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Incisor microwear of Arctic rodents as a proxy for microhabitat preference.

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4 **DECLARATIONS**
5

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9 collaboration that led to this work was developed through support from US National Science Foundation Award No:
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11

12
13 **Conflicts of interest/Competing interests.** The authors have no conflicts of interest or competing interests.
14

15 **Ethics approval.** No ethics approvals were required to conduct this research.
16

17 **Availability of data and material (data transparency).** All raw data presented in this study are presented in
18 Supplementary Information file (SI) 1. Original specimens are part of the permanent collection of the Institute of
19 Plant and Animal Ecology in Labytnangi, Russia but currently on loan to the University of Burgundy, France.
20

21 **Authors' contributions.** PSU, OG, AAS, NAS, SM, and AR conceived of the project, analyzed the data and wrote
22 the paper. NAS, IF, and AAS collected original specimens analyzed in this paper. LS generated the digital models
23 and photosimulations of the microwear surfaces, and PSU took the dental impressions and generated the microwear
24 data.
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32 LNG” company and Government of the Yamal Nenets Autonomous District, and the University of Arkansas Honors
33 College, for funds that allowed this work. The collaboration that led to this work was developed through support
34 from US National Science Foundation.
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4 **ABSTRACT**
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6 Current changing environmental conditions in the Arctic make it important to document and understand habitat
7 preferences and flexibility of vulnerable high-latitude mammals. Indirect proxies are especially useful for elusive
8 species such as rodents. This study explores incisor microwear as an indicator of variation in behavior and
9 microhabitat use within and between Siberian lemmings (*Lemmus sibiricus*) and narrow-headed voles
10 (*Lasiopodomys gregalis*) from the Yamalo-Nenets Autonomous District (Russian Federation). A total of 59
11 individuals were sampled at four sites along a latitudinal gradient spanning more than 700 km, from forest-tundra
12 ecotone to high tundra. Lemmings are present at the northernmost site, voles at the southernmost site, and both
13 species at the middle two sites. *Lemmus sibiricus* prefers wet, mossy lowland, whereas *La. gregalis* favors drier,
14 more open microhabitats and burrows underground. Results indicate significantly higher densities of smaller
15 features and more uniformly oriented scratches for voles than lemmings at sites with both species. Among voles,
16 individuals from open tundra sites have higher scratch densities than those from forest-tundra ecotone. Among
17 lemmings, individuals from the drier open tundra sites have higher scratch densities than those from the
18 northernmost site, which is water saturated and covered in moss. While microhabitat preferences and burrowing by
19 voles likely contribute to differences between the species, variation within species seems to reflect habitat variation
20 given differences in both exogenous and endogenous abrasive loads between sites. This suggests that incisor
21 microwear patterning reflects and can be used to track microhabitat differences among Arctic rodent populations.
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4 **INTRODUCTION**
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6 Ecologists interested in understanding changing climates and ecosystems of the Arctic have looked to
7 endemic rodents as key indicators (Post et al., 2009), or “canaries in the coal mine”. Lemming densities, for
8 example, are especially sensitive to changing winter weather (Ims et al., 2011), with fading outbreaks reported in
9 many areas (Gilg et al., 2009; Kausrud et al., 2008; Schmidt et al., 2012). Indeed, arvicoline rodents are in many
10 ways ideal model mammals for monitoring changes in the tundra biome (Christensen et al., 2013), so much so that
11 researchers associated with the Circumpolar Biodiversity Monitoring Program have focused on them over the past
12 two decades at 49 sites across the Arctic (Ehrich et al., 2020). But what do we really know about the resilience of
13 endemic high-latitude mammals, and how do these species respond to changing habitats and resources available in
14 them? We cannot simply go out and watch cryptic, elusive wild voles and lemmings to document where and what
15 they eat across the Arctic as glaciers retreat and permafrost melts. Still, this is just the sort of information
16 conservationists and policy makers need to develop strategies to protect vulnerable high-latitude populations and the
17 ecosystems they belong to.
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31 There are direct proxies available for diet of and microhabitat use by Arctic rodents, such as bite marks on
32 food plants (Dunaeva, 1948; Kopein, 1958), feces, and stomach contents of trapped individuals (Soininen et al.,
33 2013). These are, however, of limited value in and of themselves. Bite marks are found only on plant parts left
34 uneaten and can be difficult to assign to species when sympatric taxa are present. Feces and stomach contents give
35 only single-meal scale information and can be biased by differential digestion rate. Indirect proxies, or “foodprints”,
36 including stable isotope ratios (e.g., Baltensperger et al., 2015; Calandra et al., 2015; Soininen et al., 2014) and
37 dental wear pattern at both mesowear and microwear scales (Calandra et al., 2016; Kropacheva et al., 2017; Ungar et
38 al., 2020), can provide further information about individuals at longer time intervals, from days to weeks to
39 lifetimes. Such approaches have the added value of applicability to specimens gathered over considerable spans of
40 time and space and archived in research and museum collections. Thus they can be used to answer questions
41 difficult to address with fieldwork today.
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55 The current study assesses the potential of one such foodprint, dental microwear, as a proxy for
56 microhabitats of Arctic arvicolines. Previous studies have demonstrated that dental microwear of rodents can
57 provide a useful tool for inferring diet and habitat. Molar studies have shown distinctive patterns of microscopic
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4 scratching and pitting dependent on broad food preferences and habitat types (Firmat et al., 2011; Firmat et al.,
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6 2010; Hautier et al., 2009; Nelson et al., 2005; Rodrigues et al., 2009; Rodrigues et al., 2013; Townsend and Croft,
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8 2008; Winkler et al., 2016). Molar microwear may even be able to resolve subtler differences within and between
9
10 species with versatile diets (Burgman et al., 2016; Robinet et al., 2020). Indeed, a recent microwear analysis of field
11
12 vole (*Microtus agrestis*) molars showed marked seasonal differences in texture pattern consistent with changes in
13
14 diet between autumn and spring in Finnish Lapland (Calandra et al., 2016).

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17 Rodent incisor microwear appears better suited to separating groups by habitat type than by diet (but see
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19 Belmaker and Ungar, 2010). While patterns on molar teeth are driven largely by angle of approach between
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21 opposing occlusal surfaces, which may reflect fracture properties of foods (Adams et al., 2020; Hua et al., 2015),
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23 incisor microwear is free from confounding signals related to masticatory dynamics. Moreover, incisors are at the
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25 interface between environment and animal, and therefore likely reflect variation in environmental abrasive load (see
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27 Belmaker, 2018). Indeed, preliminary analysis suggests that anterior dental microwear texture patterns parse rodent
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29 species in wetter, closed settings from those in more open habitats (Caporale and Ungar, 2016). This underscores the
30
31 value of incisor microwear as a proxy for environmental abrasiveness, which varies with precipitation and
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33 vegetative cover (see Belmaker, 2018).

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36 Two species well suited to assess potential of incisor microwear as a proxy for Arctic habitat use are
37
38 *Lemmus sibiricus* (the Siberian brown lemming) and *Lasiopodomys* (formerly *Microtus* or *Stenocranius*) *gregalis*
39
40 (the narrow-headed or narrow-skulled vole). These iconic Palearctic rodents overlap substantively in range but differ
41
42 in microhabitat preference. Siberian lemmings prefer wetlands and lowland tundra with substantial moss and sedge
43
44 cover and are found today throughout the Russian Arctic (Tsytulina et al., 2016). Narrow-headed voles, in contrast,
45
46 typically inhabit more open grassy areas of tundra, plains, mountain steppes, and meadows (Batsaikhan et al., 2016).
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48 These voles were, until the Holocene warming, continuously distributed across northern Eurasia (Baca et al., 2019;
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50 Markova et al., 2019); but they are now confined to disjunct areas spread from western Russia to eastern China.

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53 This study focuses specifically on *Le. sibiricus* and *La. gregalis* in the Yamalo-Nenets Autonomous
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55 District, northwestern Siberia, Russian Federation. The Yamal Peninsula and adjacent Bely Island present an ideal
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57 natural laboratory for assessing impacts of habitat variation on high-latitude rodents. The peninsula extends over 700
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59 km from south to north with no insurmountable geographical barriers, such as impassable mountains, glaciers, or
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4 seasonally unfordable rivers. Bely is ca. 63 km x 41 km and located approximately 15 km from the northern tip of
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6 Yamal in the Kara Sea. These together represent a biogeographic gradient between forest-tundra ecotone and high
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8 Arctic. Comparisons of incisor microwear patterning between species where they overlap and especially within
9
10 species between sites in different bioclimatic subzones allows us to determine whether this footprint can serve as a
11
12 proxy for microhabitat use and, by extension, as a tool for assessing impact of climate change on the ecology of
13
14 endemic rodents of the Arctic.
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16 17 18 19 **MATERIALS AND METHODS**

20 21 **Study area**

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23 All specimens examined in this study were collected on the Yamal Peninsula and adjacent Bely Island.
24
25 Together, Yamal and Bely form a biogeographic gradient between Arctic bioclimatic subzone E (mean July
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27 temperature of 9–12.8°C, dominated by with erect shrubs, tussock sedges, and mosses) and subzone B (mean July
28
29 temperature 3–5.8°C, dominated by sedges and mosses with prostrate dwarf shrubs) (see Walker et al., 2005 and
30
31 Figure 1). All individuals were trapped at four research sites located strategically along a latitudinal gradient for
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33 sampling rodents and other endemic fauna: (1) Kharp in the forest-tundra ecotone (66.8°N, 66.4°E), (2) Erkuta in
34
35 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
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37 (4) Bely in the high Arctic (73.3°N, 70.1°E).
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41 Kharp is located just south of subzone (E) and is the only site with trees (mostly Siberian larches, *Larix*
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43 *sibirica*). Willow thickets (*Salix* spp.) extend more than two meters in height. Kharp is dominated by herbs
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45 *Calamagrostis purpurea*, *C. lapponica*, *Comarum palustre*, *Equisetum arvense*, *Rubus arcticus*, several *Carex*
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47 species and mosses (e.g., *Mnium* sp., *Polytrichum* sp., *Sphagnum* sp.). Erkuta is in the middle of bioclimatic subzone
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49 E, which is characterized by 80-100% vascular plant cover and a total phytomass reaching 100 t*ha⁻¹. Willow
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51 thickets range between one and two meters in height. Vegetation at Erkuta is dominated by *Ledum decumbens* and
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53 *Calamagrostis langsдорffii*, *Carex* spp., *Equisetum arvense*, *Poa arctica*, *Rubus arcticus*, *Veratrum lobelianum* and
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55 mosses (*Sanionia uncinata*). Sabetta is on the border of bioclimatic subzones C and D. It has approximately 50%
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57 cover of vascular plants with interrupted closed or patchy vegetation (see Walker et al., 2015). Total phytomass at
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59 Sabetta is estimated as 30 t*ha⁻¹, with willow thickets up to “knee height” (ca. 0.40 m maximum), and its vegetation
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4 is dominated by *Carex* spp., *Arctagrostis latifolia*, *Hierochloe alpine*. Bely Island is within subzone B, with cover of
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6 vascular plants (approximately 25 %) and cryptogams (up to 60 %). Total phytomass at Bely Island is estimated as
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8 20 t*ha-1 (see Walker et al., 2005). Bely has virtually no thickets, with a ground surface largely covered by mosses,
9
10 particularly *Drepanocladus*, *Calliergon*, and *Sphagnum*. Further details on Yamal vegetation can be found in
11
12 Magomedova et al. (2006).

13
14 No lemmings are found at Kharp, but vole species at the site include *Lasiopodomys gregalis*, *Microtus*
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16 *middendorffii*, *Mi. agrestis*, *Alexandromys* (formerly *Microtus*) *oeconomus*, *Myodes rutilus*, *Myodes rufocanus* and
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18 *Arvicola amphibius*. *Myodes* species dominate the rodent community at Kharp. Erkuta has both *La. gregalis* and
19
20 *Lemmus sibiricus*, though the former outnumber the latter. The rodent community at Erkuta also includes the
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22 lemming *Dicrostonyx torquatus*, and the voles *Mi. middendorffii*, and *Myodes rutilus*. Sabetta has mostly lemmings,
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24 both *Le. sibiricus* and *D. torquatus*, but also *La. gregalis*. Finally, *Le. sibiricus* is the only rodent species on Bely
25
26 Island. Therefore, specific to the taxa included in the present study, the southern site of Kharp has only *La. gregalis*,
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28 the northern site on Bely Island has only *Le. sibiricus*, and the intermediate latitude sites at Erkuta and Sabetta have
29
30 both narrow-headed voles and Siberian lemmings.
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33 A total of 59 individuals were sampled for microwear in this study. These included 31 *Le. sibiricus* ($n = 11$
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35 from Erkuta, $n = 10$ from Sabetta, and $n = 10$ from Bely Island) and 28 *La. gregalis* ($n = 7$ from Kharp, $n = 11$ from
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37 Erkuta, and $n = 10$ from Sabetta). These specimens were collected during snap-trap sessions at Kharp (June and
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39 September, 2013 and 2016), Erkuta (June and August 1999 and 2014), Sabetta (July, 2014), and Bely (July, 2015)
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41 following small-quadrat field protocol (Myllymäki et al., 1971). At each site, three traps were baited with raisins and
42
43 rolled oats at each corner of a 15x15 m permanent quadrat (i.e. twelve traps per quadrat) for two nights. Collections
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45 were made at spatially distinguished units (at least two km apart) with groups of quadrats representing a given
46
47 habitat separated by at least 200 m. Small quadrats were spread through different microhabitats in all three sites.
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49 Trapped individuals showed clear microhabitat preferences by species. On Bely Island, where only Siberian
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51 lemmings were recovered, nearly all trapping quadrats were situated in very wet lowlands. Erkuta and Sabetta had a
52
53 combination of overwet mossy lowlands and dry sandy microhabitats in willow thickets and riverbanks. All *Le.*
54
55 *sibiricus* individuals at Erkuta and Sabetta were trapped in the wetter mossy areas, whereas all *La. gregalis* were
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57 recovered from drier sandy areas. All narrow-headed voles at Kharp were also trapped in dry sandy microhabitats.
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59 The trapping protocol used is described in detail in Sokolova et al. (2014).
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6 **Specimen preparation and data acquisition**
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8 Specimens were dissected in the field, with heads removed and kept in a 20-40% ethanol solution. Skulls
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10 were then processed in the laboratory at the Institute of Plant and Animal Ecology Arctic Research Station in
11 Labytngangi by boiling and drying. Only adult and subadult individuals were considered in this study (age categories
12 follow Bashenina, 1962). Dental replicas were produced following conventional microwear specimen preparation
13 techniques for a sample on loan to UMR CNRS 6282 Biogéosciences at the University of Burgundy (Dijon, France).
14 First, mandibular incisor (I_1) enamel surfaces were cleaned with alcohol-soaked cotton swabs and allowed to dry.
15 Dental impressions were taken with President's Jet Regular Body polyvinylsiloxane dental impression material
16 (Coltène-Whaledent Corp., Cuyahoga Falls, OH, USA). High-resolution replicas were later prepared at the
17 University of Arkansas using Epotek 301 cold-cure epoxy (Epoxy Technologies, Billerica, MA), centrifuged into the
18 molds, and allowed to set before analysis. All replicas were subsequently screened by confocal profilometry at 100x,
19 and analysis was limited to those specimens with unobscured antemortem microwear (see Teaford, 1988 for
20 criteria).
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32 Microwear sampling focused the I_1 labial surface just below the incisal edge. High-resolution replicas were
33 scanned using a Sensofar Pl μ standard white-light scanning confocal profiler (Solarius Development Inc.,
34 Sunnyvale, CA). Each surface was scanned at 100x, for a work envelope of 138 μm x 102 μm , a lateral point
35 spacing of 0.18 μm , vertical step of 0.2 μm , and vertical resolution (as reported by the manufacturer) of 0.005 μm .
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40 Resultant surfaces were leveled using SensoMap Premium Software (MountainsMap 8, Digital Surf Corp,
41 Besançon, France) and thresholded to exclude elevations below 0.1% and above 99.9% of the data to remove spikes.
42 Dust and debris on the surface were erased digitally when present and resultant missing data were filled using a
43 nearest-neighbor algorithm. Next, a 2nd-order polynomial was applied to remove background form (Arman et al.,
44 2016; Martin et al., 2020).
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50 Because rodent incisors tend to lack flat facets, such as those on molars resulting from mastication, furrows
51 forming the background surface can swamp effects of shallow scratches on conventional texture measurement. As
52 such, two distinct data collection protocols were employed in an effort to best characterize microwear signatures: 1)
53 microwear feature analysis (Ungar, 1995; Ungar et al., 1991), and 2) microwear texture analysis (Ungar et al., 2003;
54 et seq.). See the discussion for further consideration and rationale.
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6 **Microwear feature analysis.** For microwear feature analysis, a digital photosimulation of each surface was
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8 generated in MountainsMap 8 and resampled to a resolution of 0.6 μm per pixel. This resolution was selected to
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10 allow discrimination and measurement of individual scratches while minimizing the visual impact of finer-scale
11
12 background microstructure. Microware 4.02 (Ungar, 2002) was used for the measurements. A mouse-driven cursor
13
14 was employed to identify major and minor axes of each feature, and tallies (n), average length (Maj), breadth (Min),
15
16 and length of the mean vector of long-axis orientation (r) – a measure of concentration or homogeneity of scratch
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18 orientations -- were computed for each individual. Given concerns over intraobserver error, which tends to run about
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20 7% for data generated using Microware 4.0 (Grine et al., 2002), all images were assigned random numbers and de-
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22 identified then reordered prior to analysis to assure that measurements were taken blind to both species and site.
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26 **Microwear texture analysis.** First, an 8th-order polynomial form removal filter was applied to all point clouds in
27
28 MountainsMap 8 in an attempt to further eliminate background surface texture (following Merceron et al., 2017).
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30 Both ISO standard and scale-sensitive fractal analysis (SSFA) variables were calculated in MountainsMap 8 to
31
32 characterize surface texture following commonly used microwear texture analysis protocols (see Belmaker, 2018;
33
34 DeSantis, 2016 for descriptions).
35

36
37 A total of 22 attributes (ISO 25178) were included in the ISO study following past analyses of microwear
38
39 texture (Purnell et al., 2013; Schulz et al., 2010; 2013). These include 1) height parameters (Sq , Ssk , Sp , Sz), 2) a
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41 functional parameter (Sxp), 3) spatial parameters (Sal , Str), 4) hybrid parameters (Std , Sdq , Sdr), 5) volume
42
43 parameters (Vmp , Vmc , Vvc , Vvv), 6) feature parameters (Spd , $S5v$, Sda , Sdv , Shv), and 6) stratified surface
44
45 parameters (Svk , $SMr1$, $SMr2$). These together provide a robust characterization of surface texture for microwear
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47 analysis (see Purnell et al., 2013; Schulz et al., 2010; 2013 for descriptions of individual variables).
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50 Five SSFA variables were calculated using the MountainsMap Scale-Sensitive Analysis module. These
51
52 include area-scale fractal complexity ($Asfc$), the scale of maximum complexity ($Smfc$), heterogeneity of area-scale
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54 fractal complexity calculated in 3 x 3 and 9 x 9 grids ($HAsfc_9$ and $HAsfc_{81}$), and exact proportion length-scale
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56 anisotropy of relief ($epLsar$). These attributes are described in detail by Scott et al. (2006), and together provide a
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58 characterization of change in roughness with scale, variation in texture complexity across the surface, and
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60 orientation of texture.
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6 **Statistical analyses**
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8 The feature-based data, the ISO data, and the SSFA data were separated into three sets of general linear
9 models to facilitate analysis and interpretation. All data were rank-transformed to mitigate violation of assumptions
10 inherent to parametric statistical analyses (following Conover and Iman, 1981). All statistical tests were conducted
11 using SYSTAT (Systat Software Inc., San Jose, CA).
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16 Each dataset was analyzed for comparisons of sites using separate MANOVAs for *La. gregalis* and *Le.*
17 *sibiricus*. The sites were the independent variables, and feature, ISO, and SSFA attributes were the dependent
18 variables. Separate ANOVAs and pairwise comparisons tests were used to determine sources of significant
19 variation. Both Tukey's HSD and Fisher's LSD tests were used to balance risks of Type I and Type II error (Cook
20 and Farewell, 1996). Where Fisher's LSD but not Tukey's HSD test *p* values were < 0.05, results were considered
21 suggestive but of marginal significance.
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28 Each dataset was analyzed for comparisons of Siberian lemmings and narrow-headed voles at Sabetta and
29 Erkuta (the two sites where they co-occur) using a two-factor MANOVA, with species and site as the independent
30 variables and feature, ISO, and SSFA attributes as the dependent variables. This allowed assessment of site and
31 species effects, as well as interaction between the two factors. Again, separate ANOVAs, Tukey's HSD, and
32 Fisher's LSD tests were used to determine sources of significant variation where appropriate.
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39 In addition, a principal component analysis (PCA) was conducted on the raw texture data, including both
40 ISO and SSFA variables, to compare species at Erkuta and Sabetta. Many of the microwear texture variables
41 analyzed here are likely interrelated, and a PCA reduced dimensionality for visualization of differences between
42 species in bivariate space (the first two principal components). Furthermore, a MANOVA was conducted on rank-
43 transformed PCA data for PC1 and PC2 to compare species at Erkuta and Sabetta, with single-classification
44 ANOVAs to determine source(s) of significant variation.
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53 **RESULTS**
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4 Raw data are provided in Supplementary Information File (SI) 1. Statistics are presented in Tables 1-5 and
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6 results are illustrated in Figure 2-5. Supplemental exploratory analyses are available in SI 2. Results are here
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8 considered by dataset type.
9

10 11 12 13 **Feature-based analysis**

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15 Results for the feature-based analysis are presented in Table 2 and Figure 3. The MANOVA considering
16
17 individual taxa showed significant variation between sites for both *Lemmus sibiricus* ($p < 0.001$) and *Lasiopodomys*
18
19 *gregalis* ($p = 0.034$). Individual ANOVAs indicate that Siberian lemmings differ in microwear scratch density (n)
20
21 and that narrow-headed voles differ in both microwear scratch density (n) and orientation homogeneity (r). More
22
23 specifically, lemmings from Bely have significantly lower n values compared with those from Erkuta or Sabetta,
24
25 whereas voles from Kharp have significantly lower n values than those from Erkuta and marginally lower ones than
26
27 those from Sabetta. Further, voles from Sabetta have higher r values compared with those from Kharp and
28
29 marginally higher ones than those from Erkuta. In sum, lemmings from Bely and voles from Kharp have low
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31 striation densities and voles from Sabetta have more homogeneously oriented scratches.
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35 When comparing *Le. sibiricus* and *La. gregalis* from Sabetta and Erkuta, the two-way MANOVA indicates
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37 significant variation between taxa ($p < 0.001$), but not between Erkuta and Sabetta. Furthermore, there is no
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39 interaction between species and sites in the model. Lemmings and voles thus differ in microwear feature pattern
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41 independent of site but not by site independent of species comparing values for these two localities. *Le. sibiricus* has
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43 lower r values and lower n values than *La. gregalis* at Erkuta and Sabetta. In other words, voles have higher striation
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45 densities and more homogeneously oriented scratches than lemmings at these sites.
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51 **Microwear Texture analyses**

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53 Results for the microwear texture analyses are presented in Tables 3-4 and Figure 4. Neither the ISO or
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55 SSFA datasets separated samples by site. MANOVA results with site as the independent variable for *Le. sibiricus*
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57 were $p = 0.619$ (ISO data) and $p = 0.658$ (SSFA data) and for *La. gregalis* were $p = 0.147$ (ISO data) and $p = 0.378$
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59 (SSFA data).
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4 The two-way MANOVAs comparing *Le. sibiricus* and *La. gregalis* from Sabetta and Erkuta, on the other
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6 hand, indicate significant variation between taxa with $p = 0.004$ (ISO data) and $p = 0.003$ (SSFA data). Neither
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8 dataset shows significant variation between Sabetta and Erkuta, nor an interaction between species and sites. Again,
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10 lemmings and voles differ in microwear textures independent of site, but Sabetta and Erkuta samples do not differ
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12 significantly from one another for these species.
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15 Individual ANOVAs indicate that the two species differ significantly in 14 of 22 ISO attributes (*Sq, Sp, Sz,*
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17 *Sxp, Str, Vmp, Vmc, Vvc, Vvv, Spd, S5v, Sda, Sdv, Shv*) and 2 of 5 SSFA variables (*Smfc, epLsar*). *Le. sibiricus* has
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19 higher values than *La. gregalis* for 12 of the 14 significant ISO variables (*Sq, Sp, Sz, Sxp, Vmp, Vmc, Vvc, Vvv, S5v,*
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21 *Sda, Sdv, Shv*). These variables relate largely to the heights of peaks and the areas and volumes of hills and dales
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23 on the surface. *La. gregalis* has higher values for *Str* (texture aspect ratio, a measure of uniformity of texture) and
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25 *Spd* (density of peaks, number of peaks per unit area) than does *Le. sibiricus*. These attributes together suggest
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27 surfaces with larger features for lemmings and smaller features, but more of them, for voles. The SSFA attributes
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29 indicate lower *Smfc* and higher *epLsar* values for *La. gregalis* than *Le. sibiricus*. This is also consistent with more
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31 small features, but also more texture anisotropy of those features for voles than lemmings.
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34 Finally, the PCA confirmed variation in microwear texture between lemmings and voles at Erkuta and
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36 Sabetta (Table 5, Figure 5). Nearly 42% of the variance was explained by component 1, with component loadings $>$
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38 $|.4|$ for 20 of 27 variables, $> .6|$ for 14 variables, and $> .8|$ for 8 variables. More than 16% of the variance was
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40 explained by component 2, with component loadings $> .4|$ for 9 variables and $> .6|$ for 5 variables. The MANOVA
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42 on PC1 and PC2 confirmed significant variation in microwear texture between the *Le. sibiricus* and *La. gregalis* ($p <$
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44 0.001), and ANOVA results indicated that both PC1 and PC2 differed significantly.
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49 **DISCUSSION**

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52 Analyses presented here indicate differences between Siberian lemmings and narrow-headed voles at the
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54 same sites and differences within these species at different sites. The *Lasiopodomys gregalis* samples have more
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56 striations and more homogeneously oriented scratches at Erkuta and Sabetta than do the *Lemmus sibiricus* samples.
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58 The texture analyses confirm a higher density of smaller features and more texture anisotropy (*epLsar*) in voles than
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4 lemmings. Texture dataset MANOVAs did not resolve significant variation between sites for either species (but see
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6 below), though feature-based analyses did evince differences between sites. Narrow-headed voles individuals from
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8 the forest-tundra ecotone site of Kharp have lower striation densities than those from tundra sites of Erkuta and
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10 Sabetta. Also, *La. gregalis* from the low-high Arctic border site of Sabetta have more homogeneously oriented
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12 scratches than those from the other sites. In contrast, the *Le. sibiricus* sample from the high Arctic site on Bely
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14 Island has fewer microwear striations than either the Erkuta or Sabetta lemming samples. These differences are
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16 consistent with variation in abrasive environments between sites and differences in microhabitat preference and
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18 burrowing behavior between species at a given site.
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23 **Differences between the sites**

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27 The differences in vegetative cover between the sites likely contribute to differences in environmental
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29 abrasive load. Recall that Kharp is the only site with trees (mostly Siberian larches, *Larix sibirica*), and that its
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31 thickets (*Salix* sp., *Betula* sp.) are approximately 2 m in height. At Erkuta, willow thickets are shorter, ranging
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33 between 1 m and 2 m in height. And Sabetta willow thickets are shorter still, averaging about 40 cm in height. Thus,
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35 we expect an increase in environmental grit load from Kharp to Erkuta to Sabetta given the decreasing height of
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37 ground cover (Ungar et al., 2020). We also expect less environmental grit on Bely than either Erkuta or Sabetta
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39 because, despite a lack of trees and thickets, the site is covered in lush, wet mosses and the surrounding environment
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41 lacks the open relatively high elevation sandy areas found at the two lower-latitude tundra sites.
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45 Other factors contributing to variation in environmental abrasives include networks of rivers, streams and
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47 lakes with sandy shores at Erkuta and Sabetta, and the aeolian currents at these sites, which carry grit that settles on
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49 plants there between the end of June and August. This contrasts with conditions at the Bely Island and Kharp sites,
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51 which lack the river networks and lake settings with open sandy shores. It can also be noted that endogenous silica
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53 concentration
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55 (by weight) in open tundra dominated by phytolith grasses and sedges averages more than four times that in lower
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57 latitude boreal forests (Carey and Fulweiler, 2012). Likewise, soil amorphous silica concentration tends to be
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59 twofold to threefold higher in graminoid tundra than wetlands (Alfredsson et al., 2016).
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4 In sum, abrasive loads, both endogenous and exogenous, are likely higher at Erkuta and especially Sabetta
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6 than at Kharp or Bely Island. The higher densities of microwear striations on narrow-headed vole incisors at Sabetta
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8 and Erkuta compared with Kharp, and on Siberian lemming incisors at Sabetta and Erkuta compared with Bely, are
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10 consistent with expectations and align perfectly with them.
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15 **Differences between the species**

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18 Differences between the species in microwear patterning may relate to variation in diet, microhabitat
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20 preference, and/or substrate use (i.e., tunneling behavior). First, the two species evidently differ in both preferred
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22 foods and the variety of items they consume. Published work documenting food preferences of *Le. sibiricus* and *La.*
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24 *gregalis* in the region are limited to studies in Yamal north of Erkuta by Dunaeva (1948) and on the western shore of
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26 Baydaratskaya Bay by Kopein (1958). These mid-20th century studies documented diet based on identification of
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28 plants with gnaw marks, remains of stored food, and items consumed during *ad libitum* feeding experiments with
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30 captive individuals.
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34 According to Dunaeva (1948), Siberian lemmings on Yamal are sedge specialists, consuming mostly cotton
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36 grass (*Eriophorum vaginatum*). They do consume other plant species on occasion though, including dwarf birch
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38 leaves and young shoots, some willows (*Salix* sp.), cloudberry, and *Equisetum* sp. Kopein (1958) found that Siberian
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40 lemmings on the western shore of Baydaratskaya Bay also prefer sedges (especially *Carex* sp. also *Eriophorum* sp.)
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42 though they sometimes also consume herbs (*Equisetum* spp.), *Rubus chamaemorus*, *Salix* sp. and *Vaccinium*
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44 *uliginosum*. These lemmings are not reported to eat lichens or mosses, despite their use for nests.
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46
47 Studies of narrow-headed voles suggest that *La. gregalis* has a much broader diet, including at least 40
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49 species of sedges, grasses, and herbs of *Eriophorum*, *Carex*, *Salix*, *Equisetum*, *Artemisia*, *Tilesii*, and *Astragalus*
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51 among others (Kopein, 1958). Narrow-headed vole diet evidently varies between localities, with more grass eaten
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53 north of Erkuta, but more herbs consumed on the western coast by Baidaratskaya Bay (Kopein, 1958). These
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55 observations imply a broader, more flexible diet for the voles than for the lemmings of Yamal, though more work is
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57 needed to confirm this.
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4 It is unclear to what extent dietary differences would be reflected in variation in incisor microwear, as
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6 opposed to molar microwear, which likely more directly reflects fracture properties of foods eaten (see Caporale &
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8 Ungar, 2015; Belmaker, 2018). That said, one might speculate that the consumption of a broader range of food types
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10 could be consistent with greater use of the front teeth for gnawing a variety of items, consistent with higher
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12 frequencies of microwear striations and a broader range of feature sizes (including smaller ones) in voles at Erkuta
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14 and Sabetta. This would not, however, necessarily explain the greater anisotropy.
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17 On the other hand, microhabitat preferences and variation in substrate use associated with tunneling very
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19 likely explain much of the microwear variation between lemming and vole incisors. *Lemmus sibiricus* inhabits the
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21 wetter mossy areas of Erkuta and Sabetta as well as Bely. In the summertime, these lemmings build nests in
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23 hummocks in moist sedge-moss tundra from sedge leaves with runway tracks through dense vegetation; and in the
24
25 winter they nest in snow beds near hillsides (Dunaeva, 1948). In contrast, *La. gregalis* lives in drier sandy areas at
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27 all sites. These voles typically live in colonies consisting of individual burrows connected by paths and underground
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29 tunnels (Dunaeva, 1948; Pal'chekkh et al., 2003). Voles generally dig burrows in large part with their forelimbs, but
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31 they likely also use their incisors to loosen soil (Gromov and Polyakov, 1992); and they certainly store food in these
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33 tunnels.
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36 Higher striation densities on vole I₁s likely results in large part from greater exposure to environmental grit
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38 due to microhabitat preference, underground storage of food, and tunneling behavior. The regular use of incisors
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40 with repetitive orthal movements to loosen soil might in part explain the increased anisotropy and striation
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42 orientation concentration in the voles compared with the lemmings; though this does explain the difference in *r*-
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44 values between voles at Sabetta and the other sites. It is also possible that microwear formed predominantly by
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46 angular grit particles explains the smaller features on average seen in the voles (see Ungar, 1994 for discussion).
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48 While the relative contributions of substrate use and microhabitat preference to variation in microwear patterning is
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50 yet to be determined, both likely play a role, particularly given differences within the species between sites that vary
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52 in environmental abrasivity. We expect that further study will allow us to work out the details.
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58 **Differences between methods**

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4 As an additional note, the difference in results between traditional feature-based and microwear texture
5 analyses were unexpected. Texture analysis largely replaced feature-based methods as the gold standard for dental
6 microwear studies in the 2010s (see Calandra and Merceron, 2016; DeSantis, 2016; Ungar, 2015; 2018 for review).
7
8 Feature-based analysis relies on an observer to identify, count, and measure scratches and pits on two-dimensional
9 photomicrographs or photosimulations of enamel surfaces. It is a time-consuming process subject to observer
10 measurement error (Grine et al., 2002). In contrast, texture-based analysis uses quasi-3D point clouds (only one z
11 value for any given x-y pair) and allows rapid and quantitative automated characterization of whole surfaces.
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19 This is the first microwear study we are aware of to employ both feature-based and texture-based methods.
20 We began this study with the intent of using only texture analysis, but found that differences between individual
21 surfaces obvious to the eye (see Figure 2) were not reflected in either SSFA or ISO attribute values. It was clear that
22 texture characterizations did not distinguish I₁ surfaces with a few wispy striations from those with none -- likely
23 because the rough larger-scale background surface topography swamped the scratch "signal". This problem has not
24 arisen in the past for molar facets, which are typically polished flat by mastication. And neither 2nd-order (following
25 Arman et al., 2016) nor 8th-order polynomial filters (following Merceron et al., 2017) removed the background form
26 sufficiently to allow resolution of differences in striation density on these surfaces. We added a microwear feature
27 analysis to the study given that the human eye seems better able than either SSFA or standard ISO measures to
28 resolve wispy scratches from rough background textures. In the end, the proof is in the pudding -- significant
29 variation between species and sites in striation density and alignment match visually obvious differences between
30 the samples. This suggests that feature analysis still has an important role to play in quantitative characterization of
31 microwear patterning, at least for complex or lightly worn surfaces with background textures that obfuscate subtle
32 variation between samples.
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50 **Future directions**

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52 Dental microwear analyses often rely on large samples to separate groups given inherent variation within
53 them. Within-species variation is common because microwear reflects short-term food choice -- features can
54 accumulate and patterns can be overwritten in a matter of days or weeks (Grine, 1986; Teaford and Oyen, 1989).
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56 This can present a challenge when characterizing the microwear surfaces of species that consume a variety of items
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4 in a range of microhabitats. The samples in this study vary from $n = 7$ to $n = 11$ individuals for each site-species
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6 combination. It is possible that larger samples might have allowed resolution of microwear feature measurement
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8 differences between Erkuta and Sabetta and perhaps texture differences between sites.
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10 Indeed, exploratory analyses provide some hints (see SI 2). While the MANOVA model showed no
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12 significant variation in texture between sites for either lemmings or voles, individual ANOVAs did suggest a few
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14 attributes that might vary between samples, at least if an experiment-wise error rate is not employed (see Perneger,
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16 1998). For example, *La. gregalis* from Kharp has a higher *Ssk* average (a measure of skewness of the distribution of
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18 heights on a surface) than narrow-headed voles at Erkuta or Sabetta, and Erkuta voles have a lower *Smr2* average
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20 (percentage of measurement area in deeper valleys) than those at Kharp or Sabetta. As for variation between Erkuta
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22 and Sabetta independent of species, the lower latitude site has higher *Smfc* and the higher latitude one has higher
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24 *epLsar* than Erkuta.
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26 While we caution against the “shotgun” approach of testing all texture attributes available given the risk of
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28 Type I statistical error, some of the differences seen would not be unexpected. *Ssk* has proven particularly effective
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30 at distinguishing other small mammals on the basis of diet (Schulz et al., 2013; Purnell et al., 2013; see DeSantis,
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32 2016). Further, a higher *epLsar* value for Sabetta is consistent with more homogeneously oriented scratches (as
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34 found in the feature-based microwear study), and a lower *Smfc* average at the higher latitude site would be consistent
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36 with more small scratches (which discriminates Kharp from the tundra sites). While we do not want to overstate
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38 these results, they do hint that larger samples may facilitate better resolution of variation between samples.
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42 CONCLUSIONS

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46 This study indicates that I₁ labial surface microwear holds potential as a proxy for microhabitat use in
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48 Arctic arvicolines. The presence of higher striation densities and texture attributes suggesting more and smaller
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50 features for *La. gregalis* than *Le. sibiricus* at Erkuta and Sabetta are consistent with more open, drier, and abrasive
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52 microhabitats for narrow-headed voles and more closed, wetter ones for Siberian lemmings. This, along with more
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54 texture anisotropy (*epLsar*) and homogeneously oriented scratches, may also be consistent with an inferred
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56 propensity for voles to loosen soil with their incisors while digging subterranean tunnels. Moreover, individuals of
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58 both species from the abrasive-rich open tundra sites of Erkuta and Sabetta have higher striation densities than
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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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4 **FIGURE LEGENDS**
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7 **Fig. 1.** Map of the Yamal Peninsula and Bely Island with locations of sites sampled. Bioclimatic subzones of the
8 Circumpolar Arctic Region are derived from CAVM Team (2003) and as described in Walker et al. (2005).
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14 **Fig. 2.** Photomicrograph simulations for *Lemmus sibiricus* (left) and *Lasiopodomys gregalis* (right). Representative
15 individuals from Bely Island and Kharp (top), Erkuta (middle), and Sabetta (bottom). Note that each image
16 represents an area 102 μm x 138 μm on the original surface.
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24 **Fig. 3.** Box and whiskers plots for dental microwear feature analysis attributes. Number (left) and mean vector
25 length (right) of features considered by species and site. The hinges mark the first and third quantiles, the vertical
26 lines between them are medians, each whisker represents a value 1.5 times the interquartile range, asterisks are
27 outliers, and circles are far outliers.
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35 **Fig. 4.** Bivariate plots comparing species from Erkuta and Sabetta for all microwear texture attributes found to be
36 statistically significantly different between *Lemmus sibiricus* and *Lasiopodomys gregalis*.
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43 **Fig. 5.** Principal Component Analysis for all microwear texture attributes comparing *Lemmus sibiricus* and
44 *Lasiopodomys gregalis*.
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Table 2. Feature-based analytical statistics (all analyses using rank-transformed data).

A. General linear models comparing sites by taxon

MANOVAs *Lasiopodomys*

	<i>F</i>	<i>df</i>	<i>p</i>
<i>Wilk's</i> λ	2.344	8, 44	0.034

Lemmus

	<i>F</i>	<i>df</i>	<i>p</i>
	4.385	8, 50	0.000

ANOVAs *Lasiopodomys*

	<i>df</i>	<i>F</i>	<i>P</i>
Length	2	2.43	0.109
Error	25		
Width	2	0.232	0.794
Error	25		
<i>r</i>	2	4.264	0.026
Error	25		
<i>n</i>	2	4.511	0.021
Error	25		

Lemmus

	<i>df</i>	<i>F</i>	<i>p</i>
	2	3.211	0.056
	28		
	2	0.264	0.770
	28		
	2	1.129	0.338
	28		
	2	13.605	<0.001
	28		

Paired comparisons

Lasiopodomys r

	Erkuta	Kharp
Kharp	-0.773	
Sabetta	8.177**	8.95*

Lasiopodomys n

	Erkuta	Kharp
	-	
	10.097**	
	-1.205	8.893*

Lemmus n

	Bely	Erkuta
	10.186**	
	15.300**	5.114

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

MANOVAs

		<i>F</i>	<i>df</i>	<i>p</i>
Species	Wilk's λ	7.072	4, 35	<0.001
Site	Wilk's λ	0.724	4, 35	0.581
Interaction	Wilk's λ	2.237	4, 35	0.085

ANOVAs for species

	<i>F</i>	<i>df</i>	<i>p</i>
Length	1	0.038	0.847
Error	38		
Width	1	1.34	0.254
Error	38		
<i>r</i>	1	14.706	<0.001
Error	38		
<i>n</i>	1	12.881	0.001
Error	38		

Table 3. ISO attribute microwear texture analysis.

A. General linear models comparing sites by taxon

MANOVAs *Lasiopodomys*

	<i>F</i>	<i>df</i>	<i>p</i>
<i>Wilk's λ</i>	2.022	44, 8	0.147

Lemmus

	Value	<i>F</i>	<i>df</i>	<i>p</i>
<i>Wilk's λ</i>	0.068	0.906	44, 14	0.619

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

MANOVAs

		Value	<i>F</i>	<i>df</i>	<i>p</i>
Species	<i>Wilk's λ</i>	0.174	3.669	22, 17	0.004
Site	<i>Wilk's λ</i>	0.411	1.109	22, 17	0.420
Interaction	<i>Wilk's λ</i>	0.559	0.608	22, 17	0.864

ANOVAs for species

	<i>df</i>	<i>F</i>	<i>p</i>
<i>Sq</i>	1	7.292	0.010
Error	38		
<i>Ssk</i>	1	1.862	0.180
Error	38		
<i>Sp</i>	1	8.694	0.005
Error	38		
<i>Sz</i>	1	17.487	0.000
Error	38		
<i>Sxp</i>	1	6.004	0.019
Error	38		
<i>Sal</i>	1	0.047	0.830
Error	38		
<i>Str</i>	1	16.489	<0.001
Error	38		
<i>Std</i>	1	0.991	0.326
Error	38		
<i>Sdq</i>	1	1.372	0.249
Error	38		
<i>Sdr</i>	1	1.370	0.249
Error	38		
<i>Vmp</i>	1	4.534	0.040
Error	38		

	<i>df</i>	<i>F</i>	<i>p</i>
<i>Vmc</i>	1	14.730	<0.001
Error	38		
<i>Vvc</i>	1	14.251	0.001
Error	38		
<i>Vvv</i>	1	4.594	0.039
Error	38		
<i>Spd</i>	1	11.120	0.002
Error	38		
<i>S5v</i>	1	7.960	0.008
Error	38		
<i>Sda</i>	1	9.649	0.004
Error	38		
<i>Sdv</i>	1	7.217	0.011
Error	38		
<i>Shv</i>	1	12.956	0.001
Error	38		
<i>Svk</i>	1	2.147	0.151
Error	38		
<i>Smr1</i>	1	0.000	0.992
Error	38		
<i>Smr2</i>	1	1.061	0.309
Error	38		

Table 4. Scale-sensitive fractal analysis

A. General linear models comparing sites by taxon

MANOVAs *Lasiopodomys*

	<i>F</i>	<i>df</i>	<i>p</i>
<i>Wilk's λ</i>	1.11	10, 42	0.378

Lemmus

Value	<i>F</i>	<i>df</i>	<i>p</i>
0.743	0.768	10, 48	0.658

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

MANOVAs

		<i>F</i>	<i>df</i>	<i>p</i>
Species	<i>Wilk's λ</i>	4.382	5, 34	0.003
Site	<i>Wilk's λ</i>	2.046	5, 34	0.097
Interaction	<i>Wilk's λ</i>	0.478	5, 34	0.790

ANOVAs for species

Univariate F-Tests

Source	<i>df</i>	<i>F</i>	<i>p</i>
<i>Asfc</i>	1	0.445	0.509
Error	38		
<i>Smfc</i>	1	6.937	0.012
Error	38		
<i>HAsfc₉</i>	1	0.641	0.428
Error	38		
<i>HAsfc₈₁</i>	1	1.639	0.208
Error	38		
epLsar	1	16.318	<0.001
Error	38		

Table 5. Principal components analysis for the texture data (significant attributes only).

A. PC1 and PC2 loadings and variance explained

	1	2		1	2
<i>Sq</i>	0.969	0.078	<i>Spd</i>	-0.518	0.655
<i>Ssk</i>	0.142	-0.397	<i>S5v</i>	0.899	0.227
<i>Sp</i>	0.629	-0.295	<i>Sda</i>	0.545	-0.708
<i>Sz</i>	0.871	-0.160	<i>Sdv</i>	0.634	-0.371
<i>Sxp</i>	0.924	0.205	<i>Shv</i>	0.641	-0.579
<i>Sal</i>	0.472	0.085	<i>Svk</i>	0.79	0.404
<i>Str</i>	-0.339	0.313	<i>Smr1</i>	0.289	-0.196
<i>Std</i>	0.186	0.056	<i>Smr2</i>	0.175	-0.357
<i>Sdq</i>	0.683	0.649	<i>Asfc</i>	0.443	0.731
<i>Sdr</i>	0.666	0.659	<i>Smfc</i>	0.512	-0.599
<i>Vmp</i>	0.919	0.140	<i>HAsfc₉</i>	0.054	0.416
<i>Vmc</i>	0.923	-0.011	<i>HAsfc₈₁</i>	0.032	0.378
<i>Vvc</i>	0.947	-0.049	<i>epLsar</i>	-0.551	0.297
<i>Vvv</i>	0.896	0.287			

Variance Explained by Components

	1	2
Variance	11.334	4.469
%	41.979	16.554

B. Principal components general linear model

MANOVAs

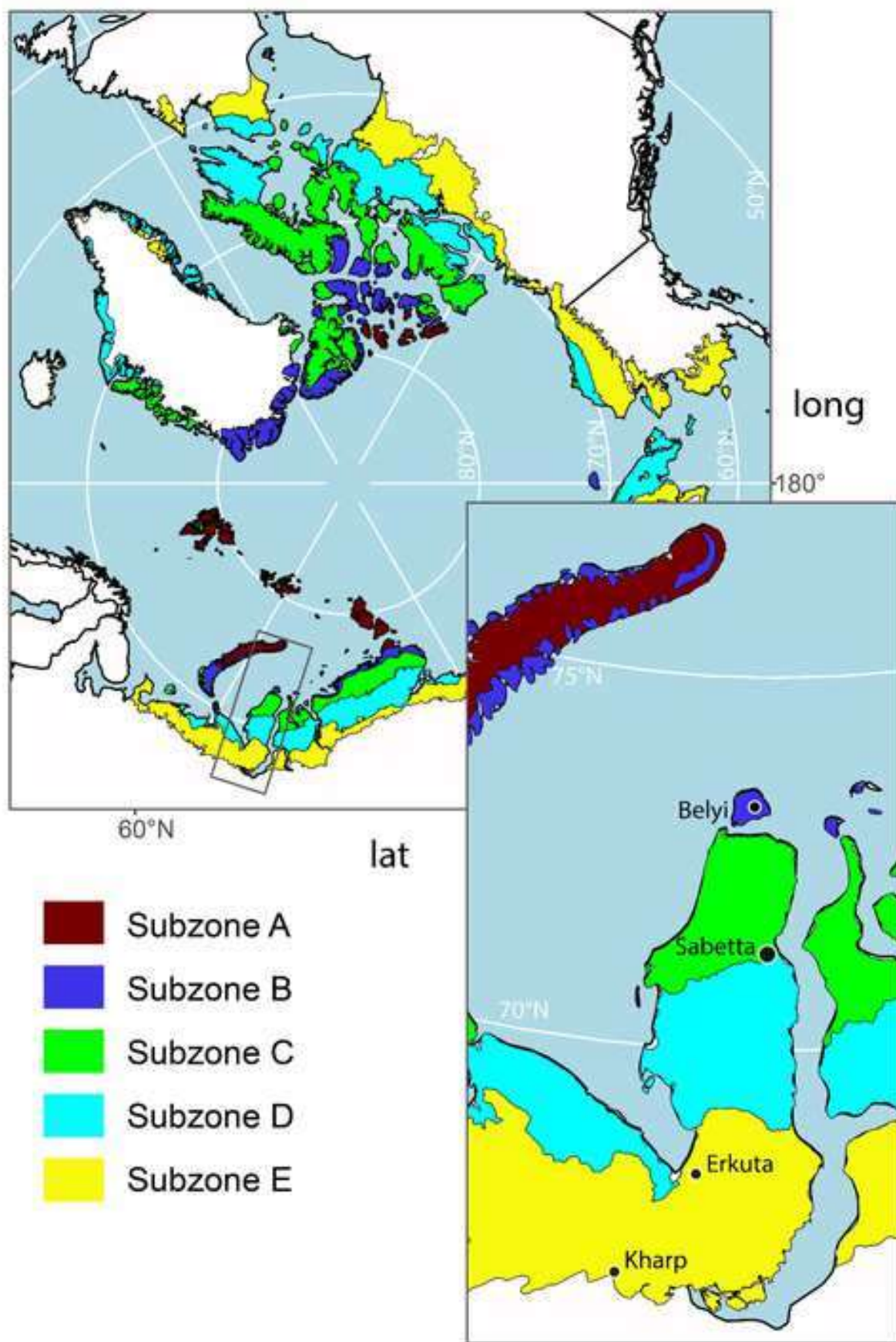
Species	<i>Wilk's λ</i>	<i>F</i>	<i>df</i>	<i>p</i>
		9.822	2, 39	<0.001

Univariate F-Tests

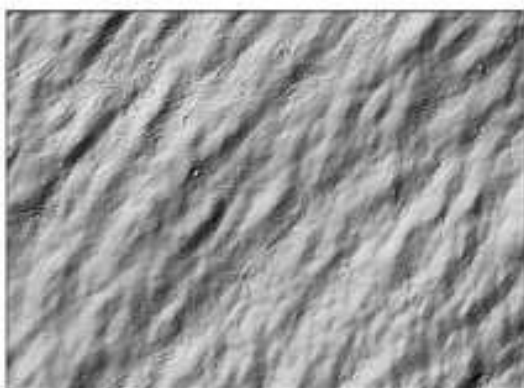
Source	<i>df</i>	<i>F</i>	<i>p</i>
PC1	1	12.579	0.001
Error	40		
PC2	1	4.695	0.036
Error	40		

Figure 1

[Click here to access/download;Figure;Fig 1.TIF](#)

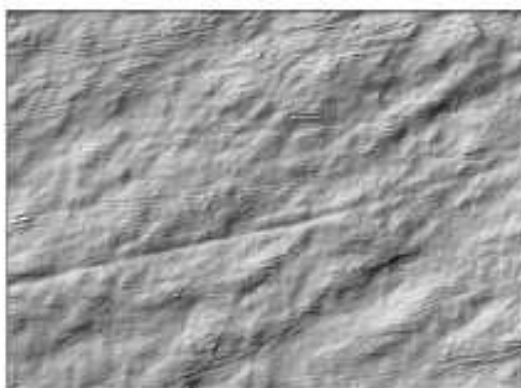


Lemmus sibiricus

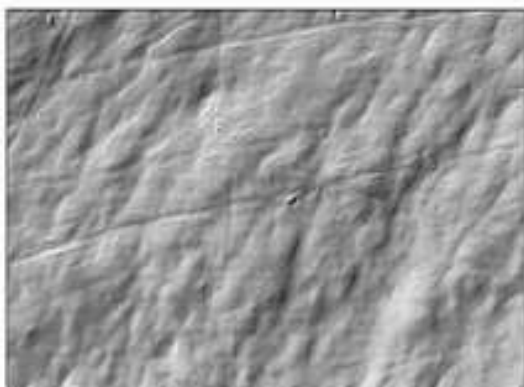


Bely 2990

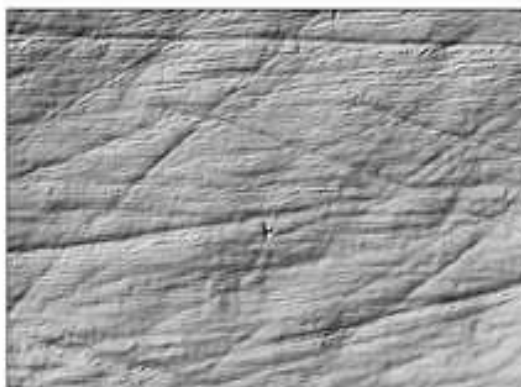
Lasiopodomys gregalis



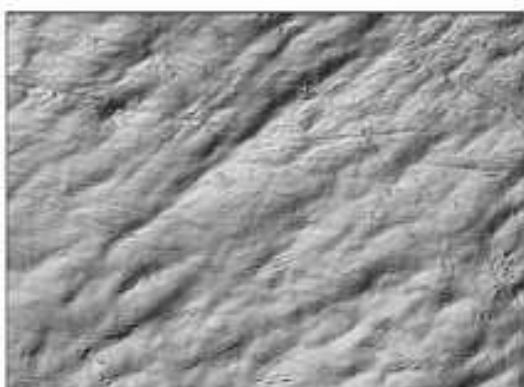
Kharp 2414



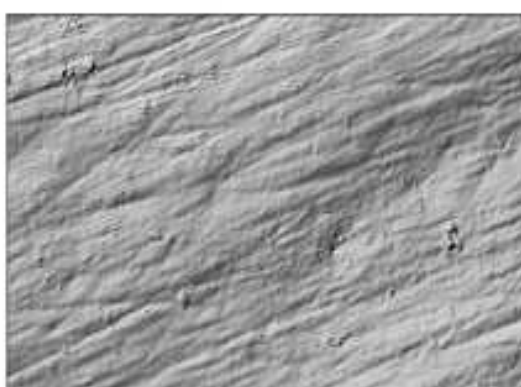
Erkuta 220



Erkuta 2496



Sabetta 2575



Sabetta 2578

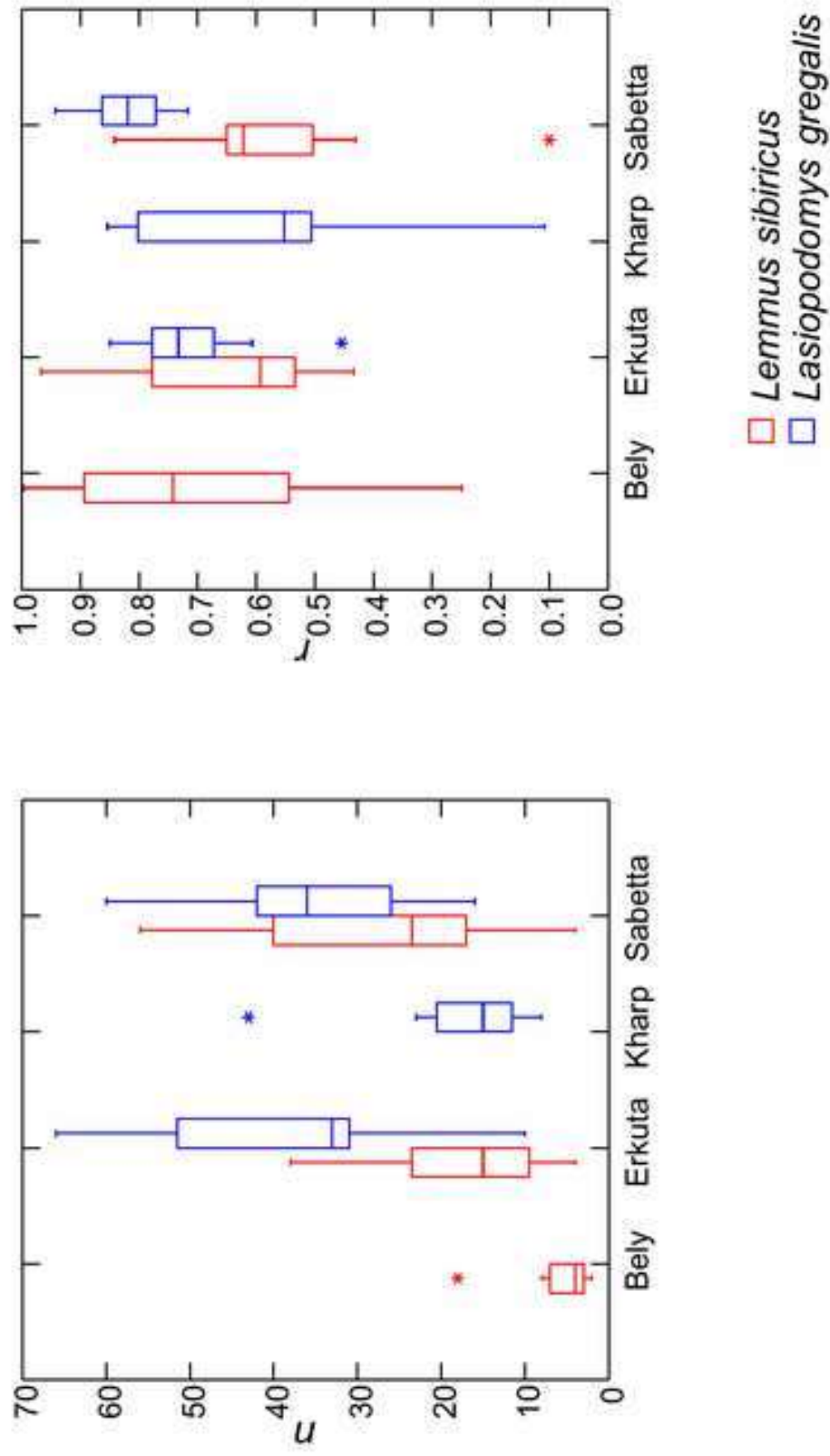


Figure 4

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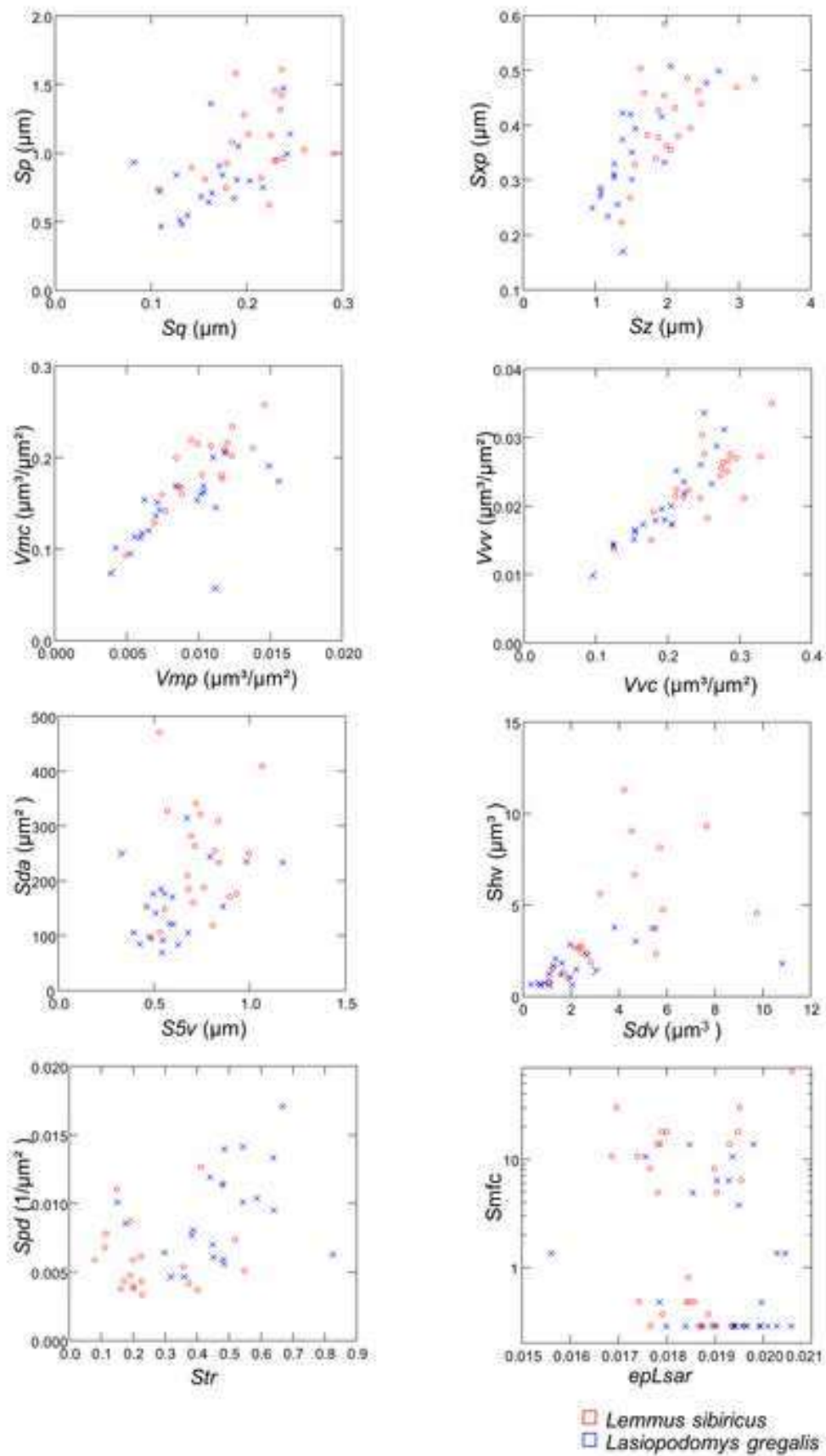


Figure 5

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