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Habitat selection, reproduction and predation of wintering lemmings in the Arctic

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Abstract Snow cover has dramatic effects on the structure and functioning of Arctic ecosystems in winter. In the tundra, the subnivean space is the primary habitat of wintering small mammals and may be critical for their survival and reproduction. We have investigated the effects of snow cover and habitat features on the distributions of collared lemming (*Dicrostonyx groenlandicus*) and brown lemming (*Lemmus trimucronatus*) winter nests, as well as on their probabilities of reproduction and predation by stoats (*Mustela erminea*) and arctic foxes (*Vulpes lagopus*). We sampled 193 lemming winter nests and measured habitat features at all of these nests and at random sites at two spatial scales. We also monitored overwinter ground temperature at a subsample of nest and random sites. Our results demonstrate that nests were primarily located in areas with high micro-topography heterogeneity, steep slopes, deep snow cover providing thermal protection (reduced daily temperature fluctuations) and a high abundance of mosses. The probability of reproduction increased in collared lemming nests at low elevation and in brown lemming nests with high availability of some graminoid species. The probability of predation by stoats was density dependent and was higher in nests used by collared lemmings. Snow cover did not affect the probability of predation of lemming nests by stoats, but deep snow cover limited predation attempts by arctic foxes. We conclude that snow cover plays a key role in the spatial structure of wintering lemming populations and potentially in their population dynamics in the Arctic.

Keywords *Dicrostonyx groenlandicus* · *Lemmus trimucronatus* · Small mammals · Snow cover · Tundra

Introduction

Some small mammal populations are famous for their phenomenal cyclic fluctuations in abundance (Elton 1924; Krebs 1964; Krebs and Myers 1974; Hornfeldt et al. 2005; Pitelka and Batzli 2007). Small mammal species with a wide geographic distribution tend to exhibit more pronounced population cycles at northern latitudes where seasonality is strongest (Hansson and Henttonen 1988; Ims and Fuglei 2005). During the cold and dark Arctic winter, small mammals may spend up to 9 months of the year under the snow. Winter remains the least known period of their annual cycle (Stenseth 1999), yet this period may play a key role in their population dynamics (Reid and Krebs 1996; Hansen et al. 1999; Kausrud et al. 2008).

At northern latitudes, snow cover dramatically changes the structure and functioning of ecosystems in winter. Temperature gradients within the snow result in the formation of a stratum of fragile and loosely arranged snow crystals near the ground, which creates a subnivean space, the primary wintering habitat of small mammals (Korslund

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and Steen 2006). Their survival is dependent upon accessibility to food and the protection against harsh temperatures and predators offered by this particular environment (Scott 1993). Freeze–thaw cycles induced by warm winter temperature disturb the subnivean space and may lead to the formation of ice at ground level, which prevents rodents from feeding on the vegetation (Korslund and Steen 2006; Coulson and Malo 2008). Small mammals require a high rate of food intake because of their low digestive efficiency and high metabolic rate increased by cold conditions (Barkley et al. 1980; Rammul et al. 2007). Therefore, limited accessibility or depletion of winter food may induce a deterioration of their physiological condition and increase mortality (Huitu et al. 2007).

Winter reproduction under the snow occurs in some species of small mammals and is especially common in lemmings (Hansen et al. 1999; Millar 2001; Gruyer et al. 2010). In fact, successful reproduction under the snow is often considered a necessary condition for the occurrence of a peak in abundance in cyclic lemming populations (Ims et al. 2008). The early onset of a thick and dry snow cover combined with the absence of freezing rain and days with above zero temperatures should favour survival and reproduction (Reid and Krebs 1996; Solonen 2006). Recent evidence suggests that population cycles of small mammals of the tundra may be fading out in some areas, especially in Fennoscandia (Hornfeldt et al. 2005; Ims et al. 2008). Increased frequencies of freeze–thaw cycles during the winter due to climate warming and their influence on snow conditions have been invoked as a possible cause for the dampening of these cycles (Hornfeldt 2004; Ims et al. 2008; Gilg et al. 2009; but see Brommer et al. 2010). Alterations in snow cover may also affect winter predator–prey interactions (Hansen et al. 1999). Even if subnivean specialist predators, such as stoats and weasels (*Mustela* sp.), should continue to be efficient predators during winter (Fitzgerald 1977; Sittler 1995), thick snow cover may reduce the success of other predators of small mammals, such as arctic foxes (*Vulpes lagopus*) or snowy owls (*Bubo scandiacus*; Hansson and Henttonen 1985; Lindstrom and Hornfeldt 1994).

During winter, lemmings build nests made of vegetation, which serves as additional insulation from the surrounding environment and allows them to breed (MacLean et al. 1974; Sittler 1995). A survey of these nests at snowmelt can provide information on the winter ecology of lemmings, including relative population levels (Gilg et al. 2006), habitat use, breeding activity (Duchesne et al. 2011) and predation rate by stoats (Fitzgerald 1977; Sittler 1995). An investigation of factors affecting the spatial distribution of these nests and the occurrence of reproduction and predation may therefore further our understanding of the winter ecology of lemmings. Surprisingly, very few studies to date have investigated these factors.

The purpose of our study was to determine the ecological factors influencing the spatial distribution of winter nests of collared (*Dicrostonyx groenlandicus*) and brown lemmings (*Lemmus trimucronatus*) at various scales and to examine the effect of habitat structure on the occurrence of reproduction and predation in those nests. Our hypotheses were that lemmings prefer areas providing protection against thermal stress and predation and maximizing energy intake. We thus predicted that, compared to random locations, sites of lemming winter nests should have (1) more features favouring snow accumulation, such as ground depressions and terrain roughness; (2) deeper snow cover; (3) lower subnivean temperature fluctuations; (4) a greater abundance of key plant species used by lemmings. We further predicted that these habitat variables should increase the probability of occurrence of lemming reproduction in winter nests. Finally, we predicted that snow depth should not affect the probability of nest predation by stoats (*Mustela erminea*), whereas nests with a shallower snow cover should be more vulnerable to predation by arctic foxes.

Materials and methods

Study area

This study was carried out on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada in 2007 and 2008 (73°08′N, 80°00′W). The study area (156 km^2) includes a large glacial valley surrounded by rolling hills and dominated by two major habitats, namely, wet and mesic tundra. The wet habitat is characterized by polygon tundra forming wet meadows, fens and shallow ponds in lowlands. Vegetation is dominated by graminoids, such as *Carex aquatilis* var. stans, *Eriophorum sheuchzeri* and *Dupontia fisheri* (Manseau and Gauthier 1993). The mesic habitat is most common in upland areas and is characterized by hummocky tundra. The most common plants are *Salix arctica*, *Cassiope tetragona* and graminoids, such as *Arctagrostis latifolia* (Audet et al. 2007). For the purpose of this study, we recognized a third habitat—streams running through the upland areas. These streams are primarily fed by spring runoff, but many of them retain some water during the summer, being fed by ponds, snow banks persisting late in the summer and/or rain. They were often located at the bottom of small gullies and were characterized by a narrow band (approx. 1 m on each side) of plants typical of wetland habitats. Previous observations led us to believe that this habitat was heavily used by wintering lemmings.

Two species of lemmings are present in the study area: the collared lemming and the brown lemming. The former is primarily associated with a dry habitat and feeds mainly on dicotyledons (Negus and Berger 1998), whereas the latter is more common in wetlands and feeds largely on monocotyledons and mosses (Batzli and Pitelka 1983; Batzli et al. 1983). These populations follow 3- to 4-year cycles at our study site and tend to fluctuate in temporal synchrony, although the amplitude of fluctuations are much larger in the brown than in collared lemming population (Gruyer et al. 2008). The abundance of both species was low in 2006. Collared lemmings increased in 2007 (although brown lemmings did not), whereas brown lemmings were very abundant in 2008.

Stoats and arctic foxes are resident lemming predators on the island. The main avian predators, which are only present during the summer, are snowy owls, rough-legged hawks (*Buteo lagopus*), long-tailed jaegers (*Stercorarius longicaudus*) and glaucous gulls (*Larus hyperboreus*) (Gauthier et al. 2004).

Winter nest survey

Lemming nest density was estimated during the winter of 2006–2007 using the line transect method (Buckland et al. 2004). In the early summer of 2007, we set out 500-m-long transect lines oriented to the north and distributed in equal proportion among our three previously defined habitat types (wet tundra, mesic tundra and streams). The starting points of these transects were randomly selected from a habitat map of the study area, and a GPS receiver was used to locate these points in the field. The transects in the stream habitat followed the meandering course of the water channel. Changes in habitat that occurred while walking transects were noted, and transects that covered <300 m in the same habitat type were discarded. We cumulated a total of 36,200 m along 74 transect lines. The position of all nests found was recorded using a GPS receiver, and perpendicular distance from the transect was measured with a measuring tape. Nests were collected in a plastic bag, air-dried in the field and sent to the laboratory for further analyses. Nests sometimes persist for more than 1 year, but older nests can be distinguished from those of the previous winter: the material of old nests is bleached and the inner layers show evidence of decomposition (MacLean et al. 1974). Based on these criteria, old nests were ignored when encountered.

In the laboratory, we identified the lemming species that used each nest based on the faeces recovered from the nests. The shape of faeces differs between the two species, with those of the collared lemming being dark reddish, about 4–6 mm long, blunt at one end and rather pointed at the other end, whereas brown lemming faeces are bright green, about 6–10 mm long and rounded at both ends (MacLean et al. 1974). We also assessed the occurrence of reproduction in winter nests on the basis of the size distribution of the faeces found in each winter nest. Duchesne et al. (2011) validated this approach in laboratory trials and found that it could reliably detect winter reproductive activity of lemmings: inspection of $\geq$30 faeces was sufficient to correctly infer reproduction of small mammals with an accuracy of >95%. Nests that had been depredated by stoats were identified based on the presence of an extensive lining of lemming fur in the nest and lemming remains, such as bones (Sittler 1995).

Nest site selection

Habitat selection was assessed by comparing nest sites to random sites at two scales (landscape and local) because resource selection is a hierarchical process, and factors affecting selection may differ according to the measurement scale (Boyce 2006). The landscape level corresponds to the scale at which individuals select their home range, whereas the local scale represents the selection of a site within the home range (Johnson 1980). Sites at the landscape level were selected along the transects randomly distributed across the whole study area. Thus, the landscape level refers to the scale of our whole study area (156 km^2). Two points per transect were located at 166-m intervals from the start of each transect. To define the local scale, we ran short transects starting in various directions from 38 lemming nests found soon after snowmelt. All signs of lemming activity, such as leaf clipping, grazing and active runways, were noted along these transects. Since 52% of signs of lemming activity were concentrated in a radius of 8.5 m around nests, we used that distance to define the local scale [Electronic Supplementary Material (ESM) Fig. A1]. Random sites at the local scale were systematically distributed in the four cardinal axes at 8.5 m from each sampled nest (ESM Fig. A2). The habitat at each winter nest and at each randomly located point at the landscape and local scales was sampled during the summer of 2007. This sampling design follows type III (landscape) and type I (local) designs of protocol A suggested by Manly et al. (2002).

The habitat variables sampled included topography (elevation, micro-topography, slope and aspect) and vegetation. Elevation (m) was estimated with a GPS. The micro-topography variables measured were the proportion of the ground covered with depressions and the depth of the deepest depression within a 1-m radius of each site. The proportion of ground depressions was measured along two 1-m-long lines perpendicular to each other. We measured the proportion of the length of these lines passing over depressions >10 cm deep (ESM Fig. A2). The slope was measured with a clinometer, and aspect was evaluated with a GPS. The percentage of non-vascular and vascular plant covers were assessed separately and estimated visually in a 50 × 50-cm quadrat centered on the site. This method was calibrated and performed by the same observer for every site.

Because the position of lemming nests during the winter of 2006–2007 could not be identified before snowmelt, we measured snow depth at these nest sites and at random sites at the end of the 2007–2008 winter. Even though snow conditions may vary from year to year, the spatial distribution of snow depth is relatively insensitive to annual variations in snowfall (Deems et al. 2008). We thus assumed that relative differences between lemming nests and random sites were constant from 2007 to 2008. Snow depth measurements were carried out from 13 to 16 May 2008 (i.e. shortly before the start of snowmelt) with a graduated metal rod. During this sampling period, we encountered many craters freshly dug into the snow by arctic foxes to attack lemmings in their nests so we measured snow depth at all these snow crater sites. These predation attempts were confirmed by the presence of destroyed lemming nests in the freshly dug craters.

We evaluated subnivean thermal conditions over the winter for a randomly selected subsample of 15 nests and 15 random sites at the landscape scale. We recorded temperature at 4-h intervals with a Smart Buttons system (ACR Systems, Surrey, BC, Canada) deployed at 2 cm above ground in August 2007. The subnivean period was defined as the time interval extending from 1 October 2007 to 1 May 2008. Mean daily temperature and mean daily temperature fluctuations (difference between daily minimum and maximum temperature) were determined from the collected data. We also determined snow density at each of these sites in May 2008 by weighing a snow core (diameter 4.13 cm) extending from the surface to the ground level and calculating average density by dividing the snow mass by its volume (kg/m^3).

Statistical analyses

Lemming nest density was estimated using a hazard-rate detection function with a simple polynomial adjustment (Buckland et al. 2004). We evaluated if habitat-specific detection probabilities should be preferred over a global model on the basis of Akaike information criterion (AIC) values (Burnham and Anderson 2002). To evaluate the fit of the detection function to the data, we used Kolmogorov–Smirnov and Cramér-von-Mises statistics with uniform and cosine weighing. Calculations were made with the software program DISTANCE ver. 5.0 of Buckland et al. (1993). The lemming nest density estimated in each habitat was compared using a Mann–Whitney *U* test; differences in nest density between the two species was assessed with Wilcoxon signed rank tests.

Habitat data expressed as proportions were normalized using arcsin square-root transformation, and all habitat variables were standardized (Sokal and Rohlf 1995). Among abiotic habitat variables (topography and snow depth), only the proportion of ground covered by depressions and the depth of depressions displayed a high correlation ($r \geq 0.7$). To avoid collinearity problems, we applied a principal component analysis (PCA) to these two variables and used the first axis as an index of micro-topography heterogeneity. For the same reasons, we conducted PCAs on plant cover data to extract a small number of components describing major non-vascular and vascular plant communities (separate analyses). There was no collinearity problem among variables (i.e. topography, snow depth and plant communities) of the resulting dataset ($r < 0.55$).

Resource selection functions (RSFs) were used to compare lemming nests to random sites (Manly et al. 2002). These were computed for each species at the landscape and local scales with lemming nest presence as the dependent variable and habitat measurements at individual lemming nests and random points as explanatory variables. To ensure a balanced design at the local scale (i.e. a roughly equal number of winter nests and random points), we used the means of habitat variables sampled at the four random sites around each nest. To estimate RSFs, we used a modification of the generalized estimating equations, which accounts for spatial autocorrelation (Carl and Kuhn 2007). As suggested by Dormann et al. (2007), spatial correlation was assumed to decrease exponentially with increasing distance, and we estimated the correlation parameter according to the robust Lagrange multiplier of model residuals using spatial software GeoDA 0.9 (Anselin 2003). Because generalized estimating equations are a non-likelihood-based method, AIC cannot be applied for model selection. Therefore, the quasi-likelihood information criterion (QIC), which is a modification of the AIC specifically designed for these situations (Pan 2001), was used. We determined a set of a priori models and did a preselection of the best variables explaining nest presence among abiotic (topography and snow depth) and biotic (plant communities) variables separately. Variables included in the best model of each group were combined in a final model selection process. To account for uncertainty in model selection, we calculated the model weight (w_i), which is an index of the relative plausibility of each model on the basis of ΔQIC values, in an analogous way to AIC (Burnham and Anderson 2002). To determine the relative importance of variables, we summed w_i of all models containing this parameter. Parameter estimates and unconditional standard errors were averaged across models to account for the effect of uncertainty in model selection on parameter estimations (Anderson et al. 2000). Two-way interaction terms and quadratic terms (for non-linear effects) associated with biological phenomenon of interest were included when the corresponding variables were present in the best model.

To determine if habitat variables could explain differences in lemming nest densities among habitat types, we used Kruskal–Wallis tests to compare habitat variables measured at random sites (landscape scale) among habitats. Post-hoc contrasts were performed using the Mann–Whitney *U* test and Dunn's procedure was used for multiple comparisons.

The effect of habitat variables on the probability of occurrence of lemming reproduction in nests of each species was examined with generalized estimating equations following the same procedure as that mentioned above. We also used generalized estimating equations to examine the effect of habitat variables on the probability of nest predation by stoats. Due to the small number of depredated nests, we pooled both species and compared these to a random subsample of intact nests stratified by habitat in the same proportion as depredated nests. Explanatory variables included snow depth, reproduction occurrence, lemming species and total lemming nest density estimated for the corresponding transect. We compared snow depth between intact nests and nests depredated by stoats using two-sample *t* tests. Finally, snow depth between a random subsample of intact nests, nests where we observed predation attempts by foxes and a subsample of random sites were compared using Mann–Whitney *U* tests.

Subnivean temperatures and snow conditions of lemming nest sites were compared to those of random locations using two-sample *t* tests or Mann–Whitney *U* tests, depending on the normality of the variables. We examined whether the effect of snow depth on the probability of occurrence of lemming nests was indirectly mediated through an effect on the subnivean microclimatic conditions (i.e. ground temperature) with path analysis. Because subnivean temperature was recorded at a relatively small number of nests, data from both species were pooled for analysis. Predictor variables included in the path analysis were snow depth, mean daily subnivean temperature fluctuations and the plant community principal component axis, which described the most variation in winter nest site selection at the landscape scale. We performed analyses on the variance–covariance matrix using the general structural equation models and the reticular action model formulation (McArdle 1980). Path analysis assumes that (1) relationships among variables are linear, (2) residuals are normally distributed and (3) correlations among predictor variables are not high. Although we detected a significant quadratic effect, linearity was obtained using a log-transformation; all other assumptions were met in our data. As recommended by Kline (1998), overall fit of the full model was assessed using four tests: the chi-square test, the Bentler–Bonett normed fit index, the Bentler–Bonett non-normed fit index and the standardized root mean square residual. We determined whether dropping non-significant path coefficients significantly reduced model fit by comparing the χ^2 goodness-of-fit statistic of the reduced model to that of the more general model. Statistical analyses were performed using R CRAN project (R Development Core Team 2008).

Results

Lemming nest density

We found 18 lemming nests in wet tundra, 58 in mesic tundra and 88 along streams ($n = 25$, 25 and 24 transects, respectively). A model with habitat-specific detection functions fitted the data better than one with a common function for all habitats (ΔAIC = 11.6). The width of the effective detection distance was estimated at 10.4 ± 1.8, 3.9 ± 1.0 and 7.1 ± 1.0 m [±standard error (SE)] in the wet, mesic and stream habitat, respectively. The detection function models displayed an adequate fit to the data ($P > 0.19$ for all habitats). Total lemming nest density (*n*/ha) was lower in wet tundra (0.71 ± 1.12) than in mesic tundra (6.14 ± 5.18, $U = 110$, $n = 50$, $P < 0.001$) and along streams (5.71 ± 5.60, $U = 87$, $n = 49$, $P < 0.001$). Nest densities of collared lemming were similar to those of brown lemmings in wet habitats ($z = 1.31$, $n = 25$, $P = 0.19$) but tended to be higher in mesic tundra ($z = 1.75$, $n = 25$, $P = 0.08$) and were much higher along streams ($z = 3.97$, $n = 24$, $P < 0.001$; Fig. 1).

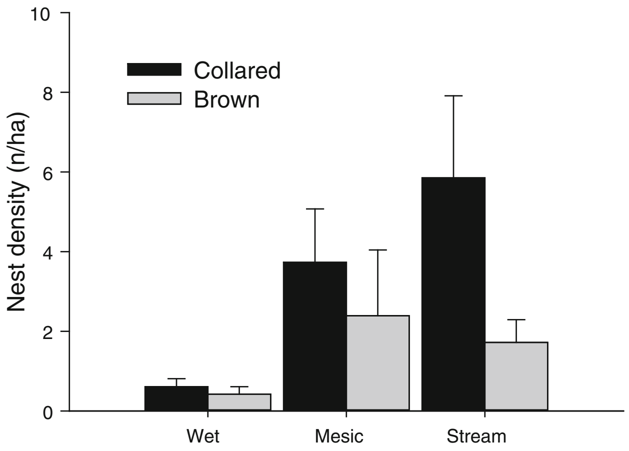

Fig. 1 Winter nest density of collared and brown lemmings in the wet, mesic tundra and stream habitat, respectively, sampled in the summer of 2007 on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada

Description of plant communities

The first three axes of the PCA explained 31% of the total variance of the original non-vascular plant cover data, which included 18 genera. On the first axis (14%), positive scores mainly discriminated the occurrence of lichen species, such as *Stereocolon fructilosa* (positive score), from that of some palatable mosses, mainly *Bryum* and *Calliergon* (negative score; palatability based on Batzli and Jung 1980). The second axis (10%) primarily distinguished the abundance of palatable mosses, such as *Polytrichum* (positive score), from the abundance of relatively unpalatable mosses, such as *Aulacomnium* and *Tomentyphnum* (negative score). On the third axis (7%), positive values principally depicted the occurrence of the relatively unpalatable *Sphagnum* and hepaticophyte species, such as *Marchantiopsida* (ESM Table A1).

For vascular plants, the first four axes explained 20% of the total variance of the original plant cover data (48 species). The first axis (7%) essentially separated forbs typical of mesic habitat (e.g. *Oxyria digyna*, *Ranunculus* sp., *Saxifraga* sp.; positive score) from deciduous shrubs (*Salix* spp.; negative score). The second axis (5%) described an index of low abundance of plants typical of wet habitats (*Carex aquatilis*, *Dupontia fisheri*, *Eriophorum scheuchzeri*). The third axis (4%) was associated with a high abundance of plants typical of drier sites, such as *Festuca brachyphylla* and *Astragalus alpinus*, and a reduced abundance of *Arctagrostis latifolia*. Finally, the fourth axis (4%) contrasted the abundance of evergreen shrubs typical of hummocky tundra (e.g. *Cassiope tetragona* or *Vaccinium uliginosum*; positive score) from other shrubs, such as *Dryas integrifolia* and *Salix reticulata* (ESM Table A2).

Lemming nest site selection

We sampled 193 winter nests (164 found along transect lines and 29 opportunistically) of which 97 were used by collared lemmings, 50 by brown lemmings and 46 by both species. Nests of both species were generally found in areas with a higher proportion of depressions, deeper depressions, steeper slopes and a deeper snow cover than the surroundings (Table 1). They also tended to be characterized by a relatively low abundance of lichens (NONVASC1), a relatively high abundance of palatable mosses (NONVASC2) and a relatively high abundance of deciduous shrubs (VASC1).

At the landscape scale, the selection of the winter nest site was generally affected by the same variables in both species, and our best models explained up to 76 and 68% (R^2) of the variability in the data for collared and brown lemmings, respectively. Micro-topography, slope and snow depth were generally the most influential variables (Table 2). The probability of encountering lemming nests increased with increasing heterogeneity of the micro-topography, slope of the terrain, and snow depth at the landscape level (Table 3, Fig. 2). The effect of snow was non-linear as its effect levelled off at depths >60 cm (Fig. 2). For the brown lemming, we also found a

Table 1 Environmental parameters measured at collared and brown lemming winter nests and at random sites at two spatial scales, namely, landscape (random-1) and local (random-2) scales (see "Materials and methods" for details) during the winter of 2006–2007 on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada

Variable	Parameter description	Random-1 (*n* = 148)	Collared lemming		Brown lemming	
			Nest (*n* = 143)	Random-2 (*n* = 572)	Nest (*n* = 96)	Random-2 (*n* = 384)
ELE	Elevation (m)	113 ± 102	158 ± 105	161 ± 107	125 ± 99	126 ± 99
MTH (1)	Micro-topography: ground depression (%)	18 ± 15	37 ± 17	22 ± 16	38 ± 18	24 ± 17
MTH (2)	Micro-topography: depression depth (cm)	10.1 ± 5.9	15.1 ± 6.8	11.5 ± 5.1	16.5 ± 8.7	12.4 ± 6.9
SDEPTH	Snow depth (cm)	39.0 ± 27.8	76.0 ± 37.8	54.4 ± 35.2	74.6 ± 42.9	52.0 ± 34.8
SINCLIN	Slope (%)	6.1 ± 2.2	18.9 ± 2.5	13.1 ± 2.5	17.4 ± 3.6	11.1 ± 3.2
EWASPECT	Aspect: E/W (1 = E/−1 = W)	0.11 ± 0.71	0.07 ± 0.71	0.02 ± 0.73	0.06 ± 0.71	−0.01 ± 0.72
NSASPECT	Aspect: N/S (1 = N/−1 = S)	0.01 ± 0.70	−0.09 ± 0.70	−0.02 ± 0.69	0.05 ± 0.70	0.02 ± 0.69
NONVASC1	Index of lichen abundance	−0.15 ± 1.85	−0.39 ± 1.34	0.18 ± 1.48	−0.57 ± 1.39	0.07 ± 1.63
NONVASC2	Index of palatable mosses abundance	−0.45 ± 1.20	0.20 ± 1.17	0.04 ± 1.34	0.35 ± 1.07	0.08 ± 1.35
NONVASC3	Index of *Sphagnum* abundance	0.34 ± 1.35	−0.12 ± 1.05	−0.09 ± 1.06	0.10 ± 0.99	−0.03 ± 1.14
VASC1	Index of forb abundance	−0.63 ± 1.41	0.23 ± 1.91	0.27 ± 1.91	0.07 ± 2.02	−0.12 ± 1.69
VASC2	Index of low abundance of wet plants	−0.31 ± 1.75	−0.16 ± 1.68	0.24 ± 1.33	−0.40 ± 2.11	−0.09 ± 1.49
VASC3	Index of dry habitat plants abundance	0.18 ± 1.24	−0.09 ± 1.31	−0.04 ± 1.44	0.16 ± 1.70	−0.09 ± 1.27

Data are presented as the mean ± standard deviation (SD) significant negative interaction between slope and snow depth, suggesting that the accumulation of deep snow was less influential in the steep slope habitat than in flat terrain (Tables 2, 3). Elevation and slope aspect did not affect nest site selection, and plant variables had a relatively weak influence on nest site selection. A high abundance of palatable bryophytes, such as *Polytrichum* (NONVASC2), positively influenced the probability of the occurrence of winter nests in both species at the landscape level (Tables 2, 3). A high abundance of lichen species (NONVASC1) negatively influenced nest site selection of brown but not collared lemmings. Finally, collared lemmings were negatively influenced by the abundance of *Sphagnum* and hepaticophytes (liverworts) (NONVASC3).

We also examined how selected habitat variables at the landscape scale varied among the three habitats. Stream habitat had the deepest snow cover, steepest slopes and lowest abundance of lichens, whereas wet tundra had the shallowest snow cover, flattest terrain, highest abundance of *Sphagnum* and lowest abundance of forbs (Table 4). Mesic tundra was generally intermediate, except for lichen (highest abundance) and *Sphagnum* (lowest abundance).

At the local scale, our best models explained up to 68 and 60% of the variability in the data for collared and brown lemmings, respectively, but fewer variables affected the probability of occurrence of lemming nests than at the landscape scale (Table 2). Heterogeneity of the microtopography was again the most influential variable in both species, but the second most important variable at this scale was lichen abundance (NONVASC1), as nest occurrence increased with a decreasing abundance of lichen and an increasing abundance of some mosses, such as *Bryum* (Tables 2, 3). Snow depth also had a positive effect on nest occurrence at this scale.

Factors affecting reproduction

We detected signs of reproduction in 38% of collared lemming nests ($n = 55$) and 9% of brown lemming nests ($n = 9$). In the 16 nests where both species were identified, reproduction was always associated with collared lemmings. Our best models explained 32 and 42% of the variation in collared and brown lemming reproduction occurrence, respectively. The probability of reproduction in collared lemming nests increased at low elevation (-0.50 ± 0.21; $\beta \pm$ SE), and we noted a weak positive effect of forbs availability (VASC1 0.38 ± 0.22; Table 2). In contrast, the probability of reproduction in brown lemming nests increased when the abundance of graminoids, such as *Arctagrostis latifolia*, was high and the abundance of plants typical of drier sites, such as *Festuca brachyphylla* and *Astragalus alpinus*, was low (VASC3 -4.71 ± 2.23; Table 2). Other habitat variables, such as snow depth and the availability of plants typical of wet habitats (VASC2), had a weak positive effect on the probability of reproduction in brown lemmings.

Factors affecting predation

We found evidence of stoat predation in nine collared lemming nests, one brown lemming nest and one nest used by both species, and six of these nests showed signs of reproduction by collared lemming. Our best model explained 44% of the variation in the data. The probability of predation by stoats increased where lemming nest density was high (1.41 ± 0.67) and when nests were used by collared lemmings (3.94 ± 1.96; Table 2). Snow depth did not affect the probability of predation by stoats as this variable did not differ between intact and depredated nests (78 ± 41 vs. 77 ± 34 cm, respectively; $t = 0.04$, $df = 20$, $P = 0.97$). We were able to measure snow depth at 21 craters dug by foxes to depredate lemmings in winter nests. Mean snow cover was deeper at intact lemming nests than at those depredated by foxes (76.6 ± 30.8 vs. 39.4 ± 18.2 cm, respectively; $U = 381$, $n = 42$, $P < 0.001$). In contrast, mean snow depth did not differ between random sites and sites where lemming nests were depredated by foxes (46.9 ± 32.5 vs. 39.4 ± 18.2 cm, respectively; $U = 230$, $n = 42$, $P = 0.82$).

Effect of subnivean temperature

The evolution of mean subnivean temperature over winter is given in Fig. 3. Mean daily temperature fluctuations recorded over the winter was lower at lemming winter nest sites than at random sites (0.96 ± 0.86 vs. 2.17 ± 1.76°C, respectively; $U = 59$, $n = 30$, $P = 0.03$). However, there was no significant difference in mean temperature between nest and random sites (-17.3 ± 3.8 vs. -20.1 ± 5.9°C, respectively; $t = 1.53$, $df = 28$, $P = 0.14$), nor in mean snow density (142 ± 51 vs. 182 ± 80 kg/m^3, respectively; $U = 80$, $n = 30$, $P = 0.18$).

The covariance matrix of the path analysis model developed to assess the effect of subnivean temperature and snow depth did not differ from the observed covariance matrix ($\chi^2 = 1.29$, $df = 1$, $P = 0.26$; all 4 goodness-of-fit tests yielded similar results). Furthermore, since the deletion of non-significant path coefficients did not affect the model fit ($\chi^2 = 0.30$, $df = 1$, $P = 0.58$), the reduced model was preferred. Our final model explained up to 35% of the total variance in nest occurrence probability and revealed that snow depth had a weak positive direct influence on the probability of nest occurrence and a strong indirect influence via an effect on subnivean thermal conditions (Fig. 4). Large subnivean temperature fluctuations

Table 2 Models explaining habitat selection and the occurrence of reproduction and predation in nests of collared and brown lemmings during the winter of 2006–2007 on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada. The best ranked models (ΔQIC < 2 and $w_i > 0.1$) are shown

Scale	Species	Variables included in the model[a]	ΔQIC	w_i
Landscape	Collared ($n = 291$)	MTH + SINCLIN + SDEPTH + SDEPTH^2 + NONVASC2 + NONVASC3 + VASC1	0.00	0.50
		MTH + (SINCLIN × SDEPTH) + SINCLIN^2 + SDEPTH2 + NONVASC2 + NONVASC3 + VASC1	0.26	0.44
	Brown ($n = 244$)	MTH + SINCLIN + NONVASC2 + NONVASC1 + SDEPTH + SDEPTH^2	0.00	0.43
		MTH + (SINCLIN × SDEPTH) + NONVASC2 + NONVASC1	0.06	0.41
Local	Collared ($n = 286$)	MTH + NONVASC1 + SDEPTH + VASC2	0.00	0.50
		MTH + NONVASC1 + SDEPTH + SDEPTH^2 + VASC2	1.18	0.28
		MTH + (NONVASC1 × VASC2) + SDEPTH	1.96	0.19
	Brown ($n = 192$)	MTH + NONVASC1 + SDEPTH	0.00	0.27
		MTH + NONVASC1 + SDEPTH + ELE	0.63	0.19
		MTH + NONVASC1 + SDEPTH + SDEPTH^2	1.11	0.15
		MTH + NONVASC1 + SDEPTH + NONVASC2	1.24	0.14
		MTH + NONVASC1 + SDEPTH + NONVASC2 + ELE	1.88	0.10
Reproduction	Collared ($n = 143$)	ELE + ELE^2 + VASC1	0.00	0.17
		ELE + VASC1	0.32	0.14
		ELE + VASC1 + NONVASC3	0.43	0.14
		ELE + SINCLIN	0.82	0.11
		ELE + VASC1 + SINCLIN	0.88	0.11
		ELE + NONVASC3 + SINCLIN	0.93	0.11
		ELE + VASC1 + NONVASC3 + SINCLIN	1.12	0.10
		ELE + NONVASC3	1.62	0.07
	Brown ($n = 50$)	VASC3 + VASC2 + SDEPTH	0.00	0.41
		VASC3 + VASC2 + SDEPTH + SDEPTH^2	1.24	0.22
		VASC3 + VASC2 + SDEPTH + NONVASC3	1.54	0.19
Predation	Collared/brown ($n = 22$)	DENSITY + SP	0.00	0.30
		DENSITY + SP + REPRO	1.52	0.14

QIC, Quasi-likelihood information criterion, w_i, model weight

Variables within each model are presented in decreasing order of importance based on the sum of the model weight (w_i) in which they appear

[a] DENSITY, Nest density (*n*/ha); SP, species (1, collared); REPRO, occurrence of reproduction. See Table 1 for definition of other variables

Table 3 Model averaged coefficient (β) estimates with unconditional standard error of significant variables in habitat selection models for collared and brown lemmings during the winter of 2006–2007 on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada

Variable	Collared lemming				Brown lemming			
	Landscape scale		Local scale		Landscape scale		Local scale	
	β	SE	β	SE	β	SE	β	SE
MTH	1.24	0.22	1.74	0.22	1.17	0.21	1.11	0.21
SINCLIN	0.86	0.26			0.53	0.22		
SDEPTH	1.32	0.26	0.50	0.15	1.00	0.27	0.44	0.17
SDEPTH^2	−0.48	0.13			−0.38	0.11		
SDEPTH × SINCLIN					−0.50	0.16		
NONVASC1			−0.95	0.22	−0.42	0.17	−1.03	0.23
NONVASC2	0.74	0.21			0.73	0.23		
NONVASC3	−0.39	0.17						
VASC1	−0.33	0.24						
VASC2			−0.54	0.18				

See Table 1 for definition of variables

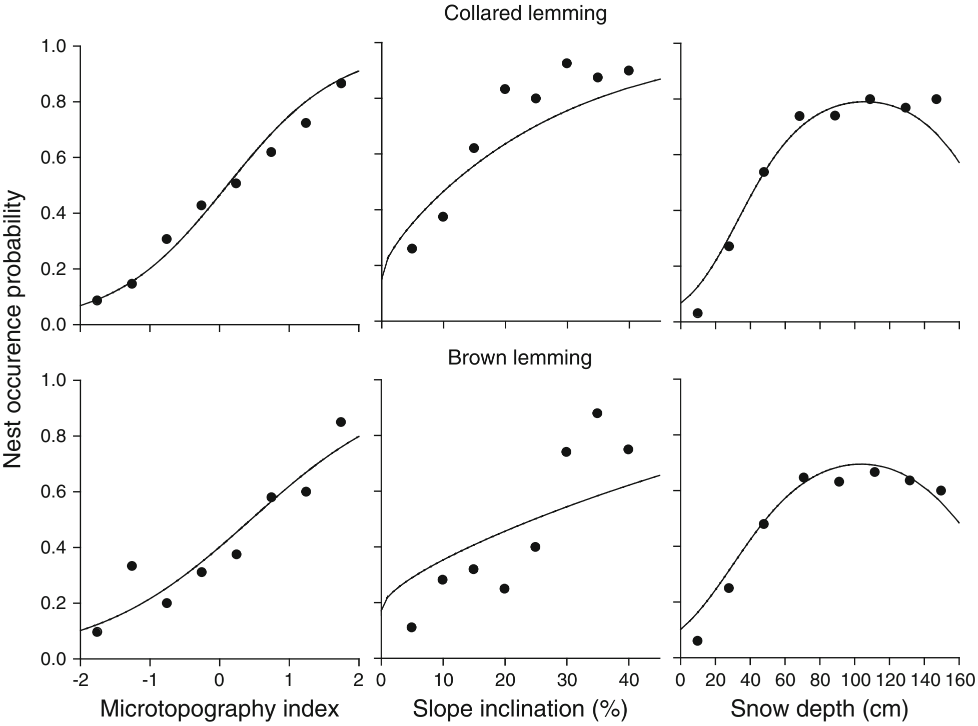

Fig. 2 Occurrence probability of collared and brown lemming winter nests in relation to micro-topography, slope and snow depth during the winter of 2006–2007 at the landscape level on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada. *Line* Prediction from the best model (Table 2) while controlling for other effects, *filled circles* observed values. Even though analyses were performed on individual data points (see "Materials and methods"), for sake of clarity the mean probability of nest occurrence observed for eight evenly spaced bins along the *x*-axis is presented for each variable

had a negative effect on lemming nest occurrence but a deeper snow cover decreased these fluctuations.

Discussion

The results of this study demonstrate that lemmings are highly selective in their use of winter habitat. We found that winter nest density varied considerably among habitats and that several abiotic and biotic factors explained their habitat selection at both the landscape and local scales. We also found strong support for the hypotheses that wintering lemmings prefer areas with heterogeneous micro-topography and deeper snow, in part because these areas provide a more favourable micro-climate. In comparison, food availability played a relatively minor role in wintering site selection, although it appeared to be more important in determining whether lemmings would reproduce at a site or not. As expected, snow depth did not affect the probability of predation by stoats, but deeper snow did appear to limit

Table 4 Comparison of habitat variables between wet tundra ($n = 50$), mesic tundra ($n = 50$) and mesic stream habitats ($n = 48$) on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada

Variable	Wet	Mesic	Stream	K–W χ^2	*P*
Index of heterogeneity in micro-topography	−0.62 ± 1.34a	−0.53 ± 1.02a	−0.41 ± 1.04a	0.9	0.64
Slope inclination (%)	12 ± 6a	28 ± 12b	35 ± 16b	75.0	<0.001
Snow depth (cm)	25.9 ± 11.4a	32.2 ± 19.3a	60.0 ± 34.8b	39.0	<0.001
Index of lichen abundance (NONVASC1)	−0.30 ± 2.09a	1.06 ± 1.35b	−1.19 ± 1.23a	39.7	<0.001
Index of palatable mosses abundance (NONVASC2)	−0.26 ± 1.12a	−0.51 ± 1.26a	−0.61 ± 1.24a	2.8	0.24
Index of *Sphagnum* abundance (NONVASC3)	1.00 ± 1.53a	−0.20 ± 1.15b	0.16 ± 0.98b	19.7	<0.001
Index of forb abundance (VASC1)	−1.52 ± 0.62a	−0.18 ± 1.29b	−0.11 ± 1.66b	39.1	<0.001

Data are presented as the mean ± standard error. Variables are compared using Kruskal–Wallis (K–W) test. Means followed by the same lowercase letter do not differ significantly

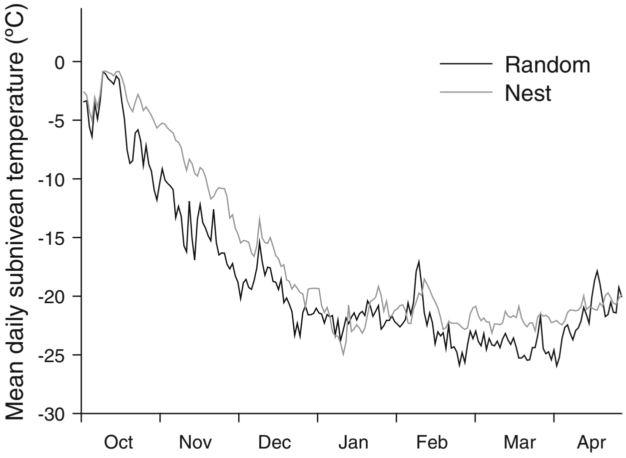

Fig. 3 Changes in the mean subnivean temperature at random sites and lemming winter nest sites during the winter of 2007–2008 on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada ($n = 15$ loggers for each treatment)

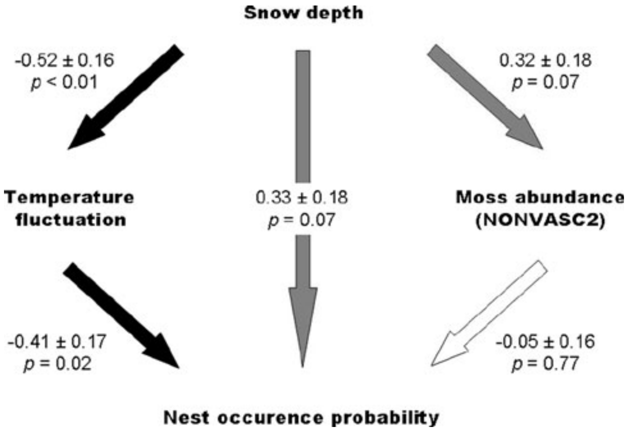

Fig. 4 Path diagram showing the direct and indirect effect of snow depth on the probability of occurrence of collared and brown lemming winter nests during the winter of 2006–2007 on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada. Path coefficient estimates, SE and *P* values are given for each tested path. *Black arrows* Significant paths, *white arrows* non-significant paths, *grey arrows* paths approaching significance. $n = 30$

arctic foxes attempting to prey on lemmings in winter nests.

Winter nest site selection

At all spatial scales, the heterogeneity of micro-topography emerges as the most important factor determining winter habitat selection of both lemming species. Previous studies have also shown that lemmings prefer sites with a rugged micro-topography, such as hummocky areas during the summer, possibly because such micro-topography provides protection against predators (Morris et al. 2000; Predavec and Krebs 2000). However, a rugged micro-topography and its associated ground depressions probably act differently during the winter. We suggest that it increases the probability of subnivean air space formation by affecting the pattern of snow drift at a small scale and increasing contact surface area at the ground–air interface (Marchand 1996). In addition, a rugged micro-topography could provide a refuge against subnivean flooding during rainy events. Accessibility to food provided by a good subnivean space is essential for overwintering small mammals in the tundra (Korslund and Steen 2006). Therefore, factors enhancing the formation of this air space are probably an essential component of the habitat selection process of overwintering lemmings. Although measuring the characteristics of this micro-habitat directly is difficult, future investigations should aim at documenting the effective distribution of the subnivean space.

At both spatial scales, snow depth was fairly important in explaining the winter habitat selection of lemmings, although less so in brown lemmings at the landscape scale. This effect was non-linear: lemmings strongly avoided areas with little snow, but the effect levelled off at approximately >60 cm of snow. The path analysis showed that the preference for areas with deeper snow is mainly explained by the more favourable subnivean thermal conditions encountered there. Our results thus confirm the previously assumed role of thermal protection offered by snow cover and corroborate previous observations of an association between lemming winter nests and deep or persistent snow cover (MacLean et al. 1974; Fuller et al. 1975; Reid and Krebs 1996). Although average temperature tended to be higher at winter nest sites than at random sites, the daily temperature fluctuations were notably reduced by deep snow cover, suggesting that snow cover may be the most important feature to wintering lemmings. This result shows that thermal protection is a critical aspect of habitat selection in wintering lemmings, presumably as a means to reduce their energetic requirement, as suggested by Chappell (1980).

Results from previous studies suggest that the distribution of preferred food is a major factor affecting lemming habitat selection (Batzli et al. 1983). Although we found that lemmings showed a preference for areas characterized by the presence of some moss species at the landscape scale, abiotic factors were clearly more important than plants in the selection process at this scale. At the local scale, however, food availability played a more important role in the habitat selection process, along with microtopography. At this scale, both lemming species preferred areas with a low abundance of lichens and a high abundance of a number of palatable mosses (e.g. *Bryum*). Collared and brown lemmings have been found to consume a greater proportion of mosses during the winter than during the summer (Rodgers and Lewis 1986; Batzli and Pitelka 1983). Although mosses have a low digestibility and occasionally a high content of phenolic compounds (Batzli and Cole 1979; Barkley et al. 1980), they are also rich in multiunsaturated fatty acids, such as arachidonic acid, which increases heat production and may help animals to survive in cold climates (Prins 1981). Overall, vascular plants had relatively weak effects on the habitat selection of both lemming species in winter.

Our observations of a higher density of lemming winter nests in the mesic tundra and associated streams than in the wet tundra are in agreement with the findings of other studies (Fuller et al. 1975; Batzli et al. 1983). Even brown lemmings, which prefer wet tundra in the summer, often perform local migrations to mesic habitat in the winter (Rodgers and Lewis 1986). The abiotic habitat variables selected by lemmings at the landscape scale can explain some of the differences in nest density observed among our three habitats. Indeed, some habitat variables preferred by lemmings, such as snow depth and slope, had their lowest values in wet tundra, intermediate values in the mesic tundra and highest values along streams. The apparent preference of wintering lemmings for steep slopes may be an indirect effect of habitat configuration in our study area. In contrast to the relatively flat wet tundra, the steep slopes of gullies associated with streams may enhance the formation of deep snow drifts, which would be favourable to wintering lemmings and thus account for the high ranking of this variable in our analysis.

Factors affecting winter reproduction

The results of our study confirm that both lemming species can reproduce under the snow in winter (MacLean et al. 1974; Krebs et al. 1995; Reid and Krebs 1996; Millar 2001) and reveal that reproductive activity was higher in collared than in brown lemmings during the 2007–2008 winter at our study site. Although some habitat variables were associated with the occurrence of reproduction, these variables differed among the two species and, globally, our models explained a relatively small proportion of the variation, which is in contrast to models explaining nest site selection. In collared lemmings, the greater occurrence of reproduction in nests at low elevation is somewhat difficult to explain. A possible explanation is that low elevation sites may benefit from a more favourable microclimate (less exposure to wind). Even though forbs are an important component of the diet of collared lemmings (Batzli and Pitelka 1983), availability of palatable forage apparently played a minor role in explaining the occurrence of reproduction in this species. In contrast, the occurrence of reproduction in brown lemmings was mostly explained by the presence of a number of monocotyledons, especially *Arctagrostis latifolia*. Interestingly, Negus and Berger (1998) showed that the presence of plant metabolites in soloniferous graminoids triggered the initiation of reproduction in brown lemmings—but not in collared lemming—thereby possibly explaining why the availability of palatable forage in our study was a relatively good predictor of the occurrence of reproduction in the former species but not in the latter.

Factors affecting predation

We found evidence that stoat predation on lemming nests was density-dependent. In Greenland, Sittler (1995) reported an aggregated pattern of lemming nest occupancy by the stoat that is consistent with density-dependent predation. We showed that lemmings are highly selective in the location of their nests, which should lead to the concentration of nests in the best habitat patches. Therefore, stoats finding one lemming nest should increase their search effort in the area as the likelihood of finding other nests is probably high. Such area-restricted searches are common in predator–prey systems (Sarnelle and Wilson 2008), especially when prey distribution is aggregated, like that of the lemmings in our area. This would be analogous to a Type III functional response at low prey density (Holling 1959) and may explain the density-dependent predation pattern observed. Furthermore, we could have underestimated the intensity of this density dependence because we could not detect predation events where stoats removed lemmings from nests without leaving any fur or bones. We also found that collared lemmings were more exposed than brown lemmings to stoat predation. Sittler (1995) reported that most lemming nests predated by stoats showed evidence of reproductive activity by lemmings, suggesting that these nests may be more vulnerable to predation. In our study, the occurrence of reproduction was higher in collared than in brown lemming nests, but we found weak evidence that nests with reproduction were more likely to be predated. We argue that stoats may show a preference for one lemming species over the other, although evidence to support this hypothesis is still weak.

Our results support previous suggestions (e.g. Fitzgerald 1977; Reid and Krebs 1996; Gilg et al. 2006) that predation pressure by subnivean specialist predators, such as the stoat, is unaffected by the depth of the snow cover in winter. In contrast, we found that predation attempts by arctic foxes on lemming nests are, at least in part, limited by deep snow, as previously suggested (Hansson and Henttonen 1985; Lindstrom and Hornfeldt 1994). Therefore, deep snow cover may provide a refuge to overwintering lemmings against at least some winter predators. Protection offered by snow cover alters the effective winter predator community and may be involved in the latitudinal cyclicity gradient observed in the dynamics of small mammal populations in Europe and Japan (Stenseth 1999).

Snow cover and lemming populations

The results of our study underline the role of snow cover as a determinant of the spatial structure of some wintering northern small mammal populations. There is increasing evidence that the winter dynamics of these populations may be dominated by the effect of stochastic climatic events on snow conditions (Ims et al. 2008). Previous studies suggested that freezing rain and frost/thaw events should reduce small mammal winter survival both directly and indirectly (Reid and Krebs 1996). Directly, such climatic events reduce the thermal protection offered by snow cover, fragment the subnivean space through the formation of an ice crust, and can induce water flooding. These phenomena may greatly reduce the probability of individuals surviving the entire winter by increasing thermal stress and reducing food availability, and possibly by the drowning of animals during floods (Korslund and Steen 2006). Indirectly, mild weather during the winter may reduce the protection offered by snow cover against some generalist predators, such as arctic foxes (Lindstrom and Hornfeldt 1994) and increase the competition among predators for lemmings during the winter (Hansson and Henttonen 1985; Hanski et al. 1991). Therefore, alterations of winter climatic conditions brought by the current global warming could reduce small mammal winter survival and destabilize their cyclic population dynamics, which would affect the whole tundra ecosystem.

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