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Spatial Association of Lemming Burrows with Landforms in the Swedish Subarctic Mountains: Implications for Periglacial Feature Stability

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Abstract

Burrowing mammals often have considerable geomorphological impacts, and their tunneling activities may decrease the stability of landforms. We document the spatial distribution of Norwegian lemming burrows in a subarctic alpine meadow to determine the preferred locations for burrow entrances and to examine the potential for burrowing to decrease the stability of periglacial landforms at the site. Burrow entrances were disproportionately common into the base and sides of landforms (>68% of burrows), probably reflecting the lower energetic cost of moving soil horizontally, rather than vertically, out of burrows. Most burrow entrances (>60%) were also located under large rocks, which probably improve burrow stability by providing a firm ceiling to the entrance. Field observations show that these burrows are relatively stable, as only 3% were associated with any signs of increased erosion or landform instability. Therefore, in contrast to some previous studies, and despite burrowing being concentrated on landforms, we suggest that these rodents have little direct impact on landform integrity at this site.

Introduction

A diversity of animals, across numerous environments, have strong geomorphological impacts (Butler, 1995). At high latitudes and altitudes, soil structure and processes are affected by a wide range of species which cause soil compaction by trampling, sediment removal by digging and burrowing, and local slope failure by altering slope loading (Price, 1971; Butler, 1995; Hall et al., 1999; Hall and Lamont, 2003). In consequence, these animals can increase surface runoff (due to compaction), enhance subsurface drainage (due to burrow systems) and exaggerate surface heterogeneity (e.g. Batzli, 1975; Reichman and Seabloom, 2002; Hall and Lamont, 2003). As a result, geomorphological processes may be strongly affected by the presence of certain animal species.

Despite their small size, rodents can have considerable geomorphological impacts in alpine and tundra environments (Batzli, 1975). For example, in the mountains of southern California, pocket gophers (*Thomomys bottae*) alter slope morphology and soil accumulation (Gabet, 2000; Yoo et al., 2005),

while rodents in the Canadian Rockies displace an estimated 200 m³ km⁻² of soil annually (Smith and Gardner, 1985; Hall et al., 1999). The geomorphological impacts of these animals may be driven simultaneously by multiple mechanisms, including tunneling, sediment transportation, and the destruction of the vegetation layer (Price, 1971). Such geomorphological impacts often vary strongly over small spatial scales. For example, in the case of the arctic ground squirrel (*Spermophilus parryii*), burrows are more common on SE-facing slopes, particularly into solifluction lobe risers (Price, 1971). Therefore, in some high-altitude and high-latitude areas, rodents exert a disproportionately strong, albeit spatially heterogeneous, influence on soil structure and processes.

In the mountains of Scandinavia, the impacts of burrowing rodents have remained largely unstudied, despite their abundance in these habitats. The Norwegian lemming (*Lemmus lemmus*) is one of the most abundant small mammals in the Scandinavian tundra, and is common on heaths above the tree line (Olofsson et al., 2004). Although lemmings prefer to use existing spaces under rocks and vegetation, they do also excavate burrows, preferentially

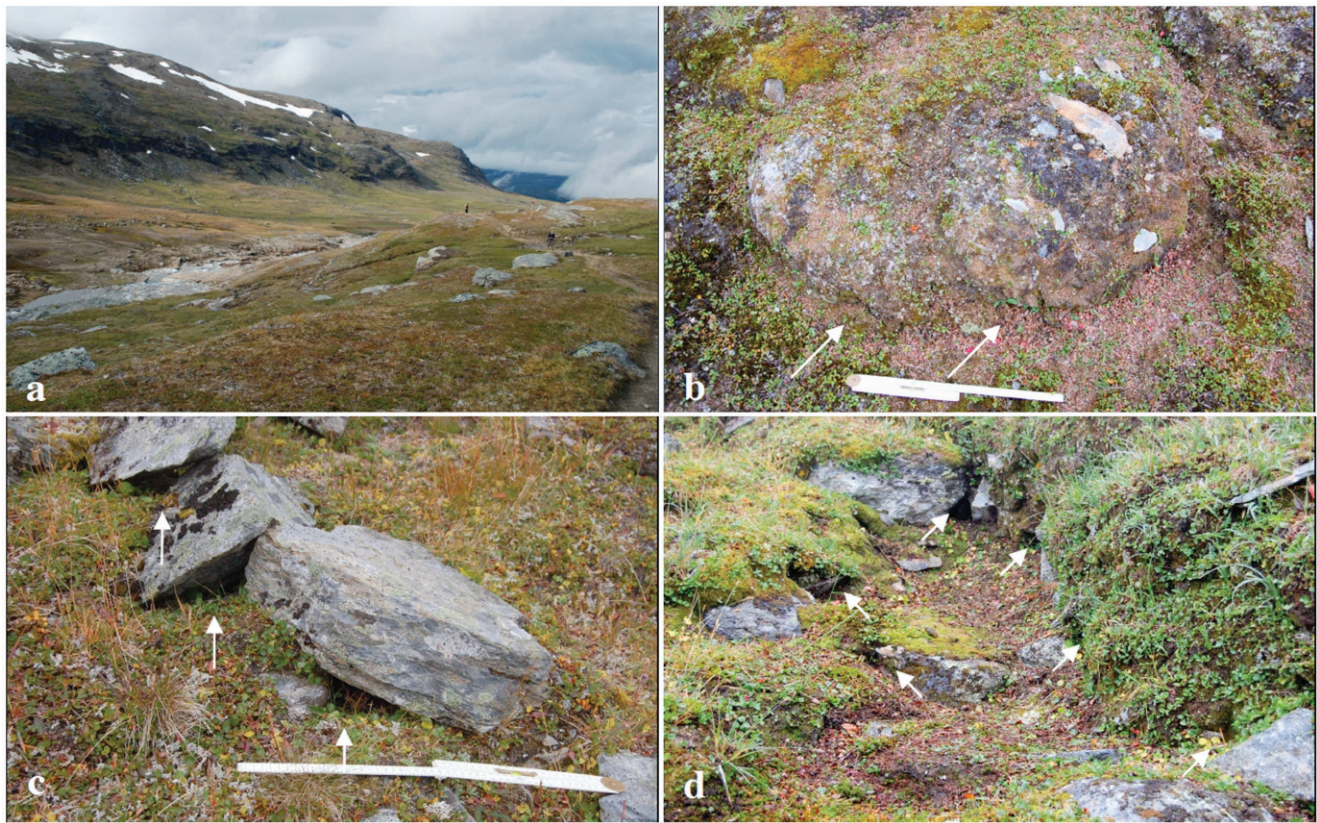


FIGURE 1. Study site: (a) the mid-elevations of the Låkkatjåkka river valley, (b) a rodent burrow entrance into a mudboil, (c) burrow entrances beneath rocks, and (d) multiple rodent burrow entrances into a collapsed riser of a solifluction lobe. Burrow entrances are indicated with arrows. Note the extensive droppings, dead plant litter and trampling effects around the base of the mudboil (b) and solifluction riser (d). The wooden ruler in (b) and (c) is 0.5 m long.

burrowing in sheltered areas where snowdrifts are more likely to form, thereby providing some thermal insulation for foraging areas during the winter (Marsden, 1964; Olofsson et al., 2004). As a result, the geomorphological impacts of their burrowing activity may be concentrated around features that promote the accumulation of thick snow cover during winter.

This study provides an investigation of the spatial pattern of lemming burrowing and its landscape impacts in the mid-alpine zone of the Abisko mountains, northern Sweden. Specifically, we document the distribution of burrowing intensity across and within landforms, and investigate if rodent burrowing could affect landform stability.

Methods

STUDY SITE

This research was conducted in August 2008 within the mid-elevations of the Låkkatjåkka river valley (68°24'N, 18°23'E; altitude 700–900 m a.s.l.), approximately 20 km west of Abisko, northern Sweden. To the west of the valley (Katterjåkk) annual precipitation averages 848 mm, with precipitation declining eastwards (Björkliden; 652 mm a⁻¹), and air temperatures averaging −1.7 °C and −0.8 °C at these sites, respectively (Swedish Meteorological and Hydrological Institute, unpublished data). The study area comprised mostly low alpine meadow vegetation, dominated by low-growing perennial shrubs (*Betula nana*, *Empetrum hermaphroditum*, *Salix herbacea*) and forbs (including *Alchemilla* spp., *Antennaria* spp., *Polygonum viviparum*; Fig. 1a).

The dominant winds across the site are westerlies, and as a result east-facing slopes usually accumulate snow (Darmody et al., 2000). Snow cover is continuous from early October until the end of May with thickness varying from tens of centimeters to a few meters at favorable (lee-side accumulation) sites. Considerable inter-annual variation exists in both the duration and the thickness of the snowpack (Kohler et al., 2006). Soil temperatures at 5 cm below the surface remain close to 0 °C beneath a fully insulating snowpack at the study site (Ridefelt and Boelhouwers, 2006), but can drop to −21 °C under snow-free conditions (Boelhouwers, unpublished data from a wind-exposed site at 900 m a.s.l. in the winter of 2009/2010). The Låkkatjåkka valley runs along a SE–NW direction and does not experience permafrost (Ridefelt et al., 2008), but solifluction landforms are widespread in the form of turf-banked lobes and terraces (Ridefelt and Boelhouwers, 2006). Mudboils and vegetated hummocks, with diameters of 0.5–2 m, are locally common on low-angled slopes.

BURROW SURVEYS

To test if rodent burrows were disproportionately associated with different landform types, a broad-scale transect was surveyed across the valley (running perpendicular to the direction of the valley, from the east-facing to the west-facing valley wall). In the transect 2 × 2 m grids were surveyed at 10 m intervals. Landform type (solifluction lobe, mudboil, hummock, or homogeneous slope), the presence of large rocks (defined as larger than the average burrow entrance), the number of burrow entrances, and the presence of other signs of rodent activity (manuring or

grazing) were recorded. Grids including streams, mires, or drainage lines were excluded from analyses to restrict the study to terrestrial features.

Additionally, fine-scale patterns of burrow distribution were quantified by surveying larger plots (25–200 m²). Plots were positioned to encompass representative examples of each landform type, and were repeated at different altitudes on both valley aspects where possible. Within each plot all burrow entrances were counted, rock cover estimated, and any association with large rocks noted. For the first six plots surveyed, we also measured burrow size (burrow entrance width and height, and the depth of the entrance tunnel before branching or turning) and recorded the distance at which rodent droppings, grazing, and trampling were evident around each entrance. Total vegetation cover and dominant species composition (i.e. species, or species groups where identification to species level was difficult, covering more than 20% of a plot) was also noted around burrow entrances in the first plots, as well as 1 m away from the entrances in a random direction.

Data were analyzed using Generalized Linear Models, assuming a Poisson error structure for the analysis of abundance data and a Gaussian distribution of errors for density data (using log and identity link functions, respectively). Where necessary, Poisson models were corrected for overdispersion, and model significance subsequently determined using an *F*-test (Dobson, 2002). Chi-square tests were used to compare the observed and expected abundance of burrows in different landforms (assuming an even distribution of burrows across all sites). Analysis of Similarity (ANOSIM) was used to compare the composition of the dominant plant species around burrow entrances and in adjacent areas without entrances (Quinn and Keough, 2002).

Results

FIELD OBSERVATIONS OF RODENT IMPACTS

Burrow entrances were typically 40–80 mm high and wide, although larger widths were observed at more complex burrow systems. While most burrow entrance tunnels were less than 0.2 m long (before branching, turning, or ending), some extended more than 0.6 m, suggesting that burrowing not only affects surface soil and vegetation but also damages root systems and may reach into the mineral soil. While damage to vegetation and roots was observed at all burrowing sites, excavated mineral soil was not recorded at burrow entrances. In addition, no signs of water drainage out of burrows or washed sediment at burrow entrances were noted. Around burrow entrances, and especially along rodent pathways, rodent trampling and grazing was associated with dead plant debris (in agreement with, e.g., Batzli, 1975; Figs. 1b–1d). These effects were restricted to superficial surface vegetation damage and did not reach through the root mat. Aggregations of dead vegetation (including leaves and grass stems) were also observed on the soil surface, probably indicating the location of subnival lemming nests.

All burrow entrances were clear of vegetation, and were therefore probably either occupied at the time of the survey or recently abandoned. Given the burrow dimensions recorded and the abundance of lemmings in similar habitats, we are confident that most, if not all, surveyed burrows were excavated by lemmings. Very few rodents were observed while surveying the burrows, but subsequent fieldwork (summer 2010) confirmed that the burrows are occupied and utilized by Norwegian lemmings (Boelhouwers, personal observation).

TABLE 1

Burrow entrance density sampled in 2 × 2 m plots across the Låkkatjåkka valley for different landforms and in the presence and absence of large rocks.

	Number of grids surveyed	Burrow density (per m ² ; mean ± S.E.)
Landforms		
Total ¹	93	0.40 ± 0.23
Homogenous slope	46	0.48 ± 0.38
Mudboil	9	0.33 ± 0.47
Hummock	15	0.17 ± 0.27
Solifluction lobe	23	0.43 ± 0.47
For solifluction lobes		
Treads	5	0.10 ± 0.39
Risers	18	0.53 ± 0.39
Large rocks		
Present	32	0.84 ± 0.49
Absent	61	0.18 ± 0.14

¹ 22 grids containing aquatic features excluded from analyses.

BURROW SURVEYS

Rodent burrows were not evenly distributed across landforms in the broad-scale transect ($\text{Chi}^2 = 11.6$, d.f. = 3, $p = 0.01$; Table 1). Solifluction lobes were the most common type of landform in the survey and burrow entrances were significantly more common on lobe risers than on treads ($\text{Chi}^2 = 6.59$, d.f. = 1, $p = 0.01$; Table 1). However, the presence of large rocks had a much stronger impact on the abundance of rodent burrow entrances than the type of landform, with a higher density of burrows associated with rocks than with areas lacking rocks ($\text{Chi}^2 = 90.6$, d.f. = 1, $p < 0.001$; Table 1). Indeed, when landform type and the presence of rocks were included in models of burrow abundance, only the presence of rocks contributed significantly to the model (Model goodness of fit: $F_{3,89} = 15.46$, $p < 0.001$, deviance explained = 34.3%; Presence of landform: Log-likelihood ratio = -137.8 , $\text{Chi}^2 = 1.39$, $p = 0.24$; Presence of rocks: Log-likelihood ratio = -157.7 , $\text{Chi}^2 = 41.25$, $p < 0.001$; Interaction between the presence of a landform and the presence of rocks: Log-likelihood ratio = -137.3 , $\text{Chi}^2 = 0.37$, $p = 0.54$). This same result was observed when repeating the analyses using other signs of rodent activity (e.g. rodent grazing and manuring were also most strongly associated with the presence of rocks). While landforms were unevenly distributed between the two sides of the valley (on the west-facing valley slope only one grid contained hummocks and none contained mudboils), the abundance of burrows did not differ between valley aspects ($F_{1,91} = 0.13$, $p = 0.28$).

In the fine-scale plots, similar patterns were observed in the location of burrow entrances (Figs. 1b–1c). The number of burrows associated with rocks was greater than expected on the basis of rock cover ($\text{Chi}^2 = 124.1$, d.f. = 12, $p < 0.001$), with 93% of these entrances occurring under rocks (Table 2). Similarly, across all plots the mean density of burrows was four times higher in plots containing landform features compared to plots on slopes without landforms (Table 2). Burrow entrances were more common at the base of landform features than on the side or top of landforms (approximately twice as common; Table 2, see e.g. Fig. 1b). Only five of the surveyed burrows were associated with any degradation of the landforms. These burrows (aggregated in one portion of plot 6; Fig. 1d) were on a collapsed riser of a solifluction lobe. Interestingly, only one of the 164 burrows surveyed in the fine-scale plots was not associated with either a rock or a landform feature.

TABLE 2

The association between burrow entrances and landforms and rocks, including the number of burrows associated with the different portions of landforms.

Plot	Landform	Plot size (m ²)	Density of burrows (m ⁻²)	Number of burrows surveyed	% surveyed burrows associated with landforms or rocks	Number of burrows into:			% surveyed burrows associated with solifluction lobes	Number of burrows into:		
						The base of landform / under rock ¹	The side of landform / next to rock	The top of landform / above rock		Risers	Tread	Bottom slope
1	Slope (none)	100	0.39	10	100	0 / 10	0 / 0	0 / 0	— ²			
2	Slope (none)	100	0.04	3	100	1 / 2	0 / 0	0 / 0	—			
3	Slope (none)	100	0.03	3	67	0 / 1	0 / 1	0 / 0	—			
4	Slope (none)	25	0.08	2	100	0 / 2	0 / 0	0 / 0	—			
5	Mudboils	100	0.21	9	100	3 / 6	0 / 0	0 / 0	—			
6	Mudboils	100	0.15	15	100	9 / 6	1 / 2	4 / 0	—			
7	Mudboils	100	0.16	16	100	11 / 4	1 / 0	2 / 0	—			
8	Gully	200	0.04	7	100	0 / 7	7 / 0	0 / 0	—			
9	Solifluction lobe	100	0.47	47	100	4 / 42	7 / 1	3 / 1	28	10	3	0
10	Solifluction lobe	100	0.14	8	100	2 / 6	2 / 0	2 / 1	75	4	2	0
11	Solifluction lobe	100	0.23	23	100	13 / 8	4 / 0	5 / 0	96	17	0	5
12	Solifluction lobe	100	0.11	11	100	5 / 3	5 / 1	1 / 0	100	10	0	1
13	Solifluction lobe	100	0.10	10	80	7 / 3	1 / 0	0 / 0	80	2	6	0

¹ Some burrows were associated with rocks on landforms and therefore fall into two categories.

² No solifluction lobes in these plots.

Signs of rodent activity were more frequent around burrow entrances than in adjacent areas. Evidence of grazing and manuring was evident around 88% and 64% of the burrows surveyed, respectively. However, 1 m away from burrow entrances these signs of activity were 70% less frequent. Trampling of the vegetation by rodents was observed less frequently around burrows than grazing and manuring (recorded around 39% of burrows) and was rare away from burrow entrances (observed in 3% of sites away from burrows). As a result, signs of rodent activity were mostly restricted to within 1 m of burrow entrances, with 50% of the signs of activity within 0.3 m of entrances. Nonetheless, there was no significant difference in vegetation cover between burrows and adjacent areas (although noting the small number of samples for which this data were collected: Wilcoxon matched pairs test: $T = 2.5$, d.f. = 15, $p = 0.18$). The composition of the dominant vegetation types also did not differ around burrows and in adjacent areas (ANOSIM $R = -0.05$, $n = 16$ pairs of plots, $p = 0.96$).

Discussion

In the mid-alpine zone of northern Sweden, lemming burrow entrances were disproportionately common under rocks and at the base of landforms. Four potentially complementary mechanisms have been suggested in previous studies of similar systems which may explain this pattern of burrow locations. First, burrowing under rocks and into the base of landforms may be more energetically efficient for the lemmings than burrowing elsewhere. Digging is energetically expensive (Vleck, 1981; Seabloom et al., 2000), and by burrowing under rocks rodents can exploit existing natural cavities. Similarly, burrowing into the base or sides of a landform can be more energetically efficient since moving the sediment vertically out of a burrow (i.e. when the burrow is on the top of a landform) requires more energy than moving it out laterally (Seabloom et al., 2000; Luna and Antinuchi, 2006). Additionally, the lemmings probably expend less energy burrowing into active (or recently active) periglacial landforms, because those sediments are likely to be less compacted and rocks are likely to be concentrated in specific areas.

Second, burrowing under rocks and into the base of landforms may offer greater burrow stability. Due to the energetic cost of excavating burrows (Vleck, 1981) and the high risk of mortality associated with burrow collapse (see e.g. Thomsen et al., 2004), species are likely to maximize burrow stability where possible. Burrow entrances associated with rocks, especially when the rocks form the ceiling of the burrow, probably have a much lower risk of collapse than other burrows.

Third, burrowing sites may be located in areas with more favorable microclimatic conditions. For example, Price (1971) observed that the burrows of the arctic ground squirrel were disproportionately common into the bases of solifluction lobes on SE-facing slopes. These sites accumulated more snow in winter and received greater solar radiation in summer, providing a more favorable microclimate in both seasons. In our study area, preferential burrowing at the base of landforms may also be related to higher and more stable winter temperatures beneath thick snow cover, which is known to be an important winter habitat requirement for lemmings (Marsden, 1964; Olofsson et al., 2004). However, in contrast to Price (1971), higher summer temperatures are unlikely around the burrow entrances in the Låkkatjåkka valley because most burrows were on north-facing slopes (due to the orientation of the valley). It is also unlikely that there are any thermal benefits for the rodents associated with locating burrow entrances under rocks.

Finally, burrow sites could also be chosen based on an area's vegetation. For example, the preferential location of arctic ground squirrels' burrows at the base of solifluction lobes corresponds with good vegetation development in that microsite (Price, 1971). Indeed, in our study, plant cover was more complete at the base of mudboils than on top of the same landform, and vegetation height was greater at the base of solifluction lobe risers than on their treads. These vegetation patterns could be important determinants of burrow entrance location for the lemmings, as these species benefit from the presence of tall shrubs which maintain open spaces between the snowpack and the ground, act as a food source and provide cover from predators (Marsden, 1964). However, as there is probably little connection between vegetation development

and the presence of rocks, it is unlikely that vegetation patterns explain the rodents' preference for burrowing under rocks. Therefore, lemming burrow locations probably reflect a tendency for the rodents to minimize energy expenditure and maximize burrow stability, while burrows extending into the base of landforms may also have additional foraging and microclimatic benefits, especially during winter.

EFFECTS ON LANDFORM STABILITY

Compared to reports from other arctic and alpine regions, the rodents in this study have smaller geomorphological impacts than recorded for some other species (e.g. arctic ground squirrels and pocket gophers; Price, 1971; Thorn, 1978; Hall et al., 1999; Schütz, 2005; Yoo et al., 2005). For example, substantial fine-scale slope instability is associated with the burrowing activity of arctic ground squirrels (Price, 1971). However, there was little direct evidence of burrowing disrupting landforms in our study, as indicated by the scarcity of collapsed burrows and the absence of bare mineral soil around burrow entrances. At least in part, the lack of a large biogeomorphological impact may be due to thick insulating winter snow cover which reduces the necessity for lemmings to excavate burrows to escape low temperatures. Furthermore, because the burrows have a relatively low risk of collapse (due to their positioning under rocks or deep into landforms), there is a lower chance that they will compromise the stability of the landforms by initiating local collapse. Thus, it appears that landscape response to the impact of burrowing is species- and/or site-specific and cannot be generalized without some understanding of species' burrowing behavior.

The potential impacts of selective rodent burrowing into lobe risers may also be considered in the light of recent discussion on solifluction lobe advance mechanisms (Kinnard and Lewkowicz, 2006; Ridefelt et al., 2009). For example, in the adjacent Kärkevagge valley, rapid advancement of solifluction lobes has been associated with lobe front collapse and subsequent colluviation (e.g. Strömquist, 1983), although the internal structures of lobes does not always show such abrupt movement (Rapp and Åkerman, 1993). Therefore, it was hypothesized that preferential rodent burrowing at lobe fronts could provide a destabilizing trigger mechanism through the disruption of the supporting vegetation root mat and the consequent reduction of the soil shear strength. Similarly, preferential drainage along burrow channels could lead to localized front collapse and enhanced sediment removal (Thorn, 1978; Grab and Deschamps, 2004). However, our results provide no support for these hypotheses, but rather suggest that lemming burrows do not accelerate the degradation of solifluction lobes.

EFFECTS ON VEGETATION

Despite signs of rodent activity being highly localized around burrow entrances, there appeared to be no effect on vegetation cover in the immediate vicinity of burrow entrances. The absence of an effect at our site may reflect the timing of our study (surveys conducted at the end of summer; see e.g. Olofsson et al., 2004), or the influence of a positive effect of rodent activity offsetting their grazing impact (e.g. nutrient enrichment through manuring or enhanced mineralization; Batzli, 1975). Nonetheless, the lack of a difference in vegetation cover around rodent burrows and in adjacent areas suggests that even under rodent grazing and burrowing the top soil layers appear to remain effectively bound by plant roots. As a result, it is possible that surface erosion processes are not strongly favored

by rodent activity in the Låkkatjåkka valley. It is, however, worth noting that even though our methods did not record a difference in vegetation cover or the dominant plant types, rodent grazing in Scandinavian tundra can affect the relative abundance of individual plant species (see e.g. Olofsson et al., 2004). It is therefore likely that, as with landform stability, the effect of rodents on vegetation is species- and site-specific.

CONCLUSIONS

This study demonstrates that lemmings in the Låkkatjåkka valley have strong preferences for burrowing under rocks and into the bases of landforms. These burrow locations probably minimize energetic expenditure and the risk of burrow collapse, and may also offer some microclimatic and foraging benefits. As a consequence of the tendency for the species to burrow under rocks, burrows appear to have little impact on landform integrity, in contrast to previous studies. Thus, these rodents have a small direct geomorphological impact in our study site, suggesting that the biogeomorphic influence of lemmings may be substantially less than documented for pocket gophers and other burrowing rodents.

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