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Lemming winter habitat choice: a snow-fencing experiment

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Abstract The insulative value of early and deep winter snow is thought to enhance winter reproduction and survival by arctic lemmings (*Lemmus* and *Dicrostonyx* spp). This leads to the general hypothesis that landscapes with persistently low lemming population densities, or low amplitude population fluctuations, have a low proportion of the land base with deep snow. We experimentally tested a component of this hypothesis, that snow depth influences habitat choice, at three Canadian Arctic sites: Bylot Island, Nunavut; Herschel Island, Yukon; Komakuk Beach, Yukon. We used snow fencing to enhance snow depth on 9-ha tundra habitats, and measured the intensity of winter use of these and control areas by counting rodent winter nests in spring. At all three sites, the density of winter nests increased in treated areas compared to control areas after the treatment, and remained higher on treated areas during the treatment. The treatment was relaxed at one site, and winter nest density returned to pre-treatment levels. The rodents' proportional use of treated areas compared to adjacent control areas increased and remained higher during the treatment. At two of three sites, lemmings and voles showed significant attraction to the areas of deepest snow accumulation closest to the fences. The strength of the treatment effect appeared to depend on how quickly the ground level temperature regime became stable in autumn, coincident with snow depths near the hiemal threshold. Our results provide strong support for the hypothesis that snow depth is a primary determinant of winter habitat choice by tundra lemmings and voles.

Keywords Arctic ecology · Energetics ·
Habitat selection · Rodents · Temperature

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Introduction

The irruptive or increase phase of cyclic population fluctuations in north latitude lemmings (*Lemmus* and *Dicrostonyx* spp.) drives numerous changes in the abundance of tundra organisms, and generally occurs, at least in part of its duration, during winter and spring, as a result of subnivean reproduction (Stenseth and Ims 1993; Gruyer et al. 2009). This represents an impressive allocation of potentially limited energy to reproduction during cold weather, and raises the question of what winter snow conditions are necessary and sufficient to allow lemmings and voles to invest energy in winter and spring reproduction.

Three species of arvicolid rodent—the collared lemming (*Dicrostonyx groenlandicus*), the brown lemming (*Lemmus trimucronatus*), and the tundra or root vole (*Microtus*

oeconomus)—inhabit North American arctic tundra and experience freezing temperatures for at least 8 months of the year. They reduce their cold exposure through anatomical, physiological and behavioral means. They increase the thickness and length of pelage in winter and increase their basal metabolic rates (Scholander et al. 1950; Chappell 1980). Collared lemmings undergo photoperiod-induced changes in body size and shape that reduce rates of heat loss (Malcolm and Brooks 1993). Tundra voles tend to congregate in winter likely to conserve heat (Madison 1984). All species live in insulative burrows in the ground or in vegetation (e.g., *Eriophorum* tussocks) as long as access is not blocked by ice. Under a cover of snow, they frequently build nests of sedge, grass and other vegetation at ground level or slightly up in the snow column, and these nests provide essential insulation against below-freezing temperatures for resting individuals (MacLean et al. 1974; Fuller et al. 1975a; Casey 1981). Remaining active all winter, these rodents can reproduce under the snow with litters raised in winter nests (Krebs 1964; Fuller et al. 1975b; Krebs et al. 1995; Duchesne et al. 2011a).

Snow insulates the ground, where these rodents are living, from ambient air temperatures. This insulation increases with snow depth and decreases with the square of density (Pomeroy and Brun 2001), so small rodents should experience a warmer sub-nivean thermal regime under deeper snow and snow that is relatively uncompacted by wind re-distribution and melting. Many lemming researchers have noted an association of lemming and vole winter nests with areas of greatest winter snow accumulation, which on the tundra tend to be in the lee of topographic breaks providing shelter for the deposition of wind-blown snow in drifts (Fuller et al. 1975a; Reid and Krebs 1996). Duchesne et al. (2011b) investigated this relationship on Bylot Island and found that the probability of occurrence of brown and collared lemming winter nests increased with snow depth to about 60 cm and was fairly constant at depths from 60 to 120 cm. As well as insulating the ground, snow cover dampens the diurnal fluctuations in temperatures at ground level compared to ambient air. This dampening effect is maximized at snow depths above 20–30 cm (varying with snow density), referred to as the hiemal threshold (Pruitt 1970). At depths greater than the hiemal threshold, daily temperature fluctuations are largely absent, and ground level temperatures change slowly in response to the mean conditions in the ambient air and heat loss from the ground. Relative stability in the thermal regime offers large advantages to small rodents who have to feed repeatedly during the day.

Across most of the North American Arctic, average maximum snow depth is less than 50 cm, and less than 30 cm over much of the western Canadian archipelago (Maxwell 1980; Atlas of Canada 2010). Total winter

snowfall may be twice the maximum snow depth, but wind redistributes snow, so actual depths are highly variable depending on topography and distribution of erect vegetation (Pomeroy and Brun 2001). In addition, the maximum depth is generally not reached until February or March (Maxwell 1980). Consequently, the hiemal threshold of 20–30 cm may be reached on lee slopes quite quickly after initial winter storms, considerably later on some less protected patches, and never at all on exposed patches. The slow rates of snowfall, combined with flat and wind-blown topographies in many landscapes, together likely limit the spatial extent of a snow pack with good insulative properties for lemmings. By contrast, summer habitats for lemmings on Arctic tundra are generally widespread, and not thought to be limiting to lemming population growth at least in terms of food and shelter requirements (Stenseth and Ims 1993). At a regional scale, we hypothesize that landscapes with persistently low lemming population densities, or low amplitude fluctuations, have a low proportion of the land base with deep (minimum 30 cm) snow through the winter. This hypothesis has two components: (1) that snow depth influences habitat choice and therefore habitat suitability, and (2) that habitat suitability influences demography. Alternative regional scale hypotheses would involve heavy predation mortality and risk, and/or food limitation.

In this paper, we report an experimental manipulation of snow depths designed to test the first component of the regional scale hypothesis, specifically that winter habitat suitability for lemmings is a function of snow depth. By enhancing tundra snow depth with a snow fence treatment, we predicted: (1) an increase in the density of lemming winter nests in treated areas compared to control areas; (2) a relaxation of the treatment effect after the treatment was removed; (3) an increase in proportional use of treated areas compared to adjacent control areas indicating movement of lemmings onto the treated areas; and (4) particular attraction of lemmings to areas of deepest snow accumulation.

Materials and methods

Study sites

We undertook the fencing experiment at three sites in the Canadian Arctic: the coastal plain of southwest Bylot Island in Sirmilik National Park, Nunavut (73°N, 80°W); the east end of Herschel Island in Qikiqtaruk Territorial Park, Yukon (69°N, 138°W); the coastal plain at Komakuk Beach in Ivvavik National Park, Yukon (69°N, 140°W). Under the Arctic vegetation classification system of Walker et al. (2005), Bylot is in graminoid, prostrate

dwarf-shrub, forb tundra, Herschel is in erect dwarf-shrub tundra, and Komakuk is in non-tussock sedge, dwarf-shrub, moss tundra. Bylot is a less productive ecosystem than those in Yukon. However, in all three sites, we chose sampling grids that avoided extensive erect dwarf-shrubs (notably *Salix pulchra* and *S. richardsoni*). At Bylot, study grids were in mesic communities dominated by woody perennials (*S. arctica*, *Dryas integrifolia*, *Cassiope tetragona* and *Vaccinium uliginosum*), graminoids (*Arctagrostis latifolia*, *Alopecurus borealis* and *Poa arctica*), forbs (*Stellaria longipes*, *Oxytropis maydelliana* and *Oxyria digyna*), and mosses (see also Gauthier et al. 1996). At Herschel, two types of drier upland plant community dominated our study grids: (1) tussock tundra composed of *Eriophorum vaginatum*, *Salix pulchra*, a few forbs and mosses; (2) prostrate-shrub heath composed of *Dryas integrifolia*, *S. arctica*, *P. arctica*, *A. latifolia*, and *Lupinus arcticus*, with some other forbs and mosses. Infrequent wet communities were composed of *C. aquatilis, E. vaginatum*, *E. scheuchzeri* and *Equisetum* spp.) (see also Smith et al. 1989). At Komakuk, our grids encompassed three communities: *Eriophorum*–moss tussock, sedge/cottongrass meadow, and low-centred polygons. The tussock community was dominated by *E. vaginatum* and a variety of mosses (notably *Aulacomnium* sp.), with extensive cover of *Rubus chamaemorus*, *S. arctica*, and *V. vitis-idaea*, but few forbs or grasses. The sedge/cottongrass meadow changed along a gradient of water flow. More sloping sites were dominated by *C. aquatilis, S. pulchra, E. angustifolium*, *C. saxatilis* and *C. chordorrhiza*. On flatter sites, *E. scheuchzeri* is dominant, with a variety of mosses. The polygons combined elements of both the other habitats. *Dupontia fisheri* was not a prominent species in north Yukon.

On Bylot and Herschel, our study grids supported populations of brown and collared lemmings. Tundra voles were not found on Bylot Island, and, though present on Herschel Island, were rare on our study grids. The wetter habitats at Komakuk supported brown lemmings and tundra voles, with collared lemmings being nearly absent. Lemming population densities on Bylot fluctuate cyclically (Gruyer et al. 2008). They increased through winter 2007–2008 to a low peak in spring 2008, declined to very low densities in winter 2008–2009, and then quickly increased in winter 2009–2010 to a peak in spring 2010 (Bilodeau and Gauthier, unpublished data). The very low 2008–2009 winter densities on Bylot hampered inference at the scale of our experiment. Lemmings on Herschel Island exhibited fairly wide amplitude population fluctuations (Krebs et al. 2011), but were always sufficiently numerous to allow inference at the scale of the experimental treatment. At Komakuk, densities of lemmings and voles were persistently low, with tundra voles being slightly more numerous than brown lemmings (Krebs et al. 2011), and they were sufficiently numerous to assess an experimental effect.

The three study sites had some similarities and differences in the community of lemming predators. Bylot was more representative of a high-Arctic community, with numerous specialist predators breeding in summers of lemming abundance. These included snowy owl (*Bubo scandiaca*), long-tailed jaeger (*Stercorarius longicaudus*), parasitic jaeger (*Stercorarius parasiticus*), rough-legged hawk (*Buteo lagopus*), arctic fox (*Vulpes lagopus*) and short-tailed weasel (*Mustela erminea*) (Gauthier et al. 2004). Arctic fox and short-tailed weasel were present through the winters. Herschel had the same complement of avian predators with the addition of short-eared owl (*Asio flammeus*) and peregrine falcon (*Falco peregrinus*), but the owl species did not nest each year. Herschel's mammalian predators were also more diverse including breeding red fox (*Vulpes vulpes*) as well as arctic fox in most summers, least weasel (*Mustela nivalis*) replacing short-tailed weasel, and wolverine (*Gulo gulo*) and grizzly bear (*Ursus arctos*). At Komakuk, rough-legged hawk, peregrine falcon, common raven (*Corvus corax*), and parasitic jaeger nested, and snowy owls and short-eared owls were often present but not nesting. The mammalian community was the same as on Herschel, though foxes did not breed locally in all years. At both Yukon sites, winter predators included both species of fox, least weasel and wolverine.

Field methods

To measure the intensity of use by lemmings and voles of different habitats in winter, we mapped the distribution of their winter nests in June as soon after the snow had melted as possible. We assumed that lemmings place their winter nests in their preferred habitat, at least in terms of maximizing the energetic benefits of the nest, and therefore that nest density is a good measure of habitat use. This line of thinking was supported by studies documenting the high value of winter nests for lemming energetics (Chappell 1980; Casey 1981). Sometimes, brown lemmings and tundra voles made winter nest structures in hummocky vegetation, notably *E. angustifolium* tussocks in Yukon. We were unable to examine every tussock for this possibility, so nest counts may have underestimated resting sites for these species in some habitats. At Komakuk, tundra voles left evidence of winter travel routes as excavated earthen runways, clearly visible in spring. We mapped the distribution of these runways as further evidence of winter habitat use.

We did our nest mapping on square grids (two at each study site, at least 600 m apart) which were also used as live-trapping grids for mark–recapture studies of summer

rodent densities. At each site, one grid was an independent control and one was allocated as a treatment grid. All grids covered commonly found plant communities and topographies in the study area, and the treatment grid was chosen to include habitat that was used by lemmings in winter but considerably less so than the apparent best sites in the landscape. All grids at Herschel and Komakuk were 9 ha (300 m × 300 m), and at Bylot the control grid was 10.89 ha (330 m × 330 m) and the treatment grid 7.29 ha (270 m × 270 m). All grids were laid out with a Cartesian array of numbered wooden lathe stakes (ca. 50 cm tall) to orient systematic foot searches and mapping of winter nests. Nests locations were recorded on maps to scale and/or by digital geographic positioning system (GPS). In the first, pre-treatment, spring, nests more than 1 year old were differentiated from nests of the most recent winter by their color and degree of decomposition (MacLean et al. 1974). At that time, and in subsequent springs, all nests were removed or destroyed to avoid risk of re-counting in another year.

To experimentally enhance snow depths, we set up parallel rows of snow fences (Agriflex Tensar Co-polymer UX425016, porosity 55%), approximately perpendicular to the prevailing wind(s), to produce fairly even coverage over all or portions of the treatment grids. Fencing came in rolls 128 m long and 1.22 m tall, weighing 43 kg. To set up the fencing, we used 2.13- or 1.83-m-tall metal fence posts pounded at least 50 cm into the ground so as to reach the top of the permafrost. These were spaced 3–6 m apart in straight rows. Fencing was drawn tight and attached to each post by sandwiching the fencing between the post and a 1.22-m-long wooden lathe and wrapping at least six bands of baling wire very tightly around the lathe and post while passing through the holes in the sandwiched fence. We tried to keep the bottom of the fencing about 10–20 cm above the ground to maximize snow drifting (Tabler 1991). Unanchored fences easily blew down. We anchored them with nylon rope that ran perpendicular to the fence on both sides of each fence post and was attached to short posts (30–50 cm long) pounded to permafrost at distances of 2–5 m from the fence. Initial calculations based on Tabler (1991) suggested that we could get fairly extensive, though probably not complete, drifting over the grids with five rows of fencing (drifts as long as 35 times fence height), so we aimed to set up five rows ranging from 30 to 50 m apart on treatment grids. For logistic reasons, we were unable to achieve full coverage on the Herschel and Komakuk grids. This left portions of these grids unaffected by the treatment because they were not downwind of fences, or were >40 m from fences, a distance at which there was clearly no drifting effect. We call these untreated portions of the treatment grids at Herschel and Komakuk—"joined" controls—in contrast to the completely "independent"

control grids. Joined control and treatment spaces were approximately equal in surface area. In some winters at Bylot, portions of the fence collapsed and could not be fully restored by the next winter, so the treated space varied somewhat between years.

Our experiment ran for two winters at Komakuk (2007–2008 and 2008–2009) and four winters at Bylot and Herschel (2006–2007 through 2009–2010). At each site, the first winter was a pre-treatment control year on both grids. We took down the fences after one treatment winter at Komakuk, two treatment winters at Herschel, and the experiment is still running at Bylot (three treatment winters). At Herschel, we relaxed the treatment after the two treatment winters, giving us one subsequent post-treatment winter.
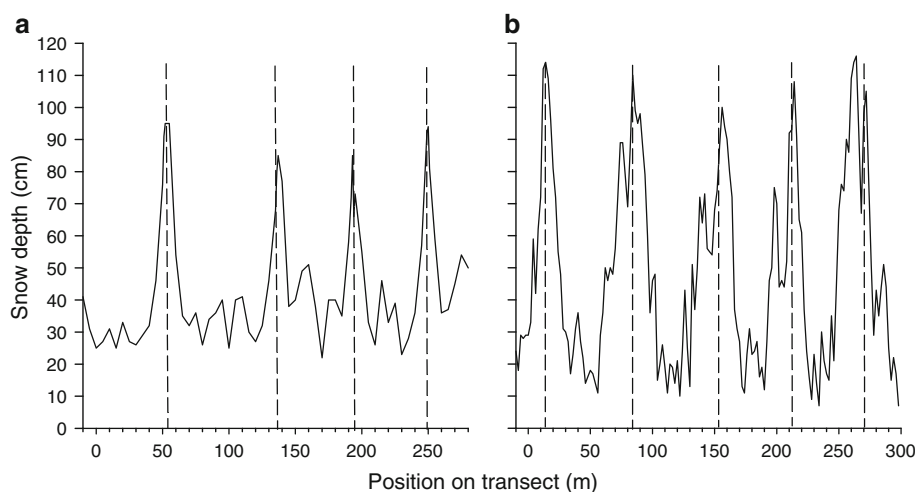
We assumed that the fences would cause snow to drift and accumulate to greater depths than the surrounding tundra, and that the ground-level temperature regime under the deeper snow would be warmer than that under snow on untreated tundra. To test the first assumption, we visited two sites in late winter (mid-April at Herschel, and May or early June at Bylot) and measured snow depths every 2 or 5 m along at least two transects oriented parallel to prevailing winds (i.e., perpendicular to the fence rows) and running the full width of the grids. We also measured snow depths at 20-m intervals along transects across the independent and joined control grids. To test the second assumption, we installed small temperature loggers (Thermocron® iButtons®; Dallas Semiconductor, USA), attached in vertical arrays to wooden stakes which were in turn attached to metal posts driven vertically into the ground at evenly spaced locations across the grids and also close to the fence rows on treatment grids. The loggers recorded temperature every 4 h at various heights above ground [minimum of ground level (0 cm), then 20, 40 and 80 cm], from late summer when they were installed through to spring when they were retrieved and data were downloaded. Our measurement of interest was the mean throughout the winter of the differences between mean daily temperatures at ground level and in ambient air.

Results

Assumptions

The snow fences successfully trapped additional snow on both sides of each row, but the resulting drifts were generally close to the fence rows and the treatment was not fully effective in the spaces between rows (Fig. 1). The parallel rows of fence relatively close together probably backed up the air downwind of each fence and disrupted the smooth air flow over the downwind drift. In addition,

Fig. 1 Snow depth profiles from representative transects across treatment grids at **a** Bylot (spring 2009) and **b** Herschel (spring 2008) to illustrate the snow trapping effect of fence rows (*vertical dashed lines*)
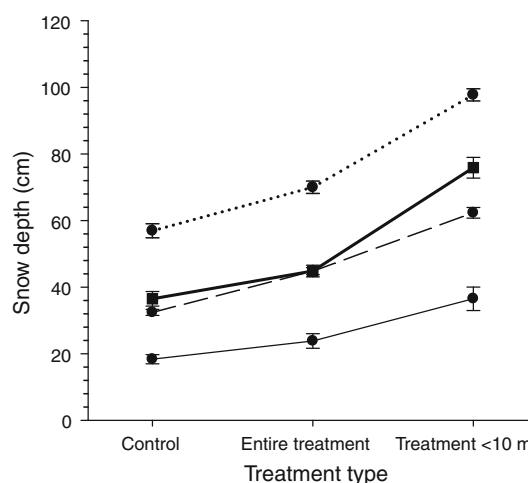

the amount of snow available to trap would have been less with each successive fence row.

Snow depth varied substantially in the areas between fence rows (Fig. 1), and some of this could have been caused by the fences, so we considered all areas between parallel fence rows, and areas up to 40 m downwind of a fence, as part of the treatment space. We chose 40 m so as to be conservative and completely inclusive of all potential drifting based on the general rule that a single fence can produce drifts up to 35 times fence height (Tabler 1991). However, the deepest drifting was consistently close to the fences, and especially <10 m from fences (Fig. 1).

Considering three winters of data from Bylot and one winter of data from Herschel, and accounting for spatial autocorrelation between points (variograms showed significant autocorrelation up to 24.8 m at Bylot and 56.7 m at Herschel), we tested if snow was deeper in the treatment than in the control grids using a generalized linear model. We corrected the model by fitting the best spatial correlation structure to the data, which was exponential. At Bylot, snow was significantly deeper over both the entire treatment grid compared to the control grid ($F = 19.93$, $df = 1, 1{,}629$, $P < 0.01$) and over portions of the treatment <10 m from the fences compared to the control grid ($F = 48.71$, $df = 1, 1{,}087$, $P < 0.01$) (Fig. 2). There was no significant grid by year interaction for both the entire treatment area ($F = 2.19$, $df = 2, 1{,}629$, $P = 0.11$) and the treatment area <10 m from fences ($F = 0.42$, $df = 2$, $1{,}087$, $P = 0.66$), indicating that different snowfall regimes among years did not affect the treatment effect. At Herschel, snow over the entire treatment area was not significantly deeper than on the control area ($F = 0.09$, $df = 1, 392$, $P = 0.77$), but was substantially deeper within 10 m of fences compared to the control area ($F = 12.64$, $df = 1, 169$, $P < 0.01$) (Fig. 2).

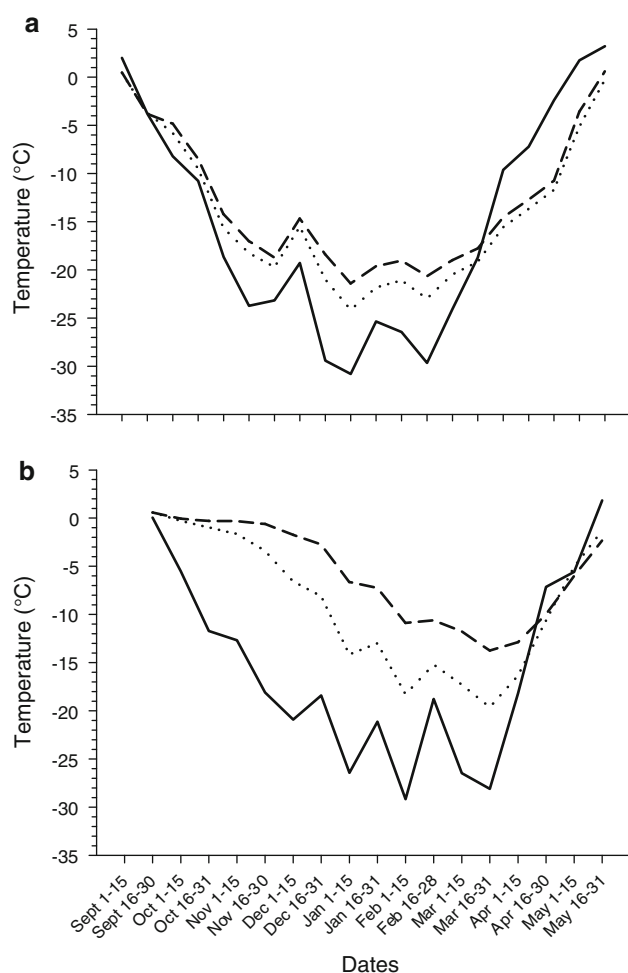At all sites, the mean daily temperatures at ground level within 10 m of the fence were warmer than those in

Fig. 2 Mean (±1 SE) snow depths from areas classed as control, entire treatment, and treatment <10 m from fences. Data are from transects run in late winter across grids at Bylot in 2008 (*solid line*), 2009 (*dashed line*) and 2010 (*dotted line*), and at Herschel in 2008 (*thick solid line, squares*)

untreated areas (Fig. 3 for examples). We calculated the differences averaged across the winter from the time when ground level temperatures start to exceed average ambient air temperatures (autumn overturn; Pruitt 1984; which coincides with the first substantial snowfall) to the time in spring when air temperatures exceed ground temperatures on average (spring overturn, Pruitt 1984). At Komakuk (2008–2009), the deeper snow close to fences provided on average 2.0°C of additional warming, at Herschel 4.5°C in 2007–2008 and 4.0°C in 2008–2009, and at Bylot 1.5°C in 2009–2010.
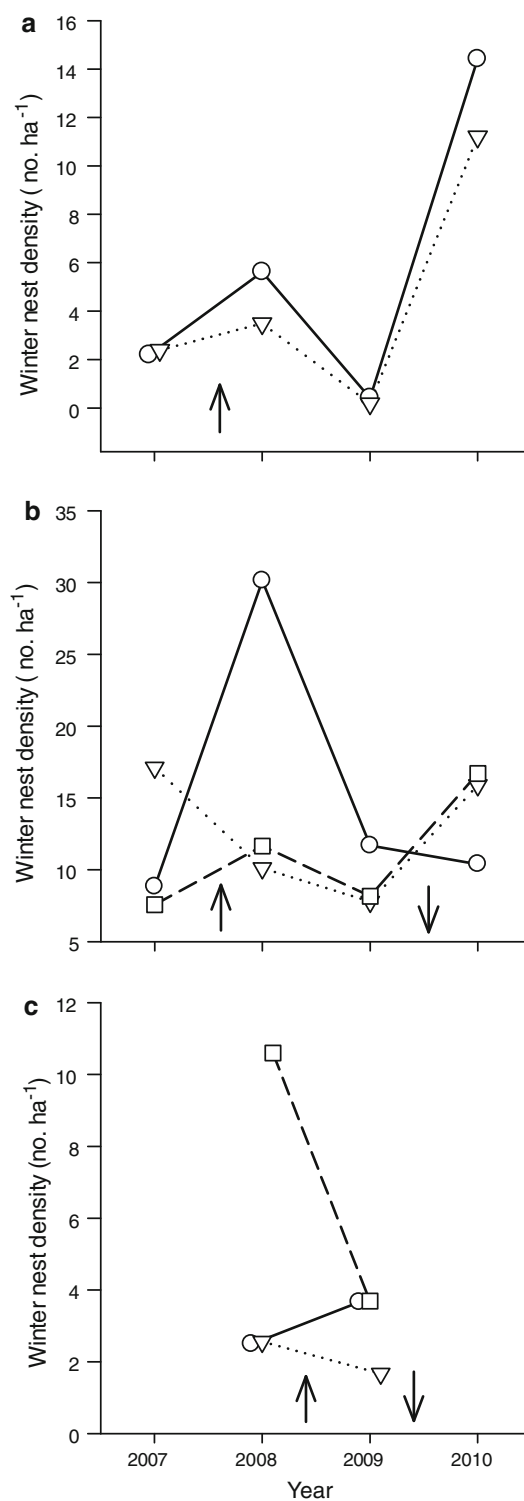
Density of winter nests

Our first prediction, that the density of winter nests would increase in treated areas compared to control areas, was

Fig. 3 Mean daily temperatures (°C) for **a** Bylot (2009–2010; $n = 13$ and 12 temperature sensors in experimental and control areas, respectively) and **b** Herschel (2008–2009; $n = 4$ sensors in each area). Data are summarized for approximately 2-week periods through the course of a winter illustrating the differences in temperature regime in ambient air (*solid lines*), at ground-level on joined control areas (*dotted lines*), and at ground level in treatment areas <10 m from fence (*dashed lines*)

supported at all three sites (Fig. 4). Nest densities on treated areas increased markedly from the winter before treatment to the first winter with treatment. This treatment effect waned in the second winter of treatment at Bylot and Herschel, but returned in the third winter at Bylot. At Bylot, lemming densities were so low in winter 2008–2009 that winter nests were almost non-existent and data too sparse to assess a treatment effect. At Herschel, the difference in the strength of the treatment effect between winters 2007–2008 and 2008–2009 needed explanation, and we provide one in our analysis of autumn temperature profiles below.

While nest densities increased in treated areas (deeper snow), densities in the joined control areas declined dramatically (Komakuk) or remained fairly stable (Herschel).

Fig. 4 Densities of winter nests at **a** Bylot, **b** Herschel and **c** Komakuk study sites, and as counted on treatment (*circles, solid lines*), joined control (*squares, dashed lines*) and independent control (*triangles, dotted lines*) areas. Data points are nest counts in June of each year, summing the accumulated winter nests from the previous winter. *Arrows up* indicate when the snow fences were erected, and *arrows down* indicate removal of the fences

Table 1 Proportion of lemming and vole winter nests recorded on treated and adjacent joined control areas in June of each year, representing accumulated nests from the previous winter

Site	Year	Experimental context	Total number of nests	Proportion in joined control area	Proportion in treated area	Z statistic	P
Herschel	2007	Before treatment	73	0.534	0.466	−0.828	0.80
	2008	Treatment	176	0.341	0.659	5.970	<0.001
	2009	Treatment	87	0.483	0.517	0.455	0.33
	2010	After treatment	126	0.683	0.317	−5.795	<0.001
Komakuk	2008	Before treatment	40	0.575	0.425	−1.342	0.91
	2009	Treatment	33	0.242	0.758	4.185	<0.001

The Z statistic is the standard normal deviate, and P is the probability that we reject the null hypothesis that the proportions are the same

At Komakuk, the decline suggested that voles and lemmings chose to occupy the deeper snow in the treatment area rather than what had previously been suitable winter habitat in the joined control area. At Herschel, the relative stability suggested fairly constant winter habitat suitability in the joined control area.

At all sites, the changing nest densities on independent control grids reflected the general changes in lemming and vole population density in the study areas, so changes on these grids that differed in direction compared to changes on treatment areas provide additional evidence for the treatment effect. At Herschel and Komakuk, nest densities on independent control grids declined from before to during the treatment, reinforcing the conclusion of a strong treatment effect. At Bylot, independent control densities showed the same pattern of increase and decline between years, but with less intensity than the treatment densities, suggesting that the treatment effect was weaker at Bylot than at the western Arctic sites.

Our second prediction, that the treatment effect would be reversed when the treatment was relaxed, was supported at Herschel, the one site where we were able to measure the response (winter 2009–2010) after removing the fences (Fig. 4). The lemming population increased during this period, with increasing nest densities on the independent control grid, but nest density on the treatment area declined a little while increasing in the adjacent joined control area. After relaxation, density in the treatment area returned to approximately the pre-treatment (winter 2006–2007) level.

Distribution of winter nests

The increase in winter nest densities on treatment areas suggested that the snow depth enhancement attracted greater numbers of lemmings and voles to occupy the treated areas. We addressed this by comparing the distribution of nests between adjacent treated and joined control areas before, during, and after treatment, predicting that the proportional use of treated areas would increase compared to joined control areas because animals would favor the deeper snow

in the treated areas compared to adjacent untreated areas such as the joined controls. This prediction was supported at both Herschel and Komakuk (Table 1). Before treatment, the proportion of nests in the two areas was not significantly different, and treatment areas tended to have fewer nests. During the first winter after treatment, the proportion of nests in treated areas increased dramatically and was significantly higher than in control areas. The pattern continued, but was statistically insignificant, in the second treatment winter at Herschel, then completely reversed in the post-treatment winter. This seemed clear evidence that lemmings and voles distributed themselves differently in various winters depending on the distribution of deeper snow.

Snow depth varied in the treated areas because the fences created relatively short drifts with the greatest enhancement of snow depth within 10 m of the fence rows (Figs. 1, 2). Given this variation, we predicted that lemmings and voles occupying treated areas would preferentially choose those portions of the treated areas within 10 m of fences—our fourth prediction. Our null hypothesis was that the observed number of nests within 10 m of fences would not differ from an expected number if animals were situating nests independent of snow depth. We calculated the expected number based on the proportion of the treated area falling within 10 m of fences (ranging from 27 to 33% of the treated areas). Our fourth prediction was supported at Herschel and Bylot, but not at Komakuk (Table 2). Before treatment, lemmings at Herschel and Bylot placed as many nests in the areas that would subsequently be within 10 m of fences as expected based on the availability of those areas. During treatment, however, they were 1.9–2.4 times more likely to place their nests within 10 m of fences than would be expected, such that the majority of nests were under the deepest snow close to fences. After the treatment was relaxed at Herschel, lemmings reverted to their pre-treatment pattern and no longer placed more nests than expected in the areas close to where fences had previously stood.

At Komakuk, we did not find a significant association of nests with the areas close to fences, either before or during

Table 2 Comparison of the observed number of lemming and vole winter nests within 10 m of snow fences in treated areas to an expected number based on random distribution of nests in the same treated areas

Site	Year	Experimental context	Total nests in treated area	Nests <10 m from fence		Chi-square statistic	P
				Observed	Expected		
Bylot	2007	Before treatment	16	4	5.9	0.118	0.74
	2008	Treatment	41	29	15.2	8.041	<0.005
	2009	Treatment	3	2	0.9	n/a	
	2010	Treatment	87	42	22.6	8.336	<0.005
Herschel	2007	Before treatment	34	9	11.3	0.119	0.74
	2008	Treatment	116	93	38.7	49.895	<0.001
	2009	Treatment	45	32	15	11.400	<0.001
	2010	After treatment	40	15	13.3	0.027	0.88
Komakuk	2008	Before treatment	17	5	5.7	0.012	0.91
	2009	Treatment	25	9	8.3	0.008	0.94

P is the probability that we reject the null hypothesis that observed and expected counts are the same

the treatment (Table 2). We did not visit this site in late winter to measure snow depths in association with fences so we do not know whether the distribution of deeper snow somehow differed at this site. We did map the distribution of other over-winter vole sign (runway diggings) and found a strong, though statistically insignificant, trend in association of runway diggings with grid cells bisected by fences compared to grid cells >40 m from fences ($\chi^2 = 3.41$, $P = 0.07$). Voles were apparently attracted to the deeper snow close to fences. Our inability to assess this choice based on winter nests was partly due to a greater use of other denning structures (notably *Eriophorum* tussocks) by voles and lemmings than at the other sites, something we observed but were unable to quantify.

Autumn temperatures

At Herschel, the treatment effect was substantially reduced in winter 2008–2009 compared to winter 2007–2008 (Fig. 4). One potential explanation was that lemmings consumed enough food in winter 2007–2008 to reduce the availability of food for the subsequent winter. We did not observe any evidence of heavy grazing in the snow enhancement area, and our live-trapping results showed that lemmings occupied this area as much in summer 2008 as summer 2007, so we do not think that food limitation was a prominent issue.

We proposed an alternative explanation which depends on the timing of deep snow accumulation on the treatment compared to joined control areas. Before the first substantial snow, lemmings experienced ambient air temperatures which generally range through several degrees in a day. As snow accumulated to reach the hiemal threshold, the daily sub-nivean temperature range declined to almost
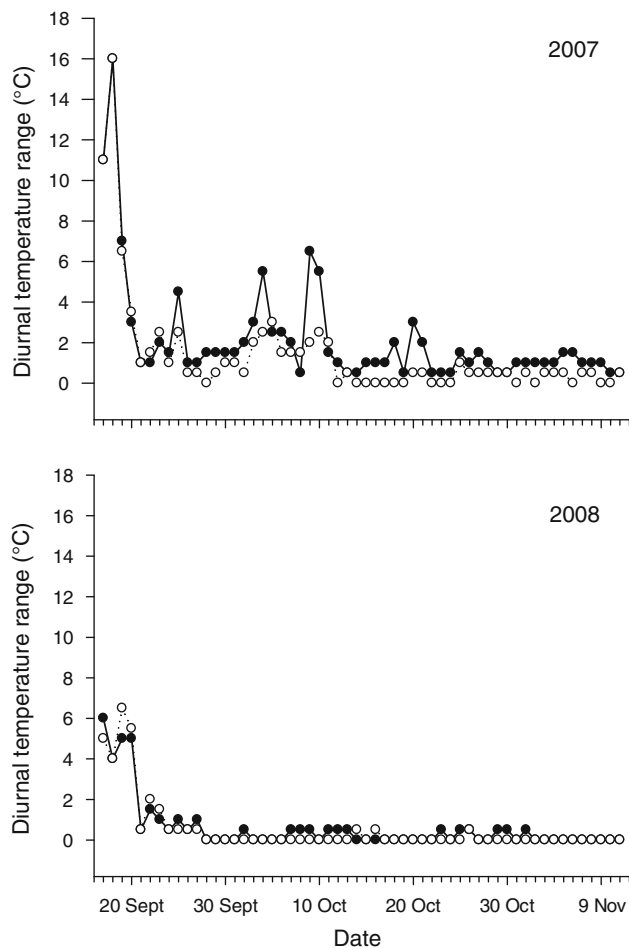
zero (i.e., a constant temperature throughout the day). We assumed that lemmings determined where the deeper snow is accumulating in early winter, with temperature range as a possible cue (Duchesne et al. 2011b). Accordingly, we hypothesized that the ability of lemmings to discriminate between the treatment and joined control areas in autumn 2008 was less than in autumn 2007. In autumn 2008, the hiemal threshold (daily temperature range of near zero) was reached on both treatment and control areas, coincidentally following a heavy snowfall on 21–24 September, after which the temperature regimes were very similar in each area (Fig. 5). In autumn 2007, by contrast, the first snowfall (20–22 September) reduced the daily temperature range more in the treated area than in the adjacent control area, and this difference persisted through a subsequent snowfall on 11 October (after which the treatment area appeared close to the hiemal threshold) until well into November (Fig. 5). The pattern of snowfall gave lemmings more temperature-based evidence for the location of relatively deep snow in 2007 than in 2008, so the attraction to the treatment area would have been greater in autumn 2007.

Discussion

Lemming winter habitat

Our experimental enhancement of snow depth increased the suitability of treated tundra as winter habitat at all three study sites, and our four predictions regarding the behaviour of lemmings were all supported in at least two of the sites. By increasing snow depth with fences, we increased the density of small rodent winter nests compared to pre-

Fig. 5 Time series of the diurnal temperature range (°C) at ground level on treatment (*open circles*) and joined control (*filled circles*) portions of the experimental grid at Herschel in autumn 2007 and 2008. Each data point portrays the daily temperature range between highest and lowest of six evenly-spaced temperature records in each 24-h period. In each graph, the range of dates is 17 September to 11 November

treatment levels and compared to concurrent control areas. When we relaxed the experimental treatment at one site, the treatment effect was reversed, and lemmings' use of the previously treated tundra returned to the pre-treatment level. The distribution of winter nests on treatment and nearby control areas showed that lemmings and voles shifted their relative use of these areas in response to the enhanced snow depths. In addition, the animals preferentially settled in the relatively restricted areas of deepest snow accumulation closest to the fences, as predicted. At a relatively localized scale, our results show that snow depth is a dominant component of winter habitat suitability for tundra lemmings and voles.

Our evidence for an experimental effect of snow depth enhancement is based on winter nests. We assume that nest density in spring is proportional to an integrative measure of actual lemming density during the winter, an assumption

that might be in question. First, tundra voles and brown lemmings may use excavated cotton-grass tussocks instead of nests, so our nest counts probably underestimated habitat use, at least by voles at Komakuk. Second, we do not know how much time lemming(s) spent using each nest. Duration of nest occupancy probably varies substantially; nests come in a range of sizes reflecting different levels of investment in their construction (therefore different insulative capacities) and also in their use, judging by size of associated latrines of fecal pellets (MacLean et al. 1974; Sittler 1995). However, we did not observe any tendency of either treatment or control areas to have larger, better built, or more heavily used nests. So we feel confident in our general assumption that the average period of nest use was similar in treatment and control areas.

Snow accumulation, and therefore winter habitat availability, has temporal and spatial dimensions. In terms of timing, earlier autumn snow accumulation provides a more favorable thermal cover earlier, thereby enhancing energy conservation for potential investment in growth and winter reproduction (Reid and Krebs 1996; Duchesne et al. 2011b). An early and deep snow cover with relatively warm temperatures but no freezing rain are the conditions associated with the strongest over-winter lemming and vole population growth (Shelford 1943; Krebs 1964; Scott 1993; Aars and Ims 2002). Early snowfall also traps the energy already in the ground under an insulative layer, keeping it in the lower snow pack much longer. This is especially powerful if the ground is not yet frozen because the latent heat released by freezing, when it occurs, is partially trapped in the lower snow pack (Pomeroy and Brun 2001).

Earlier and deeper snow also provides excellent cover from predators as most raptors have to abandon tundra foraging when snow covers the small rodents. Mammalian predators continue to forage through the snow pack, but snow removes their ability to use sight to augment sound and scent in detecting lemmings, so likely reduces capture rates (Duchesne et al. 2011b). The timing of autumn snow, and its insulative quality (depth and density), will have winter-long effects on lemming survival and habitat quality.

We stress that our study areas receive relatively little snow and have a more consistently cold winter temperature regime compared to some Scandinavian sites, where warmer temperature regimes are inversely related to rodent winter population growth rates (Aars and Ims 2002; Ims et al. 2011) and deeper snow may restrict the subnivean space and decrease access to food (Korslund and Steen 2005). It seems that, with fairly frequent winter thaw events and high humidity in Scandinavia, melting and wet snow crystal metamorphism increase snow density and hardness, thereby reducing the insulative capacity of the snow pack, and, perhaps more importantly, reducing access

to food following settling of snow layers, compaction of the subnivean space, and subsequent refreezing of melt-water as ice in or below the snow profile (Pomeroy and Brun 2001; Korslund and Steen 2005; Kausrud et al. 2008). Snow depth, and its influence on subnivean temperature regimes, is not the sole feature of the snow pack to consider across all Arctic regions. Although thaw events do occur occasionally in our study areas, our snow packs were generally quite dry and subject to dry snow crystal meta-morphism under a consistent temperature gradient from colder ambient to warmer ground temperatures, with sub-stantial hoar frost, and therefore an extensive sub-nivean space, close to the ground. We did observe basal ice for-mation but usually only after the temperature gradient reversed during spring melt.

Regarding the spatial dimension of winter habitat, our experimental results strongly support and amplify the observations from past field studies that lemmings tend to place their winter nests in areas of deepest winter snow, usually areas associated with topographic breaks providing lee slopes for deposition of wind-blown snow (Fuller et al. 1975a; Reid and Krebs 1996; Duchesne et al. 2011b). Tus-sock or hummocky vegetation and heaths with prostrate shrubs are typical arctic lemming habitats. This vegetation can create an uneven ground surface sufficient to trap some snow for insulation, perhaps even reaching the hiemal threshold in some micro-sites. However, only erect shrubs and incised topography (slopes steeper than 9°) can consis-tently trap snow well above the hiemal threshold over areas of many hectares (Pomeroy and Brun 2001). We conclude that there is substantial, though primarily site-scale, evi-dence supporting the hypothesis that the spatial extent of lee slopes and erect shrubs, with potential to trap snow, is a primary determinant of the availability of high quality lem-ming and tundra vole winter habitat. This hypothesis now needs to be addressed at a regional scale. Are areas of rela-tively deep snow accumulation (high quality winter habitat) limited in availability in any regions within the North American Arctic? The answer depends on an interaction between the amount of snowfall and the proportion of the landscape with snow-trapping topography.

Ultimately, we are interested in the potential demographic implications of differences in habitat availability regionally. We will report on any demographic effects of this site-scale experiment in a subsequent paper. In addition, we continue to investigate whether differences in winter habitat suitability could influence regional patterns in amplitude and frequency of lemming population fluctuations.

Lemming choice of winter habitat

Our results demonstrate that lemmings and voles move around soon after the first substantial snowfall in search of the best sites to establish winter ranges. Therefore, the population using a specific portion of tundra may change considerably between snow-free (summer) and snow-cover (winter) seasons, depending on the likelihood of snow accumulation.

As they move around under early winter snow, lem-mings must use some indicator to discriminate the current and future quality of different areas of the tundra. Areas with deepest early winter snow are of highest quality because of their current thermal and predator covers, and the strong likelihood that snow will continue to accumulate more on these areas than others as winter progresses. Lemmings that find substantial areas of deeper snow (i.e., areas of drifting) early in winter will have a selective advantage. Lemmings could use light intensity and/or the daily range of temperature variation at ground level as their proximate indicator of snow depth (Duchesne et al. 2011b). Snow cover rapidly attenuates the transmission of light to the ground, with approximately 10% passing through 15 cm of snow at typical early winter snow densities (Marchand 1984). Variation in light intensity is probably the most immediate indicator of deeper snow in early winter. The daily range of temperature varies in concert with light levels, with small accumulations of snow (>10 cm) quickly insulating the ground from ambient conditions, such that in uncompacted snow of 20–30 cm the daily temperature variations are essentially nil (i.e., the hiemal threshold) (Pruitt 1970; Pomeroy and Brun 2001). This indicator has the disadvantage of requiring a number of days to adequately discriminate different habitats, but the advantage of operating at any time during the winter.

Reid and Krebs (1996) concluded that the amount of cold exposure in autumn was the dominant factor influ-encing over-winter population growth rates in collared lemmings at Pearce Point, Northwest Territories, where mean maximum annual snow depth (<30 cm) is even less than at the three study sites reported here. Our results reinforce that conclusion by providing behavioral evidence for autumn cold avoidance by lemmings. We observed the strongest treatment effect on Herschel in the year when the autumn temperature regime under deepest snow close to fences differed most from the control area. A relatively stable sub-nivean temperature regime proved to be a strong attraction to lemmings (see also Duchesne et al. 2011b), probably because of the immediate energy conservation realized by a stable and, on average, warmer sub-nivean space.

Future investigations of the role of snow in tundra lemming and vole habitat choice and demography would benefit from spatially-explicit landscape modeling of snow fall and accumulation to map the dispersion and spatial extent of areas of adequate snow depth in regions of strongly contrasting topography and snowfall. The

proximate factors influencing habitat choice could be investigated with temperature controlled chambers in which lemmings' access to different thermal and light regimes is mediated by a simple maze. Future research should also focus on the energetics of lemmings in different sub-nivean thermal regimes. This could include quantifying the lower critical temperature thresholds in winter for lemming species, developing energy budgets and demographic models under divergent scenarios of snow accumulation through autumn and winter, and tracking the body size, growth rates and reproductive performance of females and their offspring in the field under diverse winter conditions which ideally would include experimental manipulations of snow depth to influence thermal regimes.

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