., least weasel, Snowy Owl, arctic fox, and red fox) eat both species readily, collared lemmings are more vulnerable because they occupy the more open upland habitat. Hypothetically, given an ample prey base, predators could curtail a peak in one species earlier than in another (e.g., decline in collared lemmings on Ridgetop grid in 2008), by prey-specific selection owing to habitat structure, thereby allowing the second species to escape strong predator limitation until the subsequent year (e.g., decline in brown

lemmings in 2009). In this paper, we cannot address these alternatives in detail, but we will investigate them in future analyses. At present we conclude only that the two lemming species were possibly out of phase on Herschel Island in 2007–2010, possibly owing to predation or owing to weather.
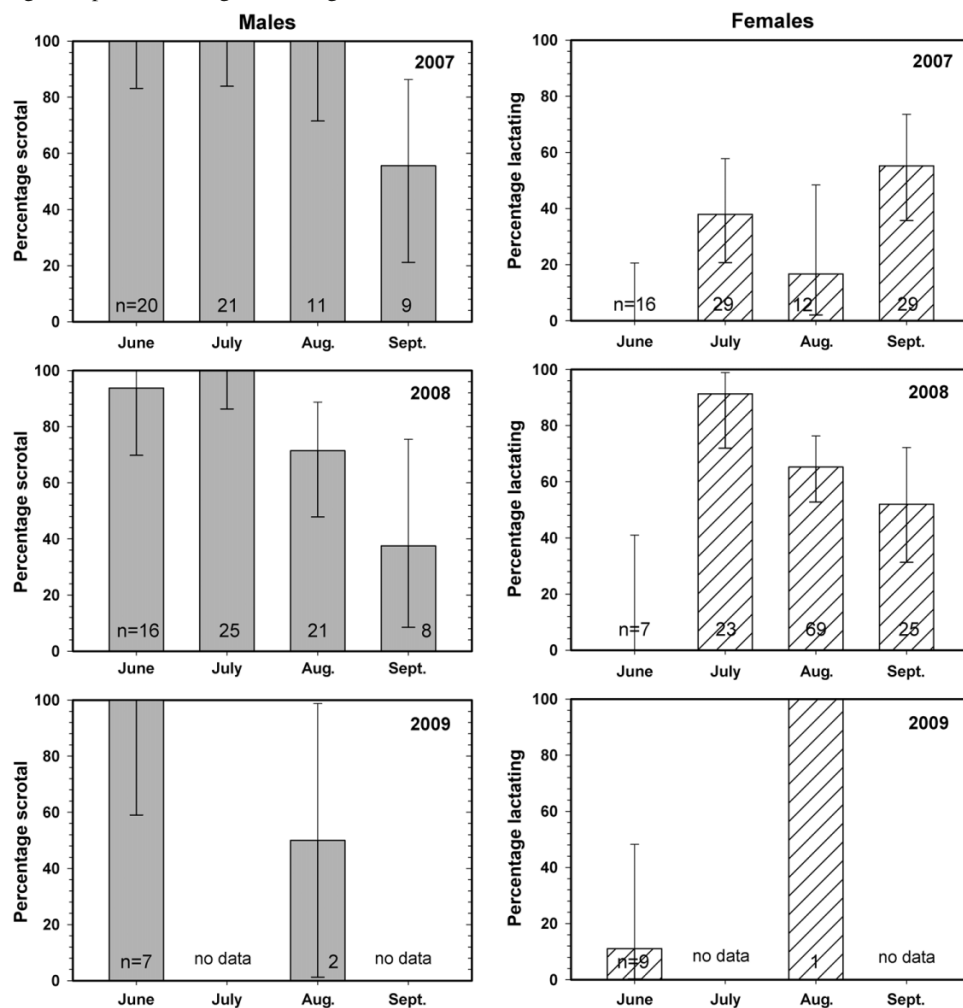
A common comment from studies of lemming populations is that population growth occurs in winter during the increase phase, whereas in summer the population always declines no matter what the phase of the population fluctuation (Gilg 2002; Gilg et al. 2009). By contrast, on Herschel Island brown lemmings increased during the summer five times out of six (Table 2: 2 grids, 3 summers) and collared lemmings increased one summer out of three. If summer declines are a signature of predation mortality (Reid et al. 1995; Gilg 2002), there is either more sporadic or less predation pressure on Herschel than seems to occur on other lemming study sites. Wilson et al. (1999) found that collared lemmings at Walker Bay on the Kent Peninsula increased in density two summers out of three, and two winters out of three. Gruyer et al. (2010) found on Bylot Island that brown lemmings typically declined during summer, consistent with the predation hypothesis, but that collared lemmings did not, perhaps because of predator preference for brown lemmings. It was clear from our natural history observations that the collapse of the brown lemming on Pauline Cove grid in 2008 from August to September was associated with a large concentration of migratory predators (Short-eared Owls (*Asio flammeus* (Pontoppidan, 1763)), Rough-legged Hawks, Northern Harriers (*Circus cyaneus* (L., 1766)), Snowy Owls) on this area in September before a heavy snowfall cut off easy prey access on 28 September. There is much more variability in summer and winter population growth than is captured in a simple generalization that summer means decline and winter increase. Primary production (food abundance) and vegetation structure (prey refugia) vary substantially across the North American ranges of these lemmings, with our north Yukon sites being relatively high in productivity and in vertical vegetation structure. We hypothesize that summer dynamics will vary with predation risk, which is a cumulative measure of prey abundance, cover, and predator abundance per capita prey.

One more remaining puzzle from our research has been the observation of a lack of population fluctuations in the rodents of the coastal plain of the north Yukon (this study; Shingle Point and Kay Point in Table 1 from Krebs et al. 2002). At Komakuk Beach, tundra voles fluctuated annually at low densities of 2–4 per ha. Brown lemmings might have been high in 2006 when we visited the site for a few days, but the population estimate is unreliable. If somehow 2006 was a peak year for brown lemmings at Komakuk, we would have expected another peak in 2009 or 2010. We do not have data for 2010, but we visited the site in June 2010 and could find few winter nests and no sign of high populations of either rodent. As with our earlier data (Krebs et al. 2002), we have no evidence of strong population fluctuations on the north Yukon coastal plain, even though we documented a peak of tundra voles and brown lemmings in 1999 above the coastal plain in the foothills 29 km away from Komakuk (site 10 in Table 3 from Krebs et al. 2003). Habitat on the coastal

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[1]B.G. Slough and R.M.P. Ward. 1987. 1986/87 Annual progress report, Furbearer Management Program. Fish and Wildlife Branch, Government of Yukon, Whitehorse. Unpublished Report.

Fig. 8. Breeding performance of adult brown lemmings (*Lemmus sibiricus*) at Herschel Island from 2007 to 2009. Adult males are >40 g; adult females are >30 g. Sample sizes are given, along with the 95% confidence limits.

plain in summer seems highly suitable for voles and brown lemmings. We hypothesize that winter snow conditions may be too severe for population persistence and growth on the coastal plain, as we found earlier in the central Arctic (Reid and Krebs 1996), which is a hypothesis that we are now investigating further. More work is required to unravel why fluctuations in brown lemming can be so pronounced on the arctic coastal plain at Point Barrow Alaska (Pitelka and Batzli 2007) and be much weaker on Herschel Island and virtually absent on the continuation of this arctic coastal plain in the mainland north Yukon. Point Barrow sits in a sedge or grass, moss wetland tundra type (CAVM Team 2003), with distinctively more graminoid and moss cover (the two principal food types of brown lemmings) than either of our study sites, except perhaps the fan habitat on Herschel Island.
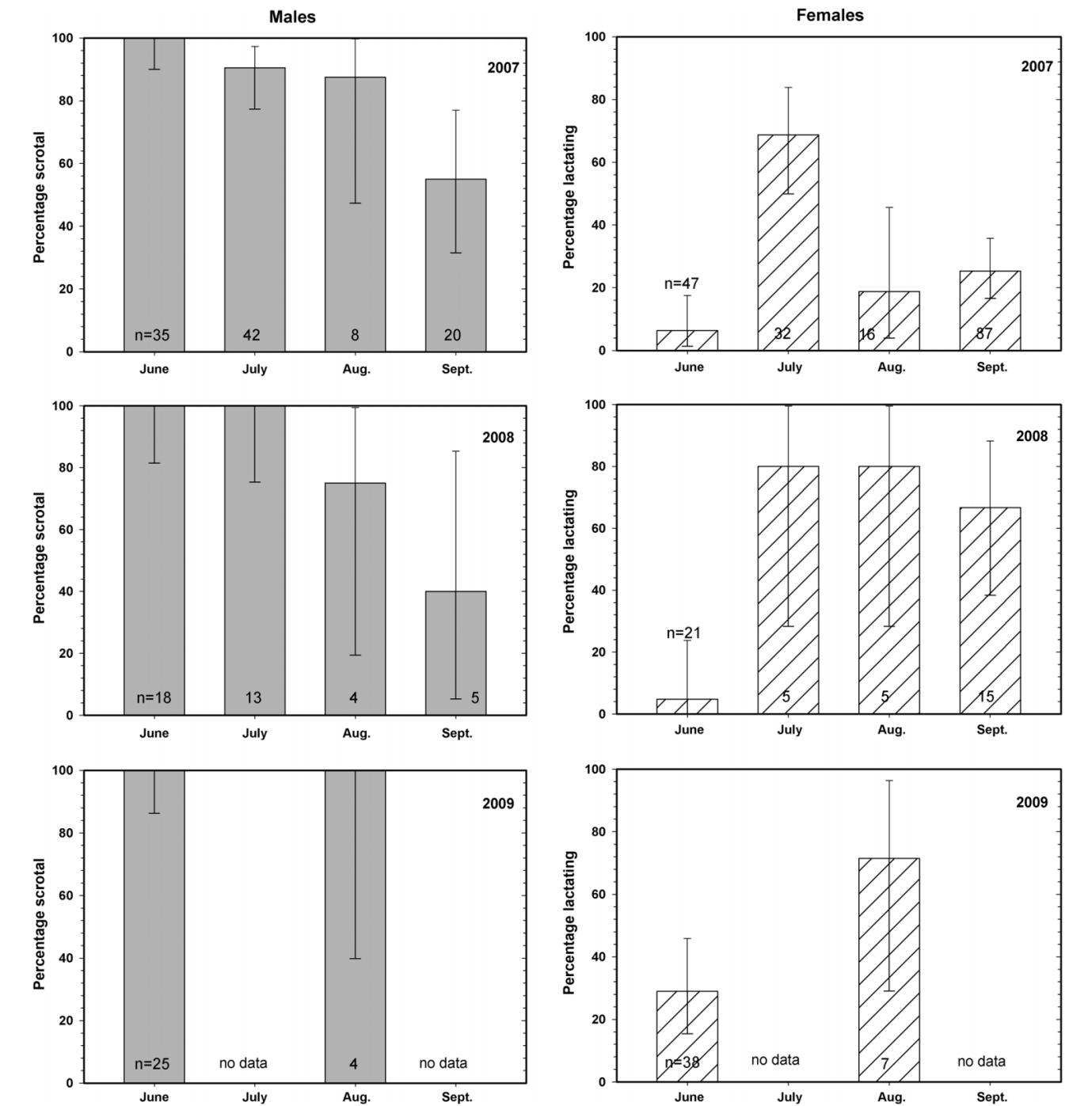
A final observation we make is that the peak density of lemming populations on the upland areas of Herschel Island is only slightly higher than those observed on Bylot Island (1–3 per ha) by Gruyer et al. (2010). Yet on a North American scale, brown lemmings can be much more abundant (e.g., >200–300 per ha; Pitelka and Batzli's (2007) data from Point Barrow), and we do not yet have any analysis of what determines peak lemming densities. We presume it has

something to do with food supplies and primary production, but exactly what the critical variables might be for the two lemming species and the tundra vole are not clear.

From the four hypotheses that we stated with in the Introduction, we have tentatively accepted 2 and 4 and tentatively rejected 1 and 3. We accept that with only a few years of data, we cannot make the kinds of definitive tests that would flow from detailed data over 10–20 years. We suggest that we have three important conclusions that can be the starting point for future research. First, synchrony between the two lemming species on the same area may or may not occur and we do not know the reasons for this. Synchrony between species with fluctuating populations can be operationally defined as having population increase, peak, and decline phases in the same years, and asynchrony means most precisely one species in the increase or peak phase while at the same time the second species is declining in density. Second, winter and spring breeding and high survival under the snow may be a key to understanding population changes in lemmings, but we do not understand what conditions permit winter breeding and promote high overwinter survival. In particular, we have no means of predicting the impacts of climate change on snow cover and winter conditions, and how this might trans-

Fig. 9. Breeding performance of adult Greenland collared lemmings (*Dicrostonyx groenlandicus*) at Herschel Island from 2007 to 2009. Adult males are >40 g; adult females >30 g. Sample sizes are given, along with the 95% confidence limits.

late into demographic effects. The patterns of reproductive changes in our populations were not good indicators of population trends, suggesting that high reproductive output may be necessary for population growth but not sufficient, particularly if predation rates are high. Third, we need to integrate our information on lemming numbers, predator abundance, and primary production to reach an ecosystem-level under-

standing of trophic dynamics on Herschel Island. This research is currently underway using the ECOPATH modelling framework (Legagneux et al. 2009; P. Legagneux, G. Gauthier, D. Berteaux, J. Bêty, M.-C. Cadieux, G. Szor, F. Bilodeau, E. Bolduc, L., McKinnon, A. Tarroux, J.-F. Therrien, M.-A. Valiquette, L. Morissette, and C.J. Krebs, unpublished data).

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