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ORIGINAL ARTICLE

Incisor microwear of Arctic rodents as a proxy for microhabitat preference

Peter S. Ungar[1] · **Lindsay Saylor**[1] · **Aleksandr A. Sokolov**[2] · **Natalia A. Sokolova**[2] · **Olivier Gilg**[3,4] · **Sophie Montuire**[5,6] · **Aurélien Royer**[6]

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Abstract

Changing environmental conditions in the Arctic make it important to document and understand habitat preferences and flexibility of vulnerable high-latitude mammals. Indirect proxies are especially useful for elusive species, such as rodents. This study explores incisor microwear as an indicator of variation in behavior and microhabitat use in Siberian lemmings (*Lemmus sibiricus*) and narrow-headed voles (*Lasiopodomys gregalis*) from the Yamal Peninsula, Russia. Fifty-nine individuals were sampled at four sites along a latitudinal gradient from forest-tundra ecotone to high-Arctic tundra. Lemmings are present at the northernmost site, voles at the southernmost site, and both species at the middle two. *Lemmus sibiricus* prefers wet, mossy lowland, whereas *La. gregalis* favors drier thickets and more open microhabitats and burrows underground. Feature-based analyses indicate higher densities of features and more uniformly oriented striations for voles than lemmings at sites with both species. The species also differ significantly in microwear texture attributes suggesting larger features for lemmings, and smaller ones, but more of them, for voles. While no texture differences were found between sites within species, voles from sites with open tundra have higher striation densities than those from the forest-tundra ecotone. Furthermore, lemmings from open tundra sites have higher striation densities than those from the water-saturated, moss-covered northernmost site. While microhabitat preferences and burrowing by voles likely contribute to differences between species, variation within seems to reflect habitat variation given differences in abrasive loads between sites. This suggests that incisor microwear patterning can be used to track microhabitat differences among Arctic rodent populations.

Keywords Siberian lemming · Narrow-headed vole · Tooth wear · Environment · Yamal Peninsula · Habitats · Tundra · Arctic · Russia

Introduction

Ecologists interested in understanding changing climates and ecosystems of the Arctic have looked to endemic rodents as key indicators (Post et al. 2009), or "canaries in the coal mine". Lemming densities, for example, are especially sensitive to changing winter weather (Ims et al. 2011), with fading outbreaks reported in many areas (Gilg et al. 2009; Kausrud et al. 2008; Schmidt et al. 2012). Indeed, arvicoline rodents are in many ways ideal model mammals for monitoring changes in the tundra biome (Christensen et al. 2013), so much so that researchers associated with the Circumpolar Biodiversity Monitoring Program have focused on them over the past two decades at 49 sites across the Arctic (Ehrich et al. 2020). But what do we really know about the resilience of endemic high-latitude mammals, and how do these species respond to changing habitats and resources available in

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✉ Peter S. Ungar
pungar@uark.edu

[1] Department of Anthropology, University of Arkansas, Fayetteville, AR, USA

[2] Arctic Research Station, Institute of Plant and Animal Ecology, Urals Branch of the Russian Academy of Sciences, Labytnangi, Russia

[3] UMR 6249 Chrono-Environnement, Université Bourgogne Franche-Comté, Besançon, France

[4] Groupe de Recherche en Ecologie Arctique, Francheville, France

[5] EPHE, PSL University, 6 Boulevard Gabriel, 21000 Dijon, France

[6] Biogéosciences, UMR 6282, CNRS, EPHE, Université Bourgogne Franche-Comté, 6 Boulevard Gabriel, 21000 Dijon, France

them? We cannot simply go out and watch cryptic, elusive wild voles and lemmings to document where and what they eat across the Arctic as glaciers retreat and permafrost melts. Still, this is just the sort of information conservationists and policy-makers need to develop strategies to protect vulnerable high-latitude populations and the ecosystems to which they belong.

There are direct proxies available for diet of and microhabitat use by Arctic rodents, such as bite marks on food plants (Dunaeva 1948; Kopein 1958), feces, and stomach contents of trapped individuals (Soininen et al. 2013). These are, however, of limited value in and of themselves. Bite marks are found only on plant parts left uneaten and can be difficult to assign to species when sympatric taxa are present. Feces and stomach contents give only single-meal scale information and can be biased by differential digestion rate. Indirect proxies, or "foodprints", including stable isotope ratios (e.g., Baltensperger et al. 2015; Calandra et al. 2015; Soininen et al. 2014) and dental wear pattern at both mesowear and microwear scales (Calandra et al. 2016; Kropacheva et al. 2017; Ungar et al. 2020), can provide further information about individuals at longer time intervals, from days to weeks to lifetimes. Such approaches have the added value of applicability to specimens gathered over considerable spans of time and space and archived in research and museum collections. Thus they can be used to answer questions difficult to address with fieldwork today.

The current study assesses the potential of one such foodprint, dental microwear, as a proxy for microhabitats of Arctic arvicolines. Previous studies have demonstrated that dental microwear of rodents can provide a useful tool for inferring diet and habitat. Molar studies have shown distinctive patterns of microscopic scratching and pitting dependent on broad food preferences and habitat types (Firmat et al. 2010, 2011; Hautier et al. 2009; Nelson et al. 2005; Rodrigues et al. 2009, 2013; Townsend and Croft 2008; Winkler et al. 2016). Molar microwear may even be able to resolve subtler differences within and between species with versatile diets (Burgman et al. 2016; Robinet et al. 2020). Indeed, a recent microwear analysis of field vole (*Microtus agrestis*) molars showed marked seasonal differences in texture pattern consistent with changes in diet between autumn and spring in Finnish Lapland (Calandra et al. 2016).

Rodent incisor microwear appears better suited to separating groups by habitat type than by diet (but see Belmaker and Ungar 2010). While patterns on molar teeth are driven largely by angle of approach between opposing occlusal surfaces, which may reflect fracture properties of foods (Adams et al. 2020; Hua et al. 2015), incisor microwear is free from confounding signals related to masticatory dynamics. Moreover, incisors are at the interface between environment and animal, and therefore more likely reflect variation in environmental abrasive load (see Belmaker 2018). Indeed, preliminary analysis suggests that anterior dental microwear texture patterns parse rodent species in wetter, closed settings from those in more open habitats (Caporale and Ungar 2016). This underscores the value of incisor microwear as a proxy for environmental abrasiveness, which varies with precipitation and vegetative cover (see Belmaker 2018).

Two species well suited to assess potential of incisor microwear as a proxy for Arctic habitat use are *Lemmus sibiricus* (the Siberian brown lemming) and *Lasiopodomys* (formerly *Microtus* or *Stenocranius*) *gregalis* (the narrow-headed or narrow-skulled vole). These iconic Palearctic rodents overlap substantively in geographic range but are reported to differ in microhabitat preference. Siberian lemmings prefer wetlands and lowland tundra with substantial moss and sedge cover and are found today throughout the Russian Arctic (Tsytsulina et al. 2016). Narrow-headed voles, in contrast, typically inhabit more open grassy areas of tundra, plains, mountain steppes, and meadows (Batsaikhan et al. 2016). These voles were, until the Holocene warming, continuously distributed across northern Eurasia (Baca et al. 2019; Markova et al. 2019); but they are now confined to disjunct areas spread from western Russia to eastern China.

This study focuses specifically on *Le. sibiricus* and *La. gregalis* in the Yamalo-Nenets Autonomous District, northwestern Siberia, Russian Federation. The Yamal Peninsula and adjacent Bely Island present an ideal natural laboratory for assessing impacts of habitat variation on high-latitude rodents. The peninsula extends over 700 km from south to north with no insurmountable geographical barriers, such as impassable mountains, glaciers, or seasonally unfordable rivers. Bely is ca. 63 km × 41 km and located approximately 15 km from the northern tip of Yamal in the Kara Sea. These together represent a biogeographic gradient between forest-tundra ecotone and high Arctic. Comparisons of incisor microwear patterning between species where they overlap and especially within species between sites in different bioclimatic subzones will allow us to better assess the potential of this foodprint as a proxy for microhabitat use and, by extension, as a tool for assessing impact of climate change on the ecology of endemic rodents of the Arctic.

While preliminary studies suggest that incisor microwear of rodents can serve as an environmental proxy, more work is needed to confirm this and to determine the potential of the approach. Yamal lemmings and voles are especially well suited to the task. Yamal is among the best studied areas for tundra ecology in the Russian Arctic, with four research stations strategically located along the latitudinal gradient for sampling endemic flora and fauna. We hypothesize that incisor microwear patterns for each species reflect variation between the sites in ground cover and vegetation type/height given differences in abrasive loads. We further expect differences between the species related to both microhabitat preference and burrowing practice (see below).

Materials and methods

Study area

All specimens examined in this study were collected on the Yamal Peninsula and adjacent Bely Island. Together, Yamal and Bely form a biogeographic gradient between Arctic bioclimatic subzone E (mean July temperature of 9–12.8 °C, dominated by with erect shrubs, tussock sedges, and mosses) and subzone B (mean July temperature 3–5.8 °C, dominated by sedges and mosses with prostrate dwarf shrubs) (see Walker et al. 2005 and Fig. 1). All individuals were trapped at four research sites located strategically along a latitudinal gradient for sampling rodents and other endemic fauna: (1) Kharp in the forest-tundra ecotone (66.8° N, 66.4° E), (2) Erkuta in the low Arctic (68.2° N, 69.2° E), (3) Sabetta at the border between the low and the high Arctic (71.2° N, 71.5° E), and (4) Bely in the high Arctic (73.3° N, 70.1° E).

Kharp is located just south of subzone (E) and is the only site with trees (mostly Siberian larches, *Larix sibirica*). Willow thickets (*Salix* spp.) extend more than two meters in height. Kharp is dominated by herbs *Calamagrostis purpurea*, *Cal. lapponica, Comarum palustre, Equisetum arvense, Rubus arcticus*, several *Carex* species and mosses (e.g., *Mnium* sp*., Polytrichum* sp*., Sphagnum* sp.). Erkuta is in the middle of bioclimatic subzone E, which is characterized by 80–100% vascular plant cover and a total phytomass reaching 100 t*ha-1. Willow thickets range between one and two meters in height. Vegetation at Erkuta is dominated by *Ledum decumbens* and *Calamagrostis langsdorffii*, *Carex* spp.*, Equisetum arvense, Poa arctica, Rubus arcticus, Veratrum lobelianum* and mosses (*Sanionia uncinata*). Sabetta is on the border of bioclimatic subzones C and D. It has approximately 50% cover of vascular plants with interrupted closed or patchy vegetation (see Walker et al. 2005). Total phytomass at Sabetta is estimated to be 30 t*ha-1, with willow thickets up to "knee height" (ca. 0.40 m maximum), and its vegetation is dominated by *Carex* spp., *Arctagrostis latifolia, Hierochloe alpine*. Bely Island is within subzone B, with cover dominated by cryptogams (up to 60%) and vascular plants (approximately 25%). Total phytomass at Bely Island is estimated to be 20 t*ha-1 (see Walker et al. 2005). Bely has virtually no thickets, with a ground surface largely covered by mosses, particularly *Drepanocladus, Calliergon,* and *Sphagnum*. Further details on Yamal vegetation can be found in Magomedova et al. (2006).

No lemmings are found at Kharp, but vole species at the site include *Lasiopodomys gregalis*, *Microtus middendorffii*, *Mi. agrestis, Alexandromys* (formerly *Microtus*) *oeconomus, Myodes rutilus, My. rufocanus* and *Arvicola amphibius*. *Myodes* species dominate the rodent community at Kharp. Erkuta has both *La. gregalis* and *Lemmus sibiricus*, though the former outnumber the latter. The rodent community at Erkuta also includes the lemming *Dicrostonyx torquatus*, and the voles *Mi. middendorffii*, and *My. rutilus*. Sabetta has mostly lemmings, both *Le. sibiricus* and *D. torquatus*, but also *La. gregalis*. Finally, *Le. sibiricus* is the only rodent species on Bely Island. Therefore, specific to the taxa included in the present study, the southern site of Kharp has only *La. gregalis*, the northern site on Bely Island has only *Le. sibiricus*, and the intermediate latitude sites at Erkuta and Sabetta have both narrow-headed voles and Siberian lemmings.

A total of 59 individuals were sampled for microwear in this study. These included 31 *Le. sibiricus* ($n = 11$ from Erkuta, $n = 10$ from Sabetta, and $n = 10$ from Bely Island) and 28 *La. gregalis* ($n = 7$ from Kharp, $n = 11$ from Erkuta, and $n = 10$ from Sabetta). These specimens were collected during snap-trap sessions at Kharp (June and September, 2013 and 2016), Erkuta (June and August 1999 and 2014), Sabetta (July, 2014), and Bely (July, 2015) following small-quadrat field protocol (Myllymäki et al. 1971). At each site, three traps were baited with raisins and rolled oats at each corner of a 15 × 15 m permanent quadrat (i.e. twelve traps per quadrat) for two nights. Collections were made at spatially distinguished units (at least two km apart) with groups of quadrats representing a given habitat separated by at least 200 m. Small quadrats were spread through different microhabitats in all three sites.

Traps were set in four distinct microhabitat types: (1) *dry* plots situated on sandy hillsides or upland dwarf-shrub tundra; (2) *wet* plots situated in moist areas in flat, low-lying tundra or small values, often in bogs dominated by *Sphagnum* moss; (3) *thicket* plots placed along the edge of willow thickets (*Salix glauca-Carex aquatilis* or *Salix lanata-Myosotis nemorosa*) on the slopes of small values or hills; and (4) *forest* plots in larch (*Larix sibirica*) forest. One specimen was recovered from a predatory bird's nest. Microhabitat classification and identification for trap placement followed Sokolova et al. (2014). Traps were set in wet, dry, and thicket habitats at both Erkuta, and Sabetta. Only the wet habitat type was present at the lemming trap site on Bely Island, and only forest and thicket habitat types were present where voles were trapped at Kharp. The microhabitat in which each individual in this study was trapped is presented in Supplementary Information File (SI) 1 and summarized by species and site in Table 1.

For lemmings, most (25 of 31) came from wet microhabitats. Five came from willow thickets and none were found in dry microhabitat traps at any of the sites. One was derived from a bird's nest. For the voles, only three individuals were trapped in wet microhabitats. Most come from thickets (15 of 27) or dry microhabitats (9 of 27). One was recovered in

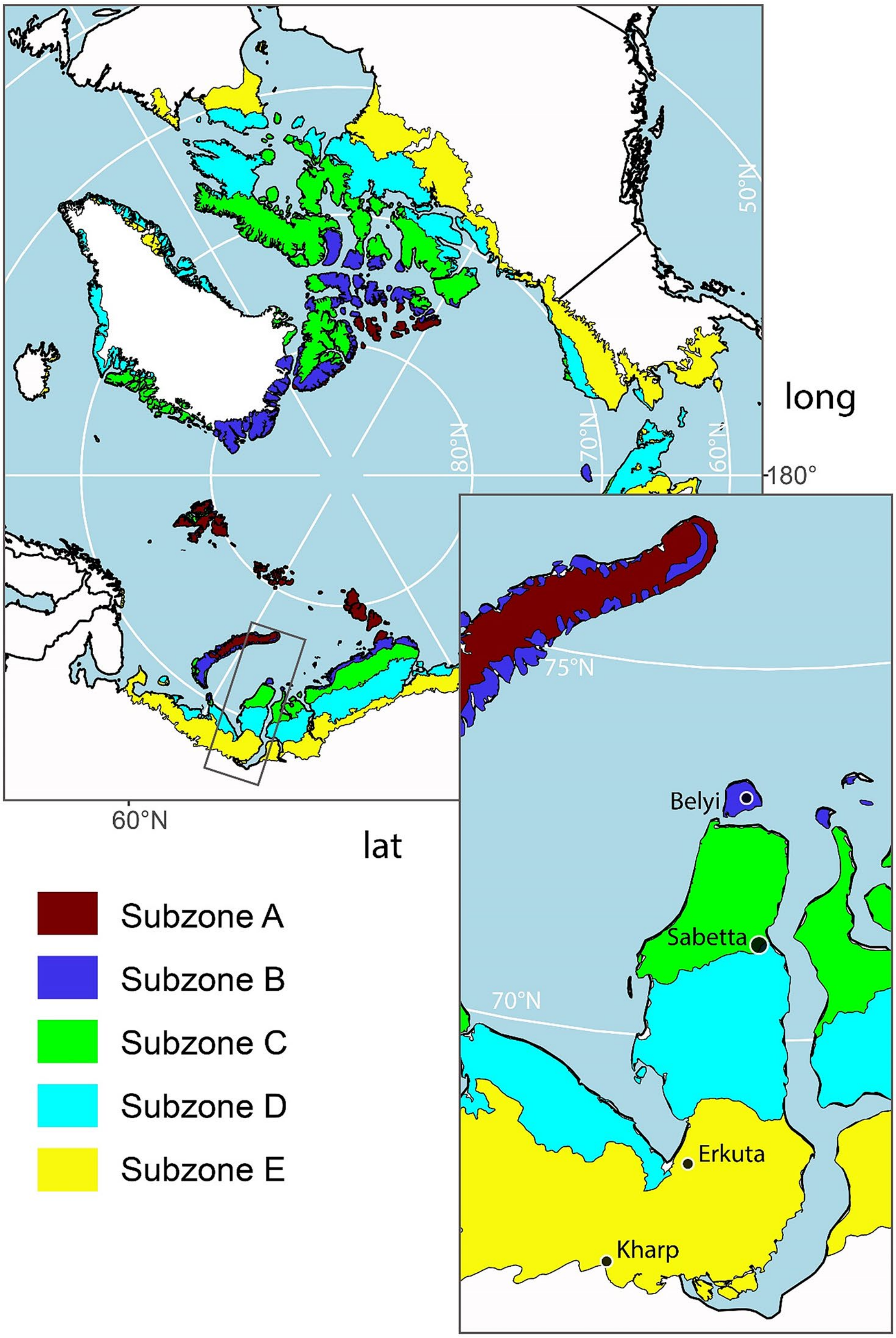


Fig. 1 Map of the Yamal Peninsula and Bely Island with locations of sites sampled. Bioclimatic subzones of the Circumpolar Arctic Region are derived from CAVM Team (2003) and as described in Walker et al. (2005)

a larch forest trap. Concerning variation between the sites, all lemmings from Bely (where there are only wet plots) and Erkuta came from wet microhabitat traps, and Sabetta specimens came from both wet and thicket traps. Furthermore, all voles at Erkuta and Sabetta came from thickets or dry traps except for two wet-trapped specimens from Sabetta. At Kharp, the forest-tundra ecotone site, most specimens derive from thicket traps, with one each from forest and wet microhabitats. There are no dry plots at Kharp.

While individual rodents are sometimes capable of moving between adjacent plots in different microhabitats, the distribution of specimens, which were randomly sampled from traps in all available microhabitats at the four sites, are in accord with our observations that lemmings prefer wet, moss-covered habitats whereas voles prefer drier willow thickets, sandy hillsides, and upland dwarf-shrub tundra. It should also be noted that microwear recorded in this study likely reflects behavior at most a day or two prior to trapping

Table 1 Trap microhabitats for specimens considered in this study by species and site (see text for descriptions)

Lemmus sibiricus				
	Wet	Forest	Thicket	Dry
Bely	10			
Sabetta	5		5	
Erkuta	10			
Lasiopodomys gregalis				
	Wet	Forest	Thicket	Dry
Sabetta	2		6	2
Erkuta			4	7
Kharp	1	1	5	

Note that one *Lemmus sibiricus* specimen from Erkuta was recovered from a predatory bird's nest

given the location of microwear sampling at the tip of the tooth (see below) and rapid rate of incisor wear. Indeed, other voles have been reported to wear their lower incisors approximately 0.3 mm/day (Coady et al. 1967; Klevezal 2010; Klevezal et al. 1990). Trapping locations of individual rodents are also consistent with habitat preferences reported for both species in the literature (Tsytsulina et al. 2016; Batsaikhan et al. 2016; see "Introduction").

Specimen preparation and data acquisition

Specimens were dissected in the field, with heads removed and kept in a 20–40% ethanol solution. Skulls were then processed in the laboratory at the Institute of Plant and Animal Ecology Arctic Research Station in Labytnangi, Russia, by boiling and drying. Only adult and subadult individuals were considered in this study (age categories follow Bashenina 1962). Dental replicas were produced following conventional microwear specimen preparation techniques for a sample on loan to UMR CNRS 6282 Biogéosciences at the University of Burgundy (Dijon, France). First, mandibular incisor (I_1) enamel surfaces were cleaned with alcohol-soaked cotton swabs and allowed to dry. Dental impressions were taken with President's Jet Regular Body polyvinylsiloxane dental impression material (Coltène-Whaledent Corp., Cuyahoga Falls, OH, USA). High-resolution replicas were later prepared at the University of Arkansas using Epotek 301 cold-cure epoxy (Epoxy Technologies, Billerica, MA), centrifuged into the molds, and allowed to set before analysis. All replicas were subsequently screened by confocal profilometry at 100x, and analysis was limited to those specimens with unobscured antemortem microwear (see Teaford 1988 for criteria).

High-resolution replicas were scanned using a Sensofar Plµ standard white-light scanning confocal profiler (Solarius Development Inc., Sunnyvale, CA). Each surface was scanned at using a Nikon L Plan super-long working distance 100 × lens (numerical aperture = 0.70, working distance = 6.5) and a work envelope of 138 µm × 102 µm, a lateral point spacing of 0.18 µm, vertical step of 0.2 µm, and vertical resolution (as reported by the manufacturer) of 0.005 µm. Microwear sampling focused the flattened distal edge of the I_1 labial surface just below the incisal edge following previous studies of rodent incisor microwear textures (see Belmaker and Ungar 2010; Caporale and Ungar 2016). This surface tends to be flatter, so I_1s have been preferred over more curved maxillary incisors given the limited depth of field of the confocal profiler used (Belmaker, personal communication).

Resultant surfaces were processed and analyzed using SensoMap Premium Software (MountainsMap Version 8.0.9173, 2020/02/12, Digital Surf Corp, Besançon, France). Each surface was leveled using the "Least squares plane" option with rotation and thresholded using the "height from mean plane" reference to exclude elevations below 0.1% and above 99.9% of the data to remove spikes. Dust and debris on the surface were erased digitally when present and resultant missing data were filled using the "smooth shape calculated from the neighbors" option. Next, a second-order polynomial was applied to remove background form (Arman et al. 2016; Martin et al. 2020).

Because rodent incisors tend to lack flat facets, such as those on molars resulting from mastication, furrows forming the background surface can swamp effects of shallow striations on conventional texture measurement. As such, two distinct data collection protocols were employed in an effort to best characterize microwear signatures: (1) microwear feature analysis (Ungar 1995; Ungar et al., 1991), and (2) microwear texture analysis (Ungar et al. 2003, et seq.). See the discussion for further consideration and rationale.

Microwear feature analysis

For microwear feature analysis, a digital photosimulation of each surface was generated in MountainsMap 8 and resampled to a resolution of 0.6 µm per pixel. This resolution was selected to allow discrimination and measurement of individual striations while minimizing the visual impact of finer-scale background microstructure. Microware 4.02 (Ungar 2002) was used for the measurements. A mouse-driven cursor was employed to identify major and minor axes of each feature, and tallies (*n*), average feature length, width, and length of the mean vector of long-axis orientation (*r*)—a measure of concentration or homogeneity of striation orientations—were computed for each surface. Given concerns over intraobserver error, which tends to run about 7% for data generated using the Microware software package (Grine et al. 2002), all images were assigned random numbers and de-identified then reordered prior to analysis to assure that measurements were taken blind to both species and site. All microwear feature data were collected by a single observer (PSU).

Microwear texture analysis

First, an eigthth-order polynomial form removal filter was applied to all point clouds in MountainsMap 8 in an attempt to further eliminate background surface texture (following Merceron et al. 2017). Both ISO standard and scale-sensitive fractal analysis (SSFA) variables were calculated in MountainsMap 8 to characterize surface texture following commonly used microwear texture analysis protocols (see Belmaker 2018; DeSantis 2016 for descriptions).

A total of 22 attributes (ISO 25178) were included in the ISO study following past analyses of microwear texture (Purnell et al. 2013; Schulz et al. 2010, 2013). These include (1) height parameters (*Sq*, *Ssk*, *Sp*, *Sz*), (2) a functional parameter (*Sxp*), (3) spatial parameters (*Sal*, *Str*), (4) hybrid parameters (*Std, Sdq*, *Sdr*), (5) volume parameters (*Vmp*, *Vmc*, *Vvc*, *Vvv*), (6) feature parameters (*Spd*, *S5v*, *Sda*, *Sdv*, *Shv*), and (7) stratified surface parameters (*Svk*, *Smr1*, *Smr2*). These together provide a robust characterization of surface texture for microwear analysis (see Purnell et al. 2013; Schulz et al. 2010, 2013 for descriptions of individual variables).

Five SSFA variables were calculated using the MountainsMap Scale-Sensitive Analysis module. These include (1) under the area-scale one-corner option, area-scale fractal complexity (*Asfc*), scale of maximum complexity (*Smfc*), and heterogeneity of area-scale fractal complexity calculated in 3 × 3 and 9 × 9 grids ($HAsfc_9$ and $HAsfc_{81}$) and (2) under the length-scale option, exact proportion length-scale anisotropy of relief (*epLsar*). These attributes are described in detail by Scott et al. (2006), and together provide a characterization of change in roughness with scale, variation in texture complexity across the surface, and orientation of texture.

Statistical analyses

The feature-based data, the ISO data, and the SSFA data were separated into three sets of general linear models to facilitate analysis and interpretation. All data were rank-transformed to mitigate violation of assumptions inherent to parametric statistical analyses (following Conover and Iman 1981). All statistical tests were conducted using SYSTAT Version 13.2 (Systat Software Inc., San Jose, CA).

Each dataset was analyzed for comparisons of sites using separate MANOVAs for *La. gregalis* and *Le. sibiricus*. The sites were the independent variables, and feature, ISO, and SSFA attributes were the dependent variables. Separate ANOVAs and pairwise comparisons tests were used to determine sources of significant variation. Both Tukey's HSD and Fisher's LSD tests were used to balance risks of Type I and Type II error (Cook and Farewell 1996). Where Fisher's LSD but not Tukey's HSD test *p* values were < 0.05, results were considered suggestive but of marginal significance.

Each dataset was analyzed for comparisons of Siberian lemmings and narrow-headed voles at Sabetta and Erkuta (the two sites where they co-occur) using a two-factor MANOVA, with species and site as the independent variables and feature, ISO, and SSFA attributes as the dependent variables. This allowed assessment of site and species effects, as well as interaction between the two factors. Again, separate ANOVAs, Tukey's HSD, and Fisher's LSD tests were used to determine sources of significant variation where appropriate.

In addition, a principal component analysis (PCA) was run on a correlation matrix of the raw texture data, including both ISO and SSFA variables, to compare species at Erkuta and Sabetta. Many of the microwear texture variables analyzed here are likely interrelated, and a PCA reduced dimensionality for visualization of differences between species in bivariate space (the first two principal components). To assess the appropriateness of using a PCA, we adapted the statistical procedure used by Stuhlträger et al. (2019). Variables not normally distributed were log-transformed (*Asfc, Std, Sdv, Shv, Sda, Svk, Spd*) or inverse-transformed ($HAsfc_9$). Kaiser's Measure of Sampling Adequacy (MSA) values were obtained for individual variables with R 4.0.5 (R Development Core Team 2021) using the function "paf" in the R package rela version 4.1 (Chajewski 2009) and variables with MSA values lower than 0.5 (Cerny and Kaiser 1977) were removed (*HAsfc81, Ssk, Smr1 and Smr2*). The Kaiser–Meyer–Olkin (KMO) statistic calculated for all remaining variables is equal 0.7, indicating that the PCA is appropriate (Budaev 2010). Furthermore, a MANOVA was conducted on rank-transformed PCA data for PC1 and PC2 to compare species at Erkuta and Sabetta, with single-classification ANOVAs to determine source(s) of significant variation.

Results

Raw data are provided in SI 1. Statistics are presented in Tables 2, 3, 4, 5, and 6 and results are illustrated in Figs. 2, 3, 4, and 5. Supplemental exploratory analyses are available in SI 2. Results are here considered by dataset type.

Feature-based analysis

Results for the feature-based analysis are presented in Table 3 and Fig. 3. The MANOVA considering individual taxa showed significant variation between sites for both *Lasiopodomys gregalis* ($p = 0.027$) and *Lemmus sibiricus* ($p = 0.002$). Individual ANOVAs indicate that narrow-headed voles differ in both microwear striation density (n) and orientation homogeneity (r) and that Siberian lemmings differ in microwear striation density (n). More specifically, voles from Kharp have significantly lower n values than those from Erkuta and marginally lower ones than those from Sabetta, whereas lemmings from Bely have significantly lower n values compared with those from Erkuta or Sabetta. Further, voles from Sabetta have higher r values compared with those from Erkuta and marginally higher ones than those from Kharp. In sum, lemmings from Bely and voles from Kharp have low striation densities and voles from Sabetta have more homogeneously oriented striations.

When comparing *La. gregalis* and *Le. sibiricus* from Erkuta and Sabetta, where both species are found, the two-way MANOVA indicates significant variation between taxa ($p < 0.001$), but not between the two sites. Furthermore, there is no interaction between species and sites in the model. Voles and lemmings thus differ in microwear feature pattern independent of site but values do not differ between Erkuta and Sabetta using this model (though, again, the model comparing only voles at all the sites did show a difference in r values between Erkuta and Sabetta). *Lasiopodomys gregalis* has higher n values and higher r values than *Le. sibiricus* at Erkuta and Sabetta. In other words, voles have higher striation densities and more homogeneously oriented striations than lemmings at these sites.

Microwear texture analyses

Results for the microwear texture analyses are presented in Tables 4, 5, and 6 and Figs. 4 and 5. Neither the ISO nor SSFA datasets separated samples by site. MANOVA results with site as the independent variable for *La. gregalis* were $p = 0.102$ (ISO data) and $p = 0.419$ (SSFA data) and for *Le. sibiricus* were $p = 0.532$ (ISO data) and $p = 0.643$ (SSFA data).

The two-way MANOVAs comparing *La. gregalis* and *Le. sibiricus* from Sabetta and Erkuta, on the other hand, indicate significant variation between taxa with $p = 0.004$ (ISO data) and $p = 0.003$ (SSFA data). Neither dataset shows significant variation between Sabetta and Erkuta, nor an interaction between species and sites. Again, voles and lemmings differ in microwear textures independent of site, but Sabetta and Erkuta samples do not differ significantly from one another for these species.

Individual ANOVAs indicate that the two species differ significantly in 14 of 22 ISO attributes (*Sq*, *Sp*, *Sz*, *Sxp*, *Str*, *Vmp*, *Vmc*, *Vvc*, *Vvv*, *Spd*, *S5v*, *Sda*, *Sdv*, *Shv*) and 2 of 5 SSFA variables (*Smfc*, *epLsar*). *Lasiopodomys gregalis* has lower values than *Le. sibiricus* for 12 of the 14 significant ISO variables (*Sq*, *Sp*, *Sz*, *Sxp*, *Vmp*, *Vmc*, *Vvc*, *Vvv*, *S5v*, *Sda*, *Sdv*, *Shv*). These variables relate largely to the heights of peaks and the areas and volumes of hills and dales on the surface. *Lasiopodomys gregalis* has higher values for *Str* (texture aspect ratio, a measure of uniformity of texture) and *Spd* (density of peaks, number of peaks per unit area) values than does *Le. sibiricus*. These attributes together suggest surfaces with larger features for lemmings and smaller features, but more of them, for voles. The SSFA attributes indicate lower *Smfc* and higher *epLsar* values for *La. gregalis* than *Le. sibiricus*. This is also consistent with more small features, but also more texture anisotropy of those features for voles than lemmings.

Finally, the PCA confirmed variation in microwear texture between lemmings and voles at Erkuta and Sabetta (Table 6, Fig. 5). More than 51% of the variance was explained by component 1, with component loadings $>|0.4|$ for 20 of 23 variables, $>|0.6|$ for 14 variables, and $>|0.8|$ for 9 variables. Nearly 19% of the variance was explained by component 2, with component loadings $>|0.4|$ for 8 variables $>|0.6|$ for 5 variables, and $>|0.8|$ for 1 variable. The MANOVA on PC1 and PC2 confirmed significant variation in microwear texture between the *Le. sibiricus* and *La. gregalis* ($p < 0.001$), and ANOVA results indicated significant variation using the $p < 0.05$ threshold for PC1 ($p = 0.002$) but not PC2 ($p = 0.069$).

Discussion

Analyses presented here indicate differences between Siberian lemmings and narrow-headed voles at the same sites and differences within these species at different sites. The *Lasiopodomys gregalis* samples have more striations and more homogeneously oriented striations at Erkuta and Sabetta than do the *Lemmus sibiricus* samples. The texture

Table 2 Descriptive statistics by samples showing significant variation

	Lemmus sibiricus			*Lasiopodomys gregalis*		
	Erkuta	Sabetta	Bely	Kharp	Erkuta	Sabetta
Sample	11	10	10	7	11	10
Features						
r						
Mean	0.648	0.563	0.706	0.590	0.709	0.822
SD	0.166	0.196	0.249	0.261	0.109	0.071
n						
Mean	17.455	28.100	5.500	18.571	39.364	35.800
SD	10.434	16.306	4.813	11.928	17.817	14.413
ISO						
Sq						
Mean	0.220	0.198	0.205	0.166	0.172	0.163
SD	0.047	0.034	0.064	0.025	0.041	0.051
Sp						
Mean	1.107	1.021	1.074	1.262	0.775	0.880
SD	0.237	0.331	0.475	0.657	0.289	0.246
Sz						
Mean	2.110	1.991	2.040	1.919	1.454	1.592
SD	0.483	0.452	0.598	0.797	0.450	0.509
Sxp						
Mean	0.420	0.397	0.398	0.326	0.355	0.328
SD	0.093	0.073	0.122	0.064	0.079	0.106
Str						
Mean	0.286	0.242	0.281	0.388	0.512	0.416
SD	0.170	0.103	0.118	0.117	0.169	0.143
Vmp						
Mean	0.011	0.009	0.011	0.009	0.009	0.008
SD	0.003	0.002	0.004	0.001	0.003	0.004
Vmc						
Mean	0.196	0.177	0.179	0.146	0.150	0.140
SD	0.043	0.032	0.060	0.024	0.033	0.038
Vvv						
Mean	0.024	0.023	0.023	0.019	0.021	0.020
SD	0.006	0.004	0.007	0.004	0.005	0.007
Spd						
Mean	0.006	0.006	0.006	0.009	0.009	0.010
SD	0.002	0.003	0.002	0.005	0.003	0.004
S5v						
Mean	0.754	0.728	0.719	0.562	0.621	0.599
SD	0.162	0.157	0.205	0.110	0.161	0.245
Sda						
Mean	239.813	237.340	230.030	226.160	158.895	156.730
SD	118.859	79.023	121.562	148.326	76.478	58.092
Sdv						
Mean	3.827	3.664	3.846	4.178	2.137	2.656
SD	2.806	1.723	3.606	4.387	1.726	2.973
Shv						
Mean	4.506	3.564	3.577	4.354	1.767	1.448
SD	3.609	2.588	2.449	5.295	1.184	0.793

Table 2 (continued)

	Lemmus sibiricus			*Lasiopodomys gregalis*		
	Erkuta	Sabetta	Bely	Kharp	Erkuta	Sabetta
Sample	11	10	10	7	11	10
SSFA						
Smfc						
Mean	10.006	5.862	10.912	4.770	3.787	0.410
SD	9.456	9.551	19.846	6.231	4.154	0.333
epLsar						
Mean	0.018	0.019	0.019	0.018	0.019	0.020
SD	0.001	0.001	0.001	0.001	0.001	0.001

analyses confirm a higher density of smaller features and more texture anisotropy (*epLsar*) in voles than lemmings. Texture dataset MANOVAs did not resolve significant variation between sites for either species (but see below), though feature-based analyses did evince differences between sites. Narrow-headed voles from the forest-tundra ecotone site of Kharp have lower striation densities than those from tundra sites of Erkuta and Sabetta. Also, *La. gregalis* from the low–high Arctic border site of Sabetta have more homogeneously oriented striations than those from the other sites. In contrast, the *Le. sibiricus* sample from the high Arctic site on Bely Island has fewer microwear striations than either the Erkuta or Sabetta lemming samples. These differences are largely consistent with variation in bioclimatic zone between sites and differences in microhabitat preference and reported burrowing behavior between species.

Differences between the sites

The differences in vegetative cover between the sites likely contribute to differences in environmental abrasive load. Recall that Kharp is the only site with trees (mostly Siberian larches, *Larix sibirica*), and that its thickets (*Salix* sp., *Betula* sp.) are approximately 2 m in height. At Erkuta, willow thickets are shorter, ranging between 1 and 2 m in height. And Sabetta willow thickets are shorter still, averaging about 40 cm in height. Thus, we expect an increase in environmental grit load from Kharp to Erkuta to Sabetta given the decreasing height of ground cover (Ungar et al. 2021). We also expect less environmental grit on Bely than at either Erkuta or Sabetta because, despite a lack of trees and thickets, the site is covered in lush, wet mosses. In contrast, Erkuta and Sabetta have networks of rivers, streams, and lakes with sandy shores and large, relatively high elevation open areas devoid of vegetation. Winds carry grit that settles on plants at Erkuta and Sabetta between the end of June and August (see Melnikov 1991; Trofimov et al. 1980). This contrasts with conditions at the Bely Island and Kharp sites, which lack the river networks and lake settings with open sandy areas (see Trofimov 1986).

As an additional note, studies from other sites have shown that endogenous silica concentration (by weight) in open tundra dominated by phytolith grasses and sedges averages more than four times that in lower latitude boreal forests (Carey and Fulweiler 2012). Likewise, soil amorphous silica concentration tends to be twofold to threefold higher in graminoid tundra than wetlands (Alfredsson et al. 2016). We hope that future study of phytolith load variation between the sites might also contribute to our understanding of microwear differences.

When we consider microhabitat types, for lemmings, while Bely Island and Erkuta specimens were all trapped in wet plots, half the Sabetta specimens come from thickets. The lack of significant variation between Sabetta and Erkuta in the two-factor MANOVA models, and lack of consistent differences in striation counts between wet- and thicket-trapped samples (See SI 1) suggest that trapping microhabitat may play less of a role in microwear patterning for lemmings than does overall habitat type characterizing each site. On the other hand, for voles, Erkuta stands out more from Kharp than does Sabetta, with seven individuals from dry microhabitat traps (compared with two for Sabetta and none for Kharp); and this is consistent with better separation of striation density from Kharp for Erkuta than Sabetta (significantly different by Tukey's HSD for the former but only by Fisher's LSD for the latter). That said, orientation concentration differences, with Sabetta significantly different from Erkuta by Tukey's HSD and from Kharp by Fisher's LSD but no difference between Kharp and Erkuta, cannot be explained by trapping microhabitat differences. More work on larger samples will likely help us better understand the role of trapping microhabitat, if any, within each larger site in rodent incisor microwear patterning.

Nevertheless, the between site differences remain and these are consistent with expectations given that abrasive loads, both endogenous and exogenous, are likely higher at Erkuta and especially Sabetta than at Kharp or Bely

Table 3 Feature-based analytical statistics (all analyses using rank-transformed data)

A. General linear models comparing sites by taxon

MANOVAs (Pillai Trace)

	V	*F*	*df*	*p*
Lasiopodomys	**0.597**	**2.445**	**8, 46**	**0.027**
Lemmus	**0.708**	**3.562**	**8, 52**	**0.002**

ANOVAs	*Lasiopodomys*			*Lemmus*		
	df	*F*	*P*	*df*	*F*	*p*
Length	2	2.43	0.109	2	3.211	0.056
Error	25			28		
Width	2	0.232	0.794	2	0.264	0.770
Error	25			28		
r	**2**	**4.264**	**0.026**	2	1.129	0.338
Error	25			28		
n	**2**	**4.511**	**0.021**	**2**	**13.605**	**< 0.001**
Error	25			28		

Paired comparisons

	Lasiopodomys r		*Lasiopodomys n*		*Lemmus n*	
	Erkuta	Kharp	Erkuta	Kharp	Bely	Erkuta
Kharp	− 0.773		− 10.097**		10.186**	
Sabetta	8.177**	8.95*	− 1.205	8.893*	15.300**	5.114

B. General linear models comparing species (Sabetta and Erkuta)

MANOVAs (Pillai Trace)	*V*	*F*	*df*	*P*
Species	**0.447**	**7.072**	**4, 35**	**< 0.001**
Site	0.076	0.724	4, 35	0.581
Interaction	0.204	2.237	4, 35	0.085

ANOVAs for species

	F	*df*	*p*
Length	1	0.038	0.847
Error	38		
Width	1	1.340	0.254
Error	38		
r	**1**	**14.706**	**< 0.001**
Error	38		
n	**1**	**12.881**	**0.001**
Error	38		

Bolded values indicate significance at $p < 0.05$

Island. The higher densities of microwear striations on narrow-headed vole incisors at Sabetta and Erkuta compared with Kharp and on Siberian lemming incisors at Sabetta and Erkuta compared with Bely make most sense in this light.

Differences between the species

Differences between the species in microwear patterning may relate to variation in diet, microhabitat preference, and/or substrate use (i.e., tunneling behavior). First, the

Table 4 ISO attribute microwear texture analysis. Bolded values indicate significance at $p < 0.05$

A. General linear models comparing sites by taxon

MANOVAs (Pillai Trace)

	V	*F*	*df*	*p*
Lasiopodomys	1.805	2.110	44, 10	0.102
Lemmus	1.464	0.993	44, 16	0.532

B. General linear models comparing species (Sabetta and Erkuta)

MANOVAs (Pillai Trace)	*V*	*F*	*df*	*p*
Species	**0.826**	**3.669**	**22, 17**	**0.004**
Site	0.589	1.109	22, 17	0.420
Interaction	0.441	0.608	22, 17	0.864

ANOVAs for species

	df	*F*	*p*		*df*	*F*	*P*
Sq	**1**	**7.292**	**0.010**	***Vmc***	**1**	**14.730**	**< 0.001**
Error	38			**Error**	**38**		
Ssk	1	1.862	0.180	***Vvc***	**1**	**14.251**	**0.001**
Error	38			Error	38		
Sp	**1**	**8.694**	**0.005**	***Vvv***	**1**	**4.594**	**0.039**
Error	38			Error	38		
Sz	**1**	**17.487**	**0.000**	***Spd***	**1**	**11.120**	**0.002**
Error	38			Error	38		
Sxp	**1**	**6.004**	**0.019**	***S5v***	**1**	**7.960**	**0.008**
Error	38			Error	38		
Sal	1	0.047	0.830	***Sda***	**1**	**9.649**	**0.004**
Error	38			Error	38		
Str	**1**	**16.489**	**< 0.001**	***Sdv***	**1**	**7.217**	**0.011**
Error	38			Error	38		
Std	1	0.991	0.326	***Shv***	**1**	**12.956**	**0.001**
Error	38			Error	38		
Sdq	1	1.372	0.249	*Svk*	1	2.147	0.151
Error	38			Error	38		
Sdr	1	1.370	0.249	*Smr1*	1	0.000	0.992
Error	38			Error	38		
Vmp	**1**	**4.534**	**0.040**	*Smr2*	1	1.061	0.309
Error	38			Error	38		

Bolded values indicate significance at $p < 0.05$

two species evidently differ in both preferred foods and the variety of items they consume. Published work documenting food preferences of *Le. sibiricus* and *La. gregalis* in the region are limited to studies in Yamal north of Erkuta by Dunaeva (1948) and on the western shore of Baydaratskaya Bay by Kopein (1958). These mid-twentieth century studies documented diet based on identification of plants with gnaw marks, remains of stored food, and items consumed during ad libitum feeding experiments with captive individuals.

According to Dunaeva (1948), Siberian lemmings in Yamal are sedge specialists, consuming mostly cotton grass (*Eriophorum vaginatum*). They do consume other plant species on occasion though, including dwarf birch leaves and young shoots, some willows (*Salix* sp.), cloudberry, and *Equisetum* sp. Kopein (1958) found that Siberian lemmings on the western shore of Baydaratskaya Bay also prefer sedges (especially *Carex* sp. also *Eriophorum* sp.) though they sometimes also consume herbs (*Equisetum* spp.), *Rubus chamaemorus*, *Salix* sp. and *Vaccinium uliginosum*. These lemmings are not reported to eat lichens or mosses, despite their use for nests.

Table 5 Scale-sensitive fractal analysis. Bolded values indicate significance at $p < 0.05$

A. General linear models comparing sites by taxon

MANOVAs (Pillai Trace)

	V	*F*	*df*	*p*
Lasiopodomys	0.386	1.051	10, 44	0.419
Lemmus	0.271	0.785	10, 50	0.643

B. General linear models comparing species (Sabetta and Erkuta)

MANOVAs (Pillai Trace)

	V	*F*	*df*	*p*
Species	**0.392**	**4.382**	**5, 34**	**0.003**
Site	0.231	2.046	5, 34	0.097
Interaction	0.066	0.478	5, 34	0.790

ANOVAs for species

Univariate *F* tests

Source	*df*	*F*	*p*
Asfc	1	0.445	0.509
Error	38		
Smfc	**1**	**6.937**	**0.012**
Error	38		
$HAsfc_{9}$	1	0.641	0.428
Error	38		
$HAsfc_{81}$	1	1.639	0.208
Error	38		
epLsar	**1**	**16.318**	**< 0.001**
Error	38		

Bolded values indicate significance at $p < 0.05$

Studies of narrow-headed voles suggest that *La. gregalis* has a much broader diet, including at least 40 species of sedges, grasses, and herbs of *Eriophorum, Carex, Salix, Equisetum, Artemisia, Tilesii,* and *Astragalus* among others (Kopein 1958). Narrow-headed vole diet evidently varies between localities, with more grass eaten north of Erkuta, but more herbs consumed on the western coast by Baidaratskaya Bay (Kopein 1958). These observations imply a broader, more flexible diet for the voles than for the lemmings of Yamal, though more work is needed to confirm this.

It is unclear to what extent dietary differences would be reflected in variation in incisor microwear, as opposed to molar microwear, which likely more directly reflects fracture properties of foods eaten (see Caporale and Ungar 2016; Belmaker 2018). That said, one might speculate that the consumption of a broader range of food types could be consistent with greater use of the front teeth for gnawing a variety of items, and consequently with higher frequencies of microwear striations and a broader range of feature sizes (including smaller ones) in voles at Erkuta and Sabetta. This would not, however, necessarily explain the greater anisotropy.

On the other hand, microhabitat preferences and variation in substrate use associated with tunneling very likely explain much of the microwear variation between lemming and vole incisors. *Lemmus sibiricus* inhabits the wetter mossy areas of Erkuta and Sabetta as well as Bely. In the summertime, these lemmings build nests in hummocks in moist sedge-moss tundra from sedge leaves with runway tracks through dense vegetation; and in the winter they nest in snow beds near hillsides (Dunaeva 1948). In contrast, *La. gregalis* often lives in drier sandy areas at all sites. These voles typically live in colonies consisting of individual burrows connected by paths and underground tunnels (Dunaeva 1948; Pal'chekh et al. 2003). Voles generally dig burrows in large part with their forelimbs, but they likely also use their incisors to loosen soil (Gromov and Polyakov 1992); and they certainly store food in these tunnels.

Higher striation densities on vole I_1s likely result in large part from greater exposure to environmental grit due

Table 6 Principal components analysis for the texture data (significant attributes only)

A. PC1 and PC2 loadings and variance explained

	1	2		1	2
Asfc	– 0.45430	0.80080	*Sdr*	– 0.63974	0.71042
Smc	– 0.49644	– 0.47954	*Vmp*	– 0.89629	0.18218
HAsfc9	– 0.34112	– 0.30617	*Vmc*	– 0.93586	0.05387
epLsar	0.52079	0.20546	*Vvc*	– 0.95345	0.02762
Sq	– 0.97729	0.12240	*Vvv*	– 0.90846	0.25695
Sp	– 0.60427	– 0.26836	*Spd*	0.56353	0.78386
Sz	– 0.86057	– 0.15437	*S5v*	– 0.89785	0.19009
Sxp	– 0.94153	0.20298	*Sda*	– 0.59925	– 0.74138
Sal	– 0.41736	0.09506	*Sdv*	– 0.68209	– 0.49803
Str	0.36740	0.26611	*Shv*	– 0.75581	– 0.56986
Std	– 0.30845	– 0.10073	*Svk*	– 0.82399	0.29764
Sdq	– 0.65972	0.71495			

Variance explained by components

	1	2
Variance	11.78	4.365
%	51.217	18.978

B Principal components general linear model

MANOVA (Pillai Trace)

	V	*F*	*df*	*p*
Species	0.332	8.380	2, 37	< 0.001

Univariate *F* tests

Source	*df*	*F*	*p*
PC1	1	11.200	0.002
Error	38		
PC2	1	3.505	0.069
Error	38		

to microhabitat preference, underground storage of food, and tunneling behavior. The regular use of incisors with repetitive orthal movements to loosen soil might in part explain the increased anisotropy and striation orientation concentration in the voles compared with the lemmings; though this does not explain the difference in *r* values between voles at Sabetta and the other sites. It is also possible that microwear formed predominantly by angular grit particles explains the smaller features on average seen in the voles (see Ungar 1994 for discussion). While the relative contributions of substrate use and microhabitat preference to variation in microwear patterning is yet to be determined, both likely play a role, particularly given differences within the species between sites that vary in environmental abrasivity. We expect that further study will allow us to work out the details.

Differences between methods

As an additional note, the difference in results between traditional feature-based microwear and texture analyses was unexpected. Texture analysis largely replaced feature-based methods as the gold standard for dental microwear studies in the 2010s (see Calandra and Merceron 2016; DeSantis 2016; Ungar 2015, 2018 for review). Feature-based analysis relies on an observer to identify, count, and measure striations and pits on two-dimensional photomicrographs or photosimulations of enamel surfaces. It is a time-consuming process subject to observer measurement error (Grine et al. 2002). In contrast, texture-based analysis uses quasi-3D point clouds (only one z value for any given x–y pair) and allows rapid and quantitative automated characterization of whole surfaces. Still, a few studies (e.g., Schulz et al. 2013; Kalthoff

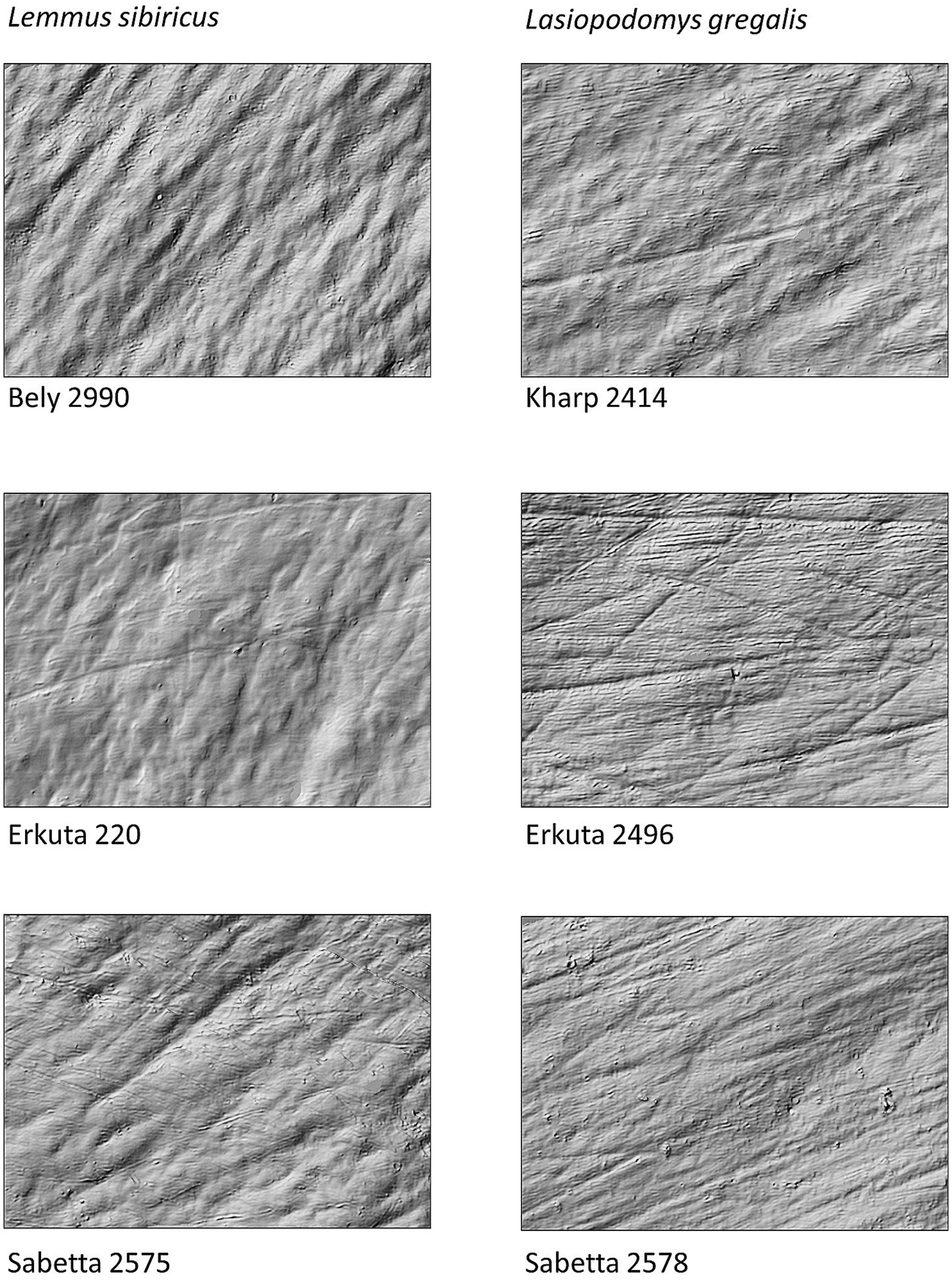


Fig. 2 Photomicrograph simulations for *Lemmus sibiricus* (left) and *Lasiopodomys gregalis* (right). Representative individuals from Bely Island and Kharp (top), Erkuta (middle), and Sabetta (bottom). Note that each image represents an area 102 μm × 138 μm on the original surface. These photosimulations employed second-order polynomial form removal only and are selected from those used in the microwear feature analysis

et al. 2019) have combined stereoscopic feature-based microwear and 3D surface texture analyses and suggested these can provide complementary data, with each approach separating groups by diet or abrasive load. Kalthoff et al. (2019) even found that microwear feature analysis separated some taxa that ISO parameters typically used in microwear texture analysis did not.

Nevertheless, microwear studies employing both feature-based and texture-based methods are rare. We began this study with the intent of using only texture analysis, but found that differences between individual surfaces obvious to the eye (see Fig. 2) were not reflected in either SSFA or ISO attribute values. It was clear that texture characterizations did not distinguish I_1 surfaces with a few wispy striations from those with none—likely because the rough larger-scale background surface topography swamped the striation “signal”. This problem has not arisen for us in the past for molar facets, which are typically polished flat by mastication. And neither second-order (following Arman et al. 2016) nor eighth-order polynomial filters (following Merceron et al. 2017) removed the background form sufficiently to allow resolution of differences in striation density on these surfaces. We added a microwear feature analysis to the study given that the human eye seems better able than either SSFA or standard ISO measures to resolve wispy striations from rough background textures. In the end, the proof is in the

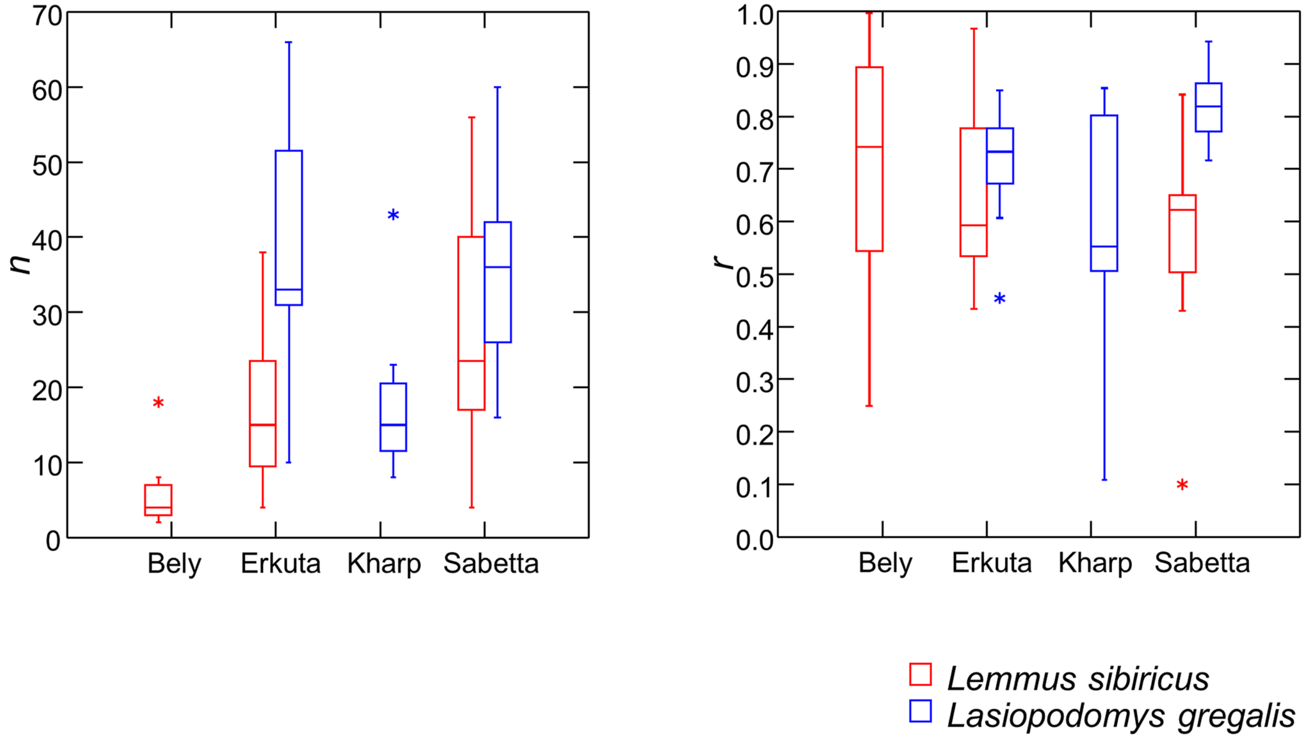


Fig. 3 Box and whiskers plots for dental microwear feature analysis attributes. Number (left) and mean vector length (right) of features considered by species and site. The hinges mark the first and third quantiles, the vertical lines between them are medians, each whisker represents a value 1.5 times the interquartile range, and asterisks are outliers

pudding—significant variation between species and sites in striation density and alignment match visually obvious differences between the samples. This affirms that feature-based analyses still have an important role to play in quantitative characterization of microwear patterning, at least for complex or lightly worn surfaces with background textures that obfuscate subtle variation between samples.

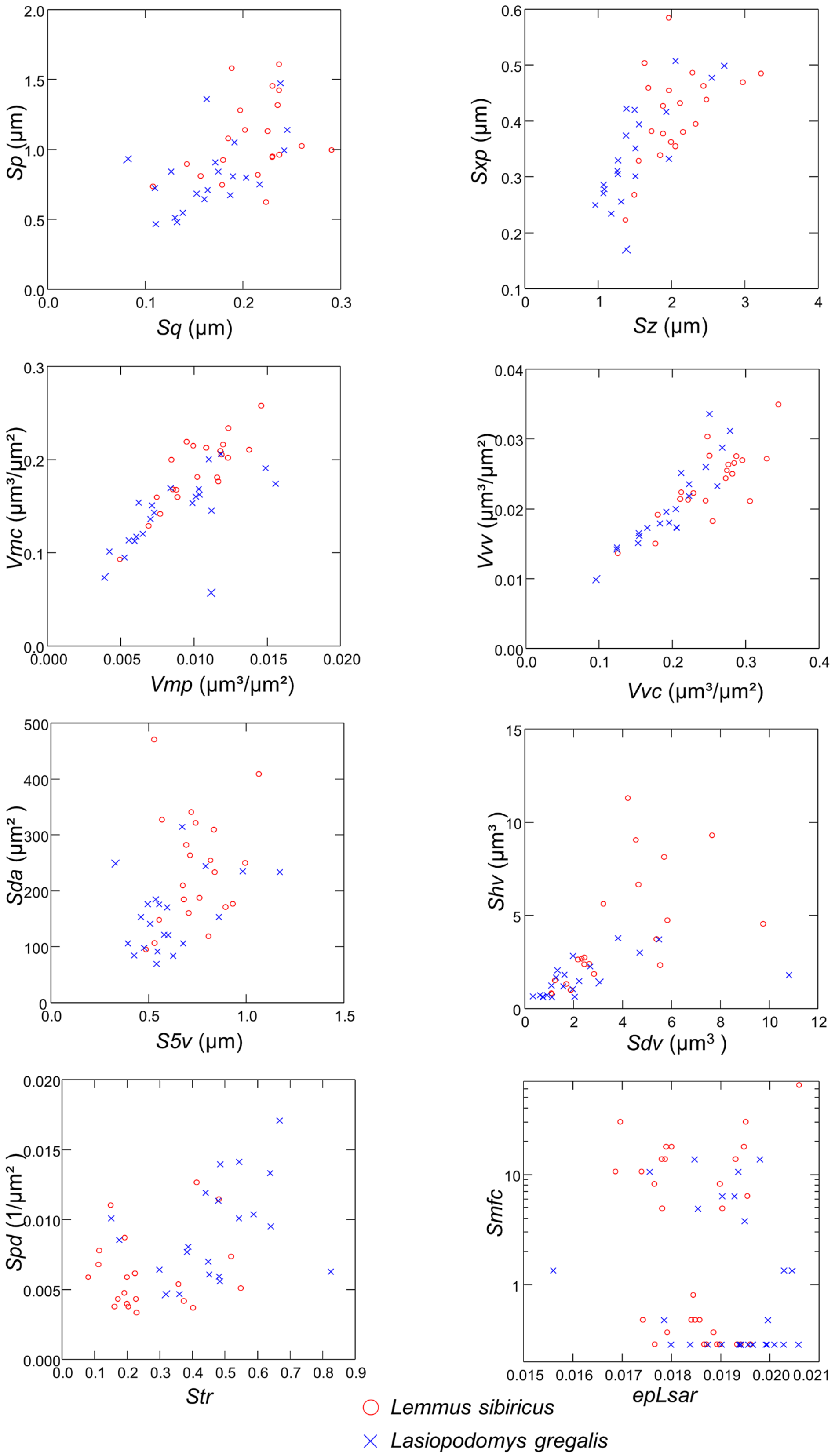
Future directions

Dental microwear analyses often rely on large samples to separate groups given inherent variation within them. Within-species variation is common because microwear reflects short-term behaviors—features can accumulate and patterns can be overwritten in a matter of days (Grine 1986; Teaford and Oyen 1989; Teaford et al. 2020). As noted above, this is especially so for microwear on the tips of fast-wearing rodent incisors. This can present a challenge when characterizing the microwear surfaces of species that move about the landscape and consume a variety of items in a range of microhabitats. The samples in this study vary from $n=7$ to $n=11$ individuals for each site-species combination. It is possible that larger samples might have allowed resolution of microwear feature measurement differences between Erkuta and Sabetta and perhaps texture differences between sites. In addition, comparisons of results for the I_1s with microwear patterns for maxillary incisors and molars might yield further insights into behavioral and diet differences between voles and lemmings and/or within each species between sites.

Exploratory analyses provide some hints regarding future directions for the I_1s (see SI 2). While the MANOVA model showed no significant variation in texture between sites for either lemmings or voles, individual ANOVAs did suggest a few attributes that might vary between samples, at least if an experiment-wise error rate is not employed (see Perneger 1998). For example, *La. gregalis* from Kharp has a higher *Ssk* average (a measure of skewness of the distribution of heights on a surface) than narrow-headed voles at Erkuta or Sabetta, and Erkuta voles have a lower *Smr2* average (percentage of measurement area in deeper valleys) than those at Kharp or Sabetta. As for variation between Erkuta and Sabetta independent of species, the lower latitude site has higher *Smfc* and the higher latitude one has higher *epLsar* than Erkuta.

While we caution against the “shotgun” approach of testing all texture attributes available given the risk of Type I statistical error, such analyses do hint that larger samples may facilitate better resolution of variation between groups. Furthermore, perhaps higher-order polynomial form removal

Fig. 4 Bivariate plots comparing species from Erkuta and Sabetta for all microwear texture attributes found to be statistically significantly different between *Lemmus sibiricus* and *Lasiopodomys gregalis*



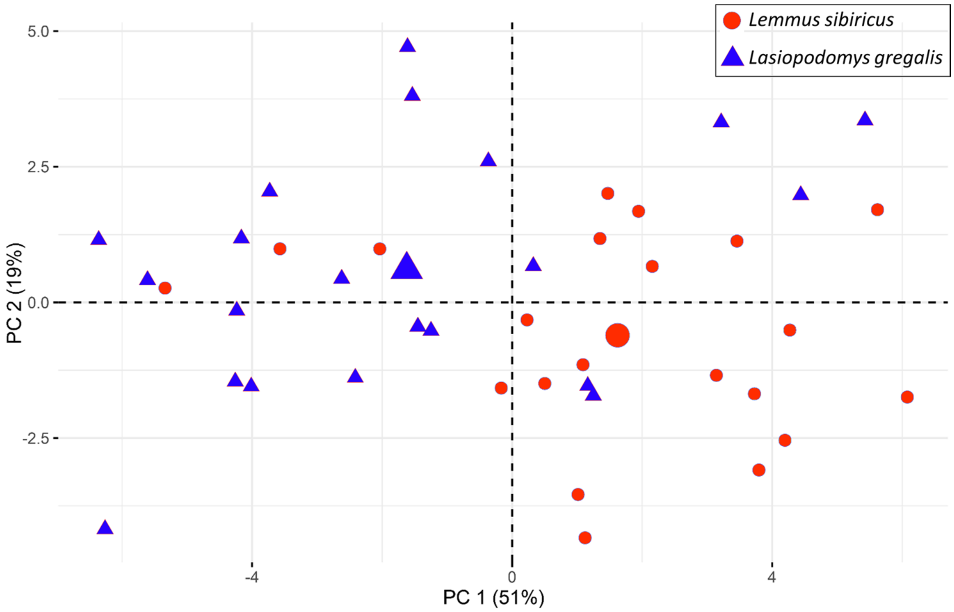


Fig. 5 Principal Component Analysis comparing *Lemmus sibiricus* and *Lasiopodomys gregalis*. The larger symbols indicate species means

(e.g., Schulz et al. 2013) or automated feature recognition algorithms may in the future help better separate microwear from background and amplify the signal to resolve more differences between groups.

Conclusions

This study indicates that I_1 labial surface microwear holds potential as a proxy for microhabitat use in Arctic arvicolines. The presence of higher striation densities and texture attributes suggesting more and smaller features for *La. gregalis* than *Le. sibiricus* at Erkuta and Sabetta are consistent with more open, drier, and abrasive microhabitats for narrow-headed voles and more closed, wetter ones for Siberian lemmings. This, along with more texture anisotropy and homogeneously oriented striations, may also be consistent with an inferred propensity for voles to loosen soil with their incisors while digging subterranean tunnels. Moreover, individuals of both species from the abrasive-rich open tundra sites of Erkuta and Sabetta have higher striation densities than conspecifics from the water-saturated, mossy site on Bely Island and the forest-tundra ecotone site of Kharp. These results suggest strongly that incisor microwear patterning varies with microhabitat use in a predictable manner, and, therefore, might serve as a useful proxy for aspects of the environment.

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Author contributions PSU, OG, AAS, NAS, SM, and AR conceived of the project, analyzed the data and wrote the paper. NAS, IF, and AAS collected original specimens analyzed in this paper. LS generated the digital models and photosimulations of the microwear surfaces, and PSU took the dental impressions and generated the microwear data.

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Data availability All raw data presented in this study are presented in Supplementary Information file (SI) 1. Original specimens are part of the permanent collection of the Institute of Plant and Animal Ecology in Labytnangi, Russia but currently on loan to the University of Burgundy, France.

Declarations

Conflict of interest The authors have no conflicts of interest or competing interests.

Ethical approval No ethics approvals were required to conduct this research.

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