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Effect of snow cover on the vulnerability of lemmings to mammalian predators in the Canadian Arctic

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In the Arctic tundra, snow is believed to protect lemmings from mammalian predators during winter. We hypothesized that snow quality (depth and hardness) should affect mammalian predation rates on lemmings, but that this effect would depend on the predator hunting strategy; and that predation by ermines (*Mustela erminea*), which can hunt lemmings under the snow, should be higher in preferred lemming habitats. We measured snow depth and hardness at tunnels made by arctic fox (*Vulpes lagopus*) predation attempts, at winter nests nonpredated and predated by ermines, and at random locations. We also determined winter nest density in 3 habitats (wet, mesic, and gully). Deep and hard snow restricted fox predation attempts made by jumping through the snow, but not those made by digging. Ermine predation was unaffected by snow depth and weakly by nest density but was higher in gully and intermediate in mesic habitats, which are conducive to high snow accumulation, compared to the wet habitat. These results indicate that habitat-related topographical features are more important than snow depth or nest density per se in affecting the winter foraging strategy of ermines. Overall, even though we found a relatively weak effect of the snow cover on predation by foxes and ermines, it is difficult to predict how upcoming changes to the snow cover will affect lemming vulnerability to mammalian predators because a wide range of snow conditions may result from climate warming.

Key words: arctic fox, ermine, predation, small mammals, snow depth, snow hardness

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In the Arctic, populations of small mammals, particulary rodents, can support a large diversity of avian and mammalian predators during the short summer (Korpimäki et al. 2005; Gilg et al. 2006; Gauthier et al. 2011). These rodents, particularly lemmings (*Dicrostonyx* and *Lemmus* spp.), are well known for their multiannual, high-amplitude population cycles (Krebs et al. 2002; Pitelka and Batzli 2007; Gruyer et al. 2008) and several studies have suggested that predation may play a role in controlling these cycles (Korpimäki and Krebs 1996; Reid et al. 1997; Angerbjörn et al. 1999; Hanski et al. 2001; Gilg et al. 2003; Legagneux et al. 2012). However, when a stable snow cover becomes established, avian predators, which represent a large proportion of the predator guild, leave the area (Gilg et al. 2006; Gauthier et al. 2011) and only mammalian predators, primarily foxes and small mustelids, remain to prey on lemmings. Although many studies have examined the interaction between lemmings and their predators during the summer (e.g., Angerbjörn et al. 1999; Wilson et al. 1999; Gilg et al. 2006), very little is known about these interactions during the long Arctic winter (up to 8 months) when snow cover is present.

Lemmings remain active under the snow throughout the winter and build winter nests made of vegetation, which they use to insulate themselves from cold temperatures (Chappell 1980; Casey 1981) and to reproduce (MacLean et al. 1974; Sittler 1995; Duchesne et al. 2011b). During winter, the snow cover over much of the wind-swept Canadian tundra is relatively thin (30–50 cm) and hard packed (McKay and Gray 1981; Pomeroy and Brun 2001; Natural Resources Canada 2010), except in areas where topographical features such as the leeside of slopes or banks promote the formation of snow drifts. Lemmings show a preference to build their nests in areas of deep snow accumulation, which provide a better insulation from the cold Arctic air (Sittler 1995; Duchesne et al. 2011b; Reid et al. 2012).

A deep snow cover has the potential to hinder predation by foxes (Hansson and Henttonen 1985; Lindstrom and Hornfeldt 1994; Gilg et al. 2006) because, to catch lemmings, they must pound through the snow or dig out their winter nests once they have detected them. However, snow depth is less likely to affect predation by small mustelids because they can hunt lemmings directly in their tunnels under the snow (Sittler 1995). Moreover, ermines (*Mustela erminea*) are known to concentrate their hunting effort in areas of high small mammal densities (Klemola et al. 1999; Hellstedt and Henttonen 2006; King and Powell 2007), and thus deep snow areas could potentially attract those predators if lemmings aggregate there. However, other factors such as snow density or hardness also have the potential to affect vulnerability of lemmings to predation during winter. As temperatures are rising, snow regimes in the Arctic are changing and episodes of winter rain or thaw–frost events are becoming more frequent (SWIPA 2011). Such conditions could contribute to hardening the snow cover and thus make it more difficult for predators to access lemmings under the snow.

With this perspective in mind, we hypothesised that a deep and hard snow cover should affect lemming predation rate by mammalian predators but that this effect should depend on their hunting strategy. We predicted that a deep and hard snow cover should hinder predation by the arctic fox (*Vulpes lagopus*) because it must forage on top of the snow, but that it should have little effect on predation by the ermine, which can forage under the snow. Because lemmings preferred habitats are conducive to high snow accumulation and densities of winter nests are generally high in such habitats (Duchesne et al. 2011b; Reid et al. 2012), we also tested the hypotheses that predation by ermines should be highest in preferred lemming habitats and in areas of high lemming density.

Materials and Methods

Study area.—The study was conducted on the south plain of Bylot Island, Sirmilik National Park, Nunavut, Canada (73°08′N, 80°00′W). The main study area (70 km^2) consists of tundra polygons, thaw lakes and ponds forming wetlands in parts of the valley bottom, and drier mesic habitat in the upland areas and nearby slopes and hills (see Duchesne et al. [2011b] and Bilodeau et al. [2012a] for details). Small, intermittent streams running through upland areas are often located at the bottom of small gullies where vegetation along the stream edge is similar to that of wetland habitat. We considered this habitat (gully) as a 3rd habitat category because it is conducive to high snow accumulation and can be heavily used by lemmings in winter (Duchesne at al. 2011b). Only 2 species of rodents are present, the brown lemming (*Lemmus trimucronatus*) and the collared lemming (*Dicrostonyx groenlandicus*); the former species is more abundant, especially in peak years (Gruyer et al. 2010). Arctic foxes and ermines are present throughout the winter on Bylot Island. Average fox density is approximately 0.1 individual/km^2 on the south plain of Bylot, where up to 25 pairs may breed in a good lemming year (Legagneux et al. 2012).

Average air temperature at our study site from October to June is –23.4°C ± 0.4°C *SE* and average temperature under the snow, where lemmings live in winter, is –15.8°C ± 0.4°C (Bilodeau et al. 2012a). A permanent snow cover is usually established in late September and melting occurs in mid-June. Maximum snow depth typically occurs in May and average snow depth at the end of the winter is 33.8 cm ± 2.5 *SE* (Bilodeau et al. 2012a), although snow can be as much as 2 m deep in areas conductive to high snow accumulation (e.g., gullies). The snowpack is very dry because of the very cold temperature prevailing during the winter.

Fox hunting behavior.—We sampled fox predation events over a 980-ha area from 19 May to 2 June 2010 and over a 240-ha area from 17 to 26 May 2011. Fresh fox tracks were found opportunistically while travelling on foot or on snowmobile through the study area. When encountered, the tracks were backtracked to find signs of predation attempts on lemmings. Tunnels in the snowpack that were going straight down to the subnivean space and that were about the size of a fox body were considered to be predation attempts. These tunnels were easy to distinguish from other holes, such as those made by foxes to locate a den, which were associated with characteristic topographical features (Szor et al. 2008). We could recognize 2 hunting techniques used by foxes. The 1st one involved digging into the snow, as evidenced by digging marks, a small pile of snow near the tunnel entrance, and the rough edges of these entrances. The attempts were primarily directed at lemming nests because nest remains were always found at the bottom of these holes. The 2nd type of tunnel was narrower with no digging marks and often no signs of lemming nests at their bottom. No obvious pile of snow appeared near the tunnel entrance, which had rather smooth edges. Observations of foxes at distance confirmed that these occurred when immobile foxes listened intensely before jumping and pounding through the snow cover, most likely to catch a lemming that they heard moving under the snow. After classifying each type of tunnel encountered (dig or jump), snow depth and hardness were measured at the site (see details below).

Ermine predation.—We sampled ermine winter predation annually from 2007 to 2011 by sampling lemming winter nests across the entire study area shortly after snowmelt. We used 500-m transects randomly distributed among our 3 habitats (wet, mesic, and gully habitats; 25, 10, and 20 transects per habitat in 2007, 2008, and 2009–2011, respectively). All winter nests found while walking along the transect line were removed and their position and perpendicular distance to the transect were noted. Nests found opportunistically, away from transects, also were collected and used for the determination of ermine predation rate.

All winter nests were dissected in the laboratory to determine whether they were used by brown or collared lemmings. We based species identification on the length, form, and color of feces found in nests (MacLean et al. 1974; Duchesne et al. 2011a). Collared lemmings have 4- to 6-mm-long, dark reddish feces, whereas brown lemmings produce 6- to 10-mm-long, green-brown feces. Lemmings reproduce under the snow in their winter nests (Stenseth and Ims 1993; Millar 2001). We determined if reproduction (defined as the production of weaned young) had occurred based on the presence of small juvenile feces in nests (Duchesne et al. 2011a). We also examined nests for signs of ermine predation. When ermines prey on lemmings, they often line the nest with their prey's fur and use the nest themselves, or they leave rodent body parts and partially eaten carcasses in the nest (MacLean et al. 1974; Sittler 1995). Fur lining and lemming body parts were thus used as evidence of predation.

Snow measurements.—We measured snow depth with a graduated rod and snow hardness with a custom-made penetrometer (McClung and Schaerer 2006). The penetrometer was a conical-shaped object of dimensions similar to a fox head and about the same mass as an adult fox (3 kg—Audet et al. 2002). The penetrometer was dropped from 60 cm above the snow and we noted how deep it penetrated the snow. Recorded depths of penetration were always < 30 cm. For ease of interpretation, we express snow hardness as $30 -$ penetration depth (highest values represent hardest snow).

Depth and hardness measurements were done at 85 locations where we had found a lemming winter nest in the previous year in 2010 ($n = 81$ in 2011), as well as at 93 random locations in 2010 and 90 in 2011. These measurements were taken during the same period as those taken at the fox tunnels, before any significant snowmelt had occurred. There was negligible precipitation during the measurement periods and average air temperature during this period was –8.8°C ± 1.4°C. Measurements could not be taken at nest locations of the current year because nests can only be found after snowmelt. To verify if areas of deep accumulation were consistent between years, we selected 30 random locations where snow depth was sampled in 2010 and 2011. Snow depth at these locations was highly correlated between years ($r = 0.76$, $t_{28} = 6.15$, $P < 0.001$).

Snow depth at winter nests where predation by ermines had been detected was estimated in the following spring using the same procedure as described above. The hardness of snow covering nests predated by ermines could not be estimated because it is unlikely to be consistent between years. Indeed, snow hardness can be affected by multiple climatic factors such as snowfall, air temperature, wind erosion, and deposition (Pielmeier and Schneebeli 2002), which vary annually.

Lemming nest density.—We estimated nest density on each transect to obtain a local index of lemming density in the area of the transect. Nest density was based on all nests found within 10 m on either side of the transect. This distance corresponds to the effective detection distance for sampling winter nests in this area (Duchesne et al. 2011b). We estimated nest density by dividing the number of nests found by the 1-ha (500 × 20-m) transect area. Nests found opportunistically, away from transects, were not used to estimate nest densities. Based on the overall abundance of winter nests (Table 1) and livetrapping conducted during the summer (see Bilodeau et al. 2012b), lemming abundance (±*SE*), was high in 2008, 2010, and 2011 (3.8 ± 0.8, 4.7 ± 0.5, and 8.0 ± 0.9 lemmings/ha respectively), intermediate to low in 2007 (0.3 ± 0.1 lemmings/ha), and very low in 2009 (0.2 lemmings/ha).

Statistical analyses.—To test if snow depth and hardness had an impact on digging and jumping predation attempts by foxes, we compared depth and hardness measurements at tunnels made by foxes, at nonpredated winter nest locations, and at random locations using analysis of variance (ANOVA; separate analyses for digs and jumps). To test if snow depth had an effect on predation by ermines, we compared snow depth at predated nest sites, nonpredated nest sites, and random locations also using an ANOVA. Interaction between year (2010–2011 for fox and 2007–2011 for ermine) and treatment (predated, nonpredated, and random) was always tested. When our treatment was significant, we used Tukey's test to compare individual means (or least square means [LSM] when there was a significant interaction).

To test the hypotheses that predation by ermines was greater in habitats preferred by lemmings in winter and in areas of high nest density, we used a logistic regression to determine if the presence or absence of predation on a nest varied according to year (2007–2011), habitat (wet, mesic, or gully), average nest density along the transect, and presence or absence of reproduction and species (brown lemming, collared lemming, or both). Two-way interactions among habitat, year, density, reproduction, and species were examined. We determined the most important variables using Akaike's information criterion adjusted for small sample size (AIC_c) and AIC_c weight (Burnham and Anderson 2002). We used model averaging to calculate the slope parameter and associated error of the most influential variables. Because there were 9 times fewer predated than nonpredated nests, we verified if this could bias our results by conducting a 2nd analysis where we reduced (through random subsampling) the number of nonpredated nests to that of the predated ones. Because of the small resulting sample size, we repeated the subsampling and associated analysis 10 times. We then calculated the average cumulative AIC_c weight of each variable across the 10 analyses. Because the analysis based on subsampling did not change our results, we only report those analyses based on the full samples. Analyses were conducted in R 2.13.1 (R Development Core Team 2010).

RESULTS

Effects of snow cover on fox hunting behavior.—We found 56 fox tunnels in 2010 (47 digs and 9 jumps) but only 9 in 2011 (all digs). Snow depth varied significantly among treatments for digs ($F_{2,385} = 5.73$, $P = 0.004$). Lemming winter nests (whether predated or not) had a deeper snow cover than random locations ($P < 0.001$), but snow depth did not differ according to whether nests had been predated or not ($P = 0.988$; Fig. 1) and this was consistent across years ($F_{2,385} =$

TABLE 1.—Proportion of transects with lemming (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus*) winter nests and average density in transect areas where winter nests were found, Bylot Island, Nunavut, Canada. 2007: $n = 25$ transects/habitat; 2008: $n = 10$ transects/habitat; 2009–2011: $n = 20$ transects/habitat.

	Year	Wet	Mesic	Gully
Proportion of transects with winter nests	2007	0.36	0.72	0.84
	2008	0.70	0.90	0.90
	2009	0.15	0.15	0.10
	2010	0.40	0.90	1.00
	2011	0.65	1.00	1.00
Average nest density (nests/ha ± *SE*) in transects with presence of winter nests	2007	2.17 ± 0.35	3.22 ± 0.42	4.20 ± 0.80
	2008	2.86 ± 0.55	6.33 ± 1.08	4.44 ± 0.80
	2009	0.90 ± 0.13	1.00	1.44 ± 0.56
	2010	2.08 ± 0.38	4.34 ± 0.85	5.84 ± 1.13
	2011	2.76 ± 0.50	5.24 ± 0.62	8.40 ± 0.83

0.74, $P = 0.480$). Snow depth also varied significantly among treatments for jumps in 2010 ($F_{2,184} = 14.84$, $P < 0.001$) but this time snow was shallower at predated than at nonpredated nests ($P < 0.001$; Fig. 1).

Snow was harder in 2011 than in 2010 (random locations, 2010: LSM = 5.17 [3.65–6.69, 95% confidence interval]; 2011: LSM = 11.08 [9.55–12.61]) and we detected a significant treatment × year interaction for the effect of snow hardness on digs ($F_{2,385} = 5.88$, $P = 0.003$; Fig. 2). In 2010, snow hardness at predated nests (LSM = 8.58 [6.81–10.35]) did not differ from that at nonpredated nests (LSM = 7.73 [6.53–8.93]), but all nests were under harder snow than random locations (LSM = 5.17 [4.03–6.32]; Fig. 2). In 2011, hardness tended to be lower at predated than at nonpredated nests but the difference was not quite significant (LSM = 4.89 [–1.13–10.91] versus 10.48 [8.46–12.49], respectively; Fig. 2). Snow hardness also varied significantly between jumps, nonpredated nests, and random locations ($F_{2,180} = 6.15$, $P = 0.003$). Lemming winter nests had a harder snow cover than random locations ($P = 0.004$) but snow hardness at jumps did not differ from that at nonpredated nest locations ($P = 0.850$; Fig. 2)

Effects of snow cover on predation by ermines.—The proportion of transects with winter nests was higher in both mesic and gully habitats than in wet habitat ($\chi^2_2 = 10.8$, $P = 0.004$) and the density of nests was generally highest in gully habitat, intermediate in mesic, and lowest in wet habitat ($F_{2,8} = 6.33$, $P = 0.022$; Table 1). On all transects sampled from 2007 to 2011, 886 winter nests were found and 33 (3.7%) of them were predated by ermines. Snow depth varied significantly among treatments ($F_{2,360} = 5.55$, $P = 0.004$) because lemming winter nests had a deeper snow cover than random locations ($P < 0.001$; Fig. 1) but snow depth at nests predated by ermines did not differ from nonpredated ones ($P = 0.330$) and this was consistent across years ($F_{2,360} = 1.70$, $P = 0.185$).

Other determinants of predation by ermines.—The probability of predation by ermines was most influenced by lemming species, year, and habitat (cumulative AIC_c weight = 0.95, 0.93, and 0.91, respectively), and to a lesser extent by nest density (cumulative AIC_c weight = 0.68; Table 2). Reproduction and 2-way interactions among variables had little or no influence (cumulative AIC_c weight < 0.33). Probability of predation was higher on collared lemmings than on brown lemmings (collared: $\beta = 1.19 \pm 0.42$ *SE*; brown was the

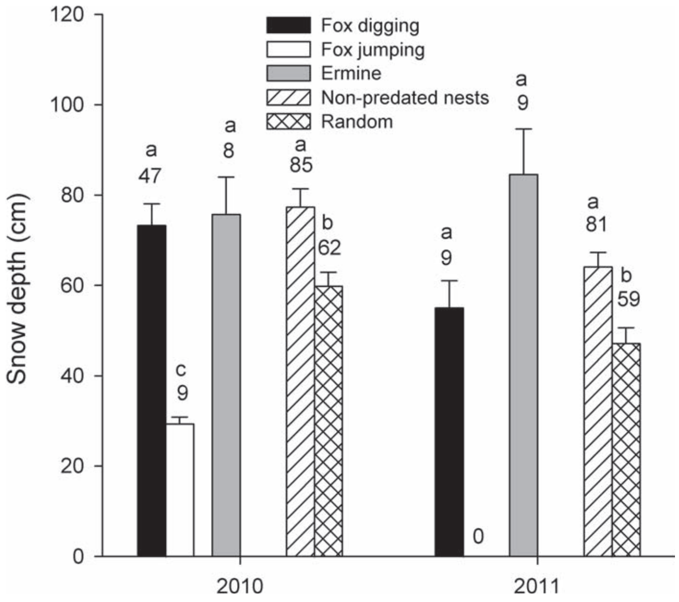

FIG. 1.—Snow depth measured at tunnels where foxes (*Vulpes lagopus*) made predation attempts on lemmings by digging or jumping, at lemming nests predated by ermines (*Mustela erminea*), at nonpredated nests, and at random locations, Bylot Island, Nunavut, Canada. Error bars represent *SE* and *n* values are shown above bars. Bars with the same letter are not significantly different ($P > 0.05$).

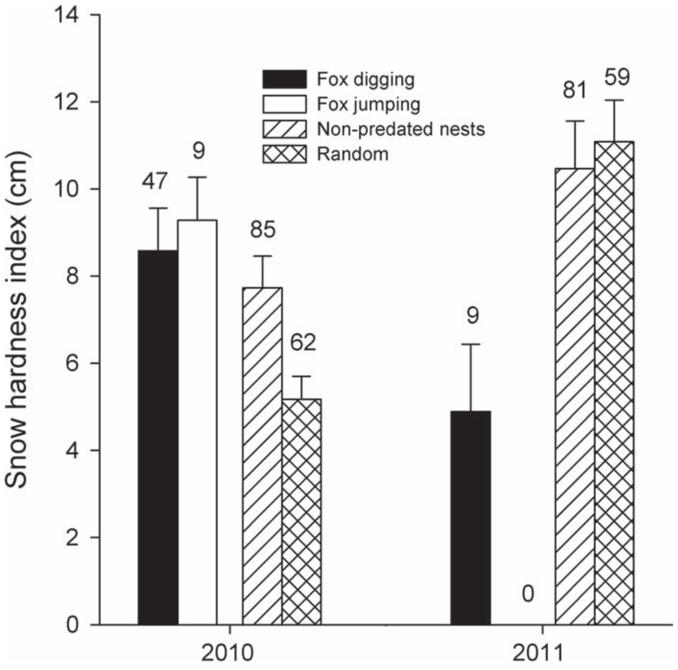

FIG. 2.—Snow hardness index measured at tunnels where foxes (*Vulpes lagopus*) made predation attempts by digging or jumping, at nonpredated lemming nests, and at random locations, Bylot Island, Nunavut, Canada. Error bars represent *SE* and *n* values are shown above bars.

TABLE 2.—Models explaining occurrence of lemming (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus*) winter nest occupancy by ermines (*Mustela erminea*) during winters 2006–2007 to 2010–2011, Bylot Island, Nunavut, Canada. ΔAIC_c: difference in Akaike's information criterion adjusted for small sample size between the current and the top-ranked model; *k*: number of parameters; w_i: model weight.

Rank	Variables in the model[a]	ΔAIC_c	w_i	*k*
1	Dens + Hab + Sp + Yr	0	0.28	7
2	Dens + Hab + Repro + Sp + Yr	0.18	0.25	8
3	Hab+ Sp + Yr	0.63	0.20	6
4	Sp + Yr	3.02	0.06	4
5	Hab + Sp + (Dens × Yr)	3.73	0.04	8
6	Hab + Repro + Sp + (Dens × Yr)	4.06	0.04	9
7	Dens + Hab + Sp	4.81	0.02	6
8	Dens + Hab + Repro + Yr	5.40	0.02	6
9	Hab + Sp	5.53	0.02	5
10	Sp	5.61	0.02	3

[a] Dens: winter nest density (nests/ha); Hab: habitat (gully, mesic, or wet); Repro: reproduction (1); Sp: species (both, brown, or collared); Yr: year (2006–2007 to 2010–2011).

reference species). Predation also varied among years and was generally highest in 2008 but rather similar in other years. Predation was higher in gully than in wet habitat and intermediate in mesic habitat (gully: $\beta = 1.58 \pm 0.92$; mesic: $\beta = 0.95 \pm 0.92$; wet was the reference habitat). Finally, probability of predation tended to decrease with increasing nest density ($\beta = -0.19 \pm 0.21$).

DISCUSSION

Fox hunting behavior.—We expected that deep snow should hinder predation attempts by foxes on lemmings but we found that this was only partially true and dependent upon the hunting tactic. Only predation attempts made by jumping were limited to sites with a shallow snow cover. Similar results were reported at Wrangel Island, Russia (Ovsyanikov 1993), although maximum snow depths at which foxes could pound through the snow appeared to be limited at 15 cm, perhaps because snow is harder at this site. Obviously, there is a physical limit at which foxes can pound through snow, and in this regard it is surprising that snow hardness did not seem to affect this hunting technique at Bylot Island. However, this was based on only 1 year when the snowpack was relatively soft, and we had a small sample size. Nonetheless, it is possible that foxes are forced to hunt rodents under hard snow because of the preference of lemmings for such sites. Indeed soft, upper snow layers may not provide adequate conditions for a stable subnivean space, where lemmings are active in winter, because a soft snowpack is more susceptible to compression (Sanecki et al. 2006).

Despite the preference of lemmings for areas of deep snow cover (Duchesne et al. 2011b; Reid et al. 2012; this study), our results show that this may offer only a limited protection from fox predation. Indeed, predation attempts made by digging, the most frequent hunting technique used in our study, were not affected by snow depth. This also was observed by Ovsyanikov (1993), who reported that foxes dug holes up to 70–80 cm deep to reach lemmings under the snow. However, accessing winter nests through digging may not always guarantee a predation success because lemmings may have enough time to escape from the attack. Nevertheless, some winter nests will hold neonates, which cannot escape, and adults also may come back after the fox has stopped digging and be caught if the fox is patient enough. Interpretation of the effect of snow hardness on predation is difficult because results were inconsistent between years. However, in 2011 when the snow was hardest, foxes showed a tendency to attack nests under a softer snow cover and no attempt to jump through the snow was detected, suggesting that harder snow has the potential to hinder their hunting efficiency. Foxes have the ability to dig through frozen ground to excavate their dens (Prestrud 1991), so digging through hard snow to access a winter nest should be feasible. However, the cost of accessing their prey under such conditions could be above the potential gains and thus not worth it. Therefore, although our results demonstrate that snow can sometimes hinder predation attempts by foxes on lemmings, foxes can apparently use different hunting techniques to bypass these limitations to some extent.

Predation by ermines.—As we expected, snow depth did not affect lemming predation rate by ermines, which suggests that snow has little effect on the activity of this predator. Moreover, the probability of predation was greatest in gully habitat, where both snow accumulation and lemming winter nest densities are generally highest (Duchesne et al. 2011b). However, contrary to what Duchesne et al. (2011b) found, nest density per se did not have an effect on probability of predation. Our results thus suggest that foraging ermines primarily use habitat features to find areas more likely to have high prey densities in winter. Unlike rodents, which may detect areas of deep snow based on local cues such as temperature or light intensity under the snow (Duchesne et al. 2011b; Reid et al. 2012), ermines could use other cues such as topographical features to detect areas where high rodent densities are likely to be found. Areas where snow tends to accumulate, such as the leeward side of slopes or along stream embankments, are visually and rapidly detectable even in winter and could be fairly reliable cues to predict the occurrence of lemmings (Duchesne et al. 2011b). The divergence in cues used by ermines to forage compared to those used by lemmings to settle could explain the absence of an effect of nest density per se on probability of predation. Ermines could successfully predict preferred winter habitats of lemmings, but not necessarily where the highest densities are.

Predation rate was higher on nests used by collared lemmings than those used by brown lemmings. This could be due to a preference of ermines for one species over the other, as previously suggested by Duchesne et al. (2011b). However, an alternative explanation may be that ermines react differently when they predate one species or the other. Our index of predation is largely based on the presence of lemming fur because ermines often line the nest with their prey's fur and use the nest for some time. Ermines may show a preference for occupying collared lemming nests because this species has a highly insulative fur (Ferguson and Folk 1970; Batzli et al. 1983; Malcolm and Brooks 1993) that could provide better insulation against the cold temperature than brown lemming fur. We found no evidence that ermines selectively prey on nests containing juveniles, contrary to what was previously suggested by Sittler (1995) and Hanski et al. (2001). This is consistent with the hypothesis that selection of winter hunting areas by ermines may primarily be based on topographical features. Finally, the absence of interaction between year and other variables suggests that the ermine hunting strategy during winter may not be affected by the phase of the lemming cycle.

A potential limitation of our study, however, is that we do not know when during the winter predation occurred, and thus actual snow depth at that time is unknown. Moreover, our study took place at the end of the winter, and thus may not be representative of conditions experienced by predators and lemmings throughout the winter. This may be especially true early in the winter, when the snowpack should be thin, and lemmings presumably more vulnerable. Additional studies at this time period would be desirable.

Snow cover, climate change, and predation.—Several characteristics of snow cover such as its depth, hardness, timing of establishment, and duration are likely to be affected by climate warming (Rouse et al. 1997; Mellander et al. 2007; Kausrud et al. 2008). Hard snow in the polar regions, which could potentially restrict predation by foxes, is a consequence of high snow density (Höller and Fromm 2008) and low air temperature (Tusima 1975). Thus, as temperature warms in the Arctic, hardness may decrease, which could increase vulnerability of lemmings to fox predation. However, it also is possible that warming will increase melt–frost and icy rain events, which would have the opposite effect on snow hardness. Therefore, it is difficult to predict how upcoming changes in snow quality due to climate warming will affect mammalian predation on lemmings. Nonetheless, considering the relatively weak effects of snow characteristics on lemming vulnerability to predation that we found, it is possible that aspects of lemming ecology other than mammalian predation will be more affected by changes to snow cover. For instance, reduced winter habitat quality (due to lower insulative properties of the snow) and food accessibility (due to ground icing or reduced movement in the subnivean space) or a prolonged period of vulnerability to avian predators due to a shorter snow season (Gilg et al. 2009) also may affect lemming populations.

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