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Dental microwear textures of reindeer from northern herding districts in Finnish Lapland

Peter S. Ungar[1,*], Caroline Groves[2], Harrison Lowe[1], Gerardo Celis[1], Jouko Kumpula[3], Ilpo Kojola[4], Mikael Fortelius[5,6] & Bruce C. Forbes[7]

[1)] *Department of Anthropology and Environmental Dynamics Program, Old Main 330, University of Arkansas, Fayetteville, Arkansas, 72701, USA (*corresponding author's e-mail: pungar@uark.edu)*
[2)] *College of Dentistry, 1395 Center Dr. University of Florida, Gainesville, Florida, 32610, USA*
[3)] *Natural Resources Institute Finland (LUKE),Toivoniementie 246, 99910 Inari, Finland*
[4)] *Natural Resources Institute Finland (LUKE), Ounasjoentie 6, 96200, Rovaniemi, Finland*
[5)] *Geosciences Unit, Finnish Museum of Natural History – LUOMUS, PB 44 (Jyrängöntie 2), FI-00014 University of Helsinki, Finland*
[6)] *Department of Geosciences and Geography, University of Helsinki, PB 64 (Gustaf Hällströmin katu 2), FI-00014 University of Helsinki, Finland*
[7)] *Arctic Centre, University of Lapland, Arktinen keskus, Pohjoisranta 4, 96200, Rovaniemi, Finland*

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Patterns of microscopic wear on fossil teeth often serve as proxies to retrodict diets of extinct species. Dental microwear can also help ecologists monitor food choices in mammals today as they relate to variation in resource availability. Here we considered reindeer from northern Finland in herding districts with varying biomasses of lichen and dwarf shrub, hay and grass pasture to determine whether dental microwear texture pattern follows resource abundance. We examined textures of 179 individuals representing nine districts. All samples fell within the "mixed feeder" to browser range (with caveats), but there was also variation between districts. Results of a generalized mixed model indicated that samples from sites with more lichen had significantly lower microwear texture complexity. This suggests that while relationships between microwear pattern and resource abundance are complex, this approach holds promise as a tool for tracking food choice with varying availability for neontological studies.

Introduction

Dental microwear analysis has served as a valuable tool to reconstruct aspects of diet and tooth use in extinct vertebrates for more than a century (Simpson 1926). Studies of tooth wear have some advantages over more traditional "adaptive" lines of evidence for diets of fossil taxa, such as tooth size, shape and structure, which focus on species-level dietary adaptations. Microwear is a "foodprint" (Ungar 2017) — it reflects actual foods eaten by specific individuals rather than those that the ancestors of a species evolved to consume. So it can be used to study within-species variation and can tell us something about food choices in a given place and at a given time (Teaford *et al*. 2023).

Most studies of microwear have focused on developing extant baselines to associate patterns with diets, on working out the etiology of those patterns and on using those associations to reconstruct diets in past vertebrates (Calandra & Merceron 2016, DeSantis 2016, Ungar 2015). Diet is clearly key to understanding evolution given its role in driving the relationship between an organism and its environment. Paleontologists need proxies like microwear to infer diet because they cannot observe animals in the past directly. However, neontologists often cannot observe animals directly either; and diet is also key to understanding ecology of living populations given its role in driving the relationship between an organism and its environment. For example, logistical constraints prevent us from watching animals eat across vast stretches of the North over decades as ice retreats and glaciers melt. This raises the question, "can microwear and other foodprints originally developed for paleontological applications be used to track food choices of animals today as environments, and the resources they make available, change?"

Some microwear researchers have begun to turn their attention to neontological questions related to climate change and human encroachment on natural habitats (*e.g.*, Bethune *et al*. 2021, Ungar *et al*. 2021a, b, 2022). It follows that studies of microwear of modern species can provide insights into food selection and resilience to resource shifts within a changing world that can contribute to development of wildlife management strategies for endangered species (Han *et al*. 2024). However, much work remains to identify how food choice relates to variation in availability in the context of microwear patterning.

This study applies current methods of dental microwear surface characterization using texture analysis (*see* Calandra & Merceron 2016, DeSantis 2016, Ungar 2015 for review) to semi-domesticated extant reindeer (*Rangifer tarandus*) from nine herding districts with documented differences in available resource abundances in the low Arctic latitudes of northern Finland. Kojola *et al*.'s (1998) study of gross tooth wear in Finnish reindeer from various districts found a significant relationship between tooth height and lichen biomass in winter habitats. Reindeer living in herding districts with less lichen had more tooth wear at a given age, presumably because of the need to masticate less preferred but more abrasive and mechanically challenging foods (e.g., dwarf shrubs, graminoids) in the winter rather than softer and more pliant lichen (*see* Kojola *et al*. 1995). Is this same pattern of difference discernible using dental microwear analysis?

Here we consider dental microwear textures of a subset of the specimens used by Kojola (1998) to assess the impacts of lichen availability on gross tooth wear. We reasoned that this sample would likewise provide an excellent case study to assess impacts of variation in lichen and other food resource availabilities on dental microwear patterning. Our hypothesis was that reindeer with a diet dominated by soft, pliant lichens would likely have low texture complexity and anisotropy values, whereas those with less access to lichens would consume tree/bush parts or graminoids, leading to higher values for texture complexity or anisotropy, respectively.

Logic dictates that tooth wear caused by lichens should generate fewer features given that pliant foods should cause less microwear than resistant ones (Hua *et al*. 2020). Further, we expect that wear caused by soft, non-abrasive lichens should be largely attritional, with less complex surfaces with fewer deep features resulting from repeated loading of hard, abrasive foods with high occlusal forces. We would likewise expect fewer long, parallel striations resulting from repeated shearing of tough foods. If it turns out that we can use microwear to infer such aspects of reindeer diet, these data could serve as a model for documenting food choice and perhaps a better understanding of the resilience of reindeer in the face of shifting resource availability over space and time, with implications for their husbandry and possibly even conservation efforts for other species.

Materials and methods

This study focused on permanent mandibular molars of female reindeer from nine herding districts, or *paliskunta*, in northern Lapland with

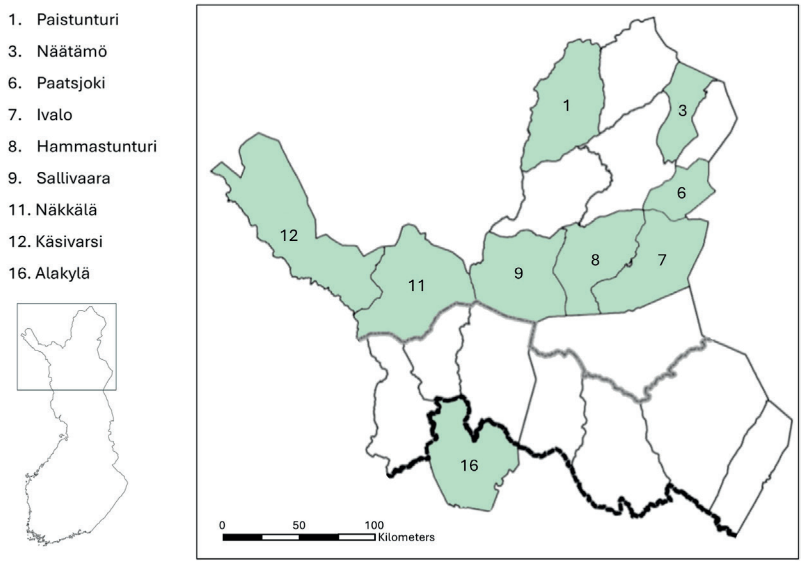

Fig. 1. Specimens used in this study come from the Finnish herding districts noted in green. The thicker gray line is the southern border of the Sámi residential area and the black one is the southern border of the area specially intended for reindeer herding.

reported differences in availability of ground lichen and dwarf shrub, hay and grass pasture (Kumpula *et al*. 1997, *see* Table 1, Fig. 1). Reindeer in most of the cooperatives considered here are constrained to their designated districts by fences. Even reindeer in cooperatives with less fencing (e.g., Alakylä) by and large stay within their home districts, given learned seasonal migration routes/rotations.

Specimens used in this study are a subset of mandibles collected in 1993–1994 from butcheries by IK and colleagues from the Natural Resources Institute, Finland (at the time the Finnish Game and Fisheries Research Institute). All individuals were slaughtered in the late Autumn (October) or early Winter (November, December). A total of 179 individuals were analyzed for microwear from the following districts: Paistunturi (n = 12), Näätämö (n = 20), Paatsjoki (n = 22), Ivalo (n = 23), Hammastunturi (n = 19), Sallivaara (n = 22), Näkkälä (n = 21), Käsivarsi (n = 21) and Alakylä (n = 19). The smaller sample size for Paistunturi reflects a lack of enamel for many specimens due to common but extreme pathological wear of the lower anterior molars. All specimens are archived at the Natural Resources Institute, Finland (LUKE), Inari field station. Only adult teeth were considered for this study. Ages for individuals are not reported as, while this affects gross wear amount, microwear patterns are not cumulative over a lifetime – they typically reflect no more than a few weeks of diet (Winkler *et al*. 2020). This is because individual microwear features are on the scale of microns in depth and so "turn over" quickly as surfaces wear (Teaford & Oyen 1989).

Table 1. Finnish Game and Fisheries Research Institute's pasture inventory data (data from Kumpula *et al.* 1997) for the herding districts considered in this study, including hectares of dwarf shrub, hay and grass pasture (SHG) and ground lichen pasture, and the number of allowed reindeer.

	SHG (ha)	Lichen (ha)	Reindeer
Alakylä	76925	31616	5500
Hammastunturi	46553	62236	6000
Ivalo	46817	87140	6000
Käsivarsi	180610	84931	13000
Näätämö	68532	105081	10000
Näkkälä	43300	43875	4000
Paatsjoki	5622	16928	1600
Paistunturi	111436	78088	8000
Sallivaara	76827	61121	9000

We first cleaned the occlusal surfaces of first and second molars (M_1s and M_2s) with alcohol-soaked cotton swabs to remove adherent dust and other particles. Dental impressions were then taken using Affinis regular body polyvinylsiloxane dental impression material (Coltène-Whaledent Inc., Alstätten, Switzerland). High-resolu-

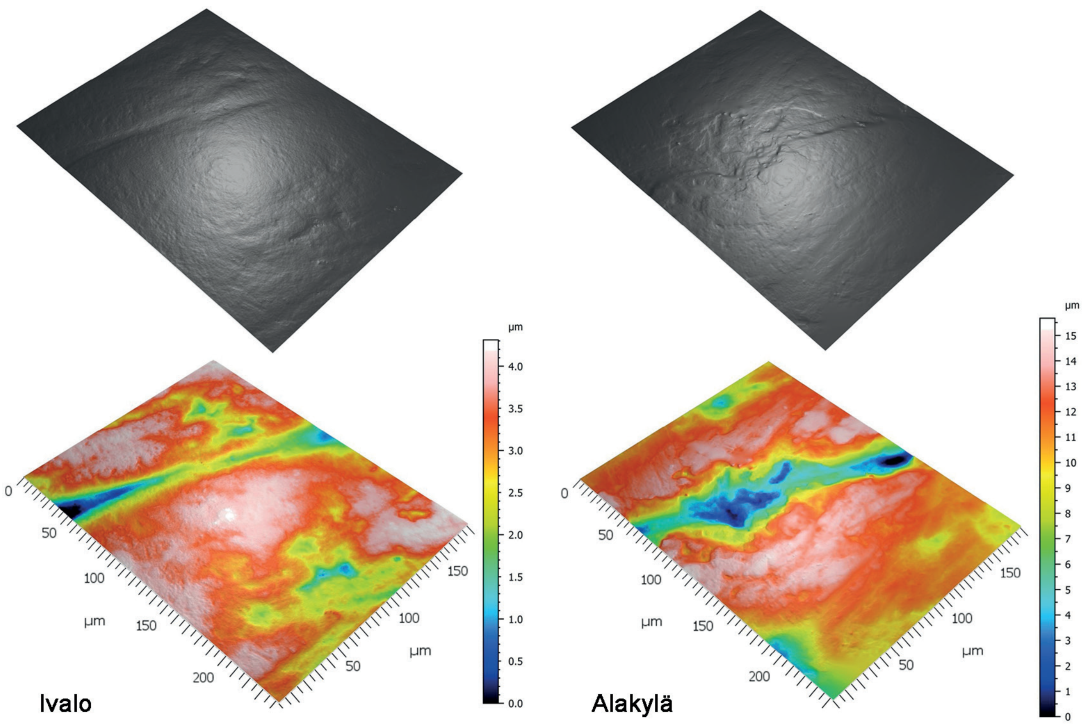

Fig. 2. Sample microwear photosimulations of surfaces representing Ivalo (7-3901) and Alakylä (16-344). Photosimulations above match elevation maps below. Note that the specimen from Ivalo has less relief and lower complexity than that from Alakylä.

tion replicas were later prepared at the University of Arkansas using Epotek 301 epoxy resin and hardener (Epoxy Technologies, Billerica, MA, USA).

All specimens were examined using a Plμ neox white-light scanning confocal profiler (Sensofar Corp., Barcelona, Spain) with a 100× objective lens in extended topography mode. Point clouds were generated for Facet 1 surfaces on the posterobuccal enamel band of each specimen, one molar per individual, following microwear analysis convention for selenodont ruminant teeth (Merceron *et al*. 2004, Scott 2012, Ungar *et al*. 2007). Each point cloud represented a field of view of 242 × 182 μm with a lateral point spacing of 0.17 μm, for a total of ~1.6 million points at a vertical step spacing of 0.2 μm (Fig. 2).

Microwear texture data were generated for each point cloud using MountainsMap 8.1 (Digital Surf. Inc., Besançon, France). Surfaces were prepared for analysis by leveling, thresholding out the top and bottom 0.1% of the data (to remove spikes) and manual deletion of minimal surface dust/debris. The scale-sensitive fractal analysis add-in was used to calculate area-scale fractal complexity (*Asfc*) and the Sfrax version of length-scale anisotropy of relief (*epLsar*) for each scan. These two texture characterizations were the focus of this study as they have together been shown to separate extant ruminants well based on diet (Ungar *et al*. 2007). These attributes are described in detail in Scott *et al*. (2006). Complexity is a measure of change in roughness with scale of observation, so surfaces with pits of varying size and shape tend to have high *Asfc* compared with more uniform surfaces. Anisotropy is a measure of texture directionality, and surfaces with long, parallel scratches tend to have higher *epLsar* values than surfaces dominated by pits or randomly oriented scratches. Scott (2012) has demonstrated that, among ruminants (i.e., African bovids), frugivores and other browsers have higher microwear texture complexity and lower anisotropy than grazers, which have lower com-

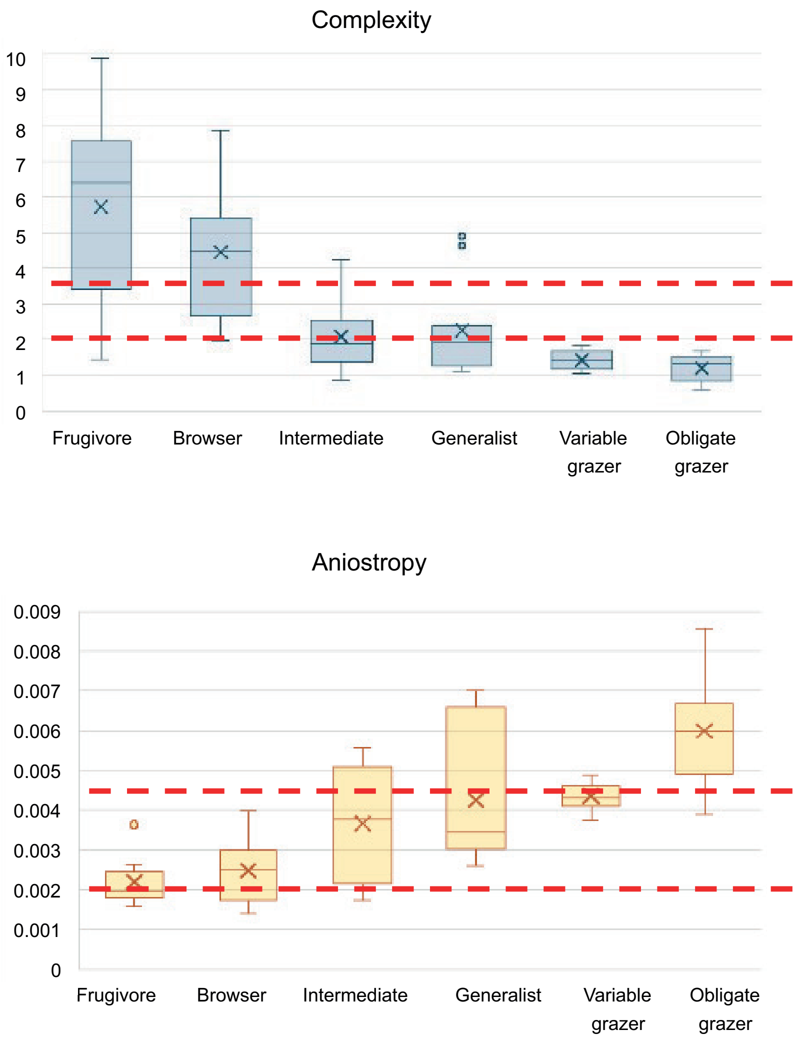

Fig. 3. Comparisons of maximum and minimum median values for Finnish reindeer (red lines) with box-and-whisker plots for values reported by Han (2024) for extant baseline bovids with known diets. Note that values for the two studies are likely offset, with higher and lower complexity and anisotropy ranges, respectively, for the reindeer relative to the baseline series given different instruments used to generate the raw data (*see* text).

plexity and higher anisotropy than browsers. Further, mixed-feeding species are intermediate and microwear texture signatures tend to reflect their position along the graze-browse continuum (*see* Fig. 3).

Unfortunately, the data presented here could not be compared directly to those generated for the ruminant baseline of Scott (2012) because the current study used a newer confocal profiler model with a higher resolution and larger work envelope and newer software to generate the texture characterizations. In fact, in comparisons of data derived from the same specimens, the Plμ standard "Connie", which was used to generate the original baseline, tended to give higher texture complexity values and lower anisotropy values than the Plμ neox "Wall-e" used in this study (Arman *et al*. 2016). The differences were of a magnitude that could potentially yield different dietary reconstructions if values for the same surfaces were compared directly. Still, results presented here are contextualized roughly by comparing high and low median values for various districts against distributions of Scott's (2012) baseline point clouds generated with the Plμ standard instrument but reanalyzed using the newer software (Han *et al*. 2024), with the caveat that the instrument used to generate those data was different.

The main focus of the research presented here though, was on a within-study comparison of microwear texture data between districts with differing food type availabilities. Rather than simply comparing results for the various districts, we used a generalized linear mixed model to evaluate the effects of food type availability in those districts on reindeer microwear texture values (*Asfc* and *epLsar*).

For the food availability variables, we used pasture inventory data reported by the Finnish Game and Fisheries Research Institute (FGFRI) on the land area (ha) of 1) dwarf shrub, hay and grass pastures and 2) ground lichen pastures. We used ground lichen rather than arboreal lichen because reindeer in these districts do not shift their preference from the former to the latter until later in the winter, well after the slaughter season during which the microwear reported here was formed (Kumpula 2001). Unfortunately, inventories do not and cannot separate grass from dwarf shrub areas because these two plant functional types largely coexist in the same pastures in the districts of northern Finland. This makes it difficult to distinguish between the two, which is something that microwear of ruminants is particularly effective at (*e.g.*, Solounias *et al*. 1988, Scott 2012). Nevertheless, reindeer consume both grass/hay and shrubs from these pastures, suggesting a mixed diet.

Finally, we also included the maximum allowed number of reindeer per district, which provides an estimate of the number of animals, as this value is used by cooperatives to regulate herd size. Pasture inventory data reported for 1996–1997 (Kumpula *et al*. 1997) were used here because these were the nearest in time available to the sampling of specimens considered in this study (1993–1994). These pasture inventory data are reproduced in Table 1.

The model for each response microwear texture variable included both pasture types and reindeer number as fixed effects, and the herding district as a random effect. We applied the *glmmTMB* function of the *glmmTMB* package (Brooks *et al*. 2024, v1.1.10) using R statistical software (R Core Team 2024, v4.4.2) for the models and adjusted the probability distribution for each response variable to *Gaussian* with "identity" link. Complexity values were log-transformed to satisfy assumptions of parametric statistical analyses, and anisotropy was multiplied by 1000 given the scale difference between the variables. All predictors were scaled using *scale* function. Model fit was assessed using the simulation-based package *DHARMa* (Hartig 2024, v0.4.7) and the *tab_model* function of the *sjPlot* (Lüdecke 2024, v2.8.16) package for model summaries. The *ggplot2* package (Wickham *et al*. 2024, v3.5.1) was used for figures.

Results

Raw microwear texture data generated for this study (*Asfc, epLsar* and other texture variables not included) are archived online in the NSF Arctic Data Center Repository (Ungar & Celis 2026). Summary statistics for both complexity and anisotropy variables, considered by herding district, are presented in Table 2. When these data are compared with those of the extant

Table 2. Summary microwear texture statistics by herding district.

		Asfc			*epLsar* (× 1000)		
	n	Median	Mean	SD	Median	Mean	SD
Alakylä	19	3.426	5.017	5.606	4.349	4.306	2.180
Hammastunturi	19	3.143	3.590	1.645	4.538	4.398	1.594
Ivalo	23	2.462	3.213	3.159	3.314	3.928	1.895
Käsivarsi	21	3.658	5.598	6.508	3.716	3.901	1.770
Näätämö	20	3.512	4.790	4.381	3.180	2.727	1.400
Paatsjoki	22	3.742	3.765	1.899	1.996	2.620	1.545
Paistunturi	12	1.998	2.477	0.977	3.495	3.936	1.949
Näkkälä	21	3.441	3.459	1.579	3.676	3.546	1.847
Sallivaara	22	3.615	3.727	1.295	3.705	3.377	1.491

baseline series reported in Han *et al*. (2024), the range of median values for the herding districts falls within the mixed-feeder to browser/frugivore range, centered squarely between browser and browse-graze intermediate (Fig. 3). This is reported with the caveat that different instruments were used to generate these data, which limits the comparability of results (*see* above and Arman *et al*. 2016). In any event, we are confident, based on the patterns observed, that none of the reindeer samples had the texture distributions of grazing ruminants.

Results indicate a great deal of variation in both complexity and anisotropy values for reindeer within each of the districts and overlap among samples (Fig. 4). Still, the observed variation in microwear was significantly related to the number of hectares of ground lichen available in each district. The generalized linear mixed model found no relationship between complexity (*Asfc*) and dwarf shrub, hay and grass pasture (ha) or reindeer number, and no relationship between anisotropy (*epLsar*) and any of the three fixed effects. On the other hand, there was a negative relationship between *Asfc* and the amount of ground lichen (ha) (p = 0.014, Table 3).

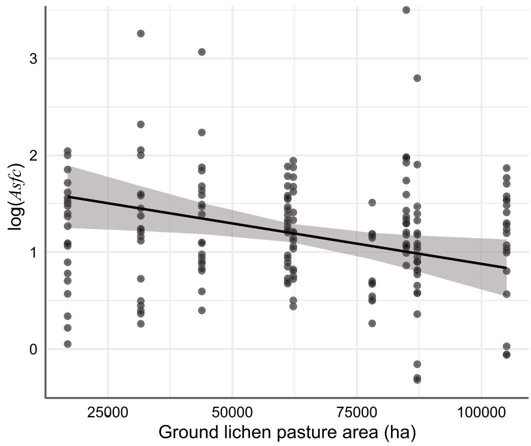

Fig. 4. Estimated marginal response (black line) based on a generalized linear mixed model for *Asfc* in relation to ground lichen pasture ha per reindeer. The confidence interval of the marginal response is depicted by the shaded area.

Discussion

Our results are consistent with consumption of both browse items and grass for herds from all nine of the Finnish districts considered (with the caveat that the baseline data were generated with a different instrument). Since all previous rein-

Table 3. Results of the generalized linear mixed models evaluating each response microwear texture variable (*Asfc* and *epLsar*). Each model included pasture type and maximum number of reindeer as fixed effects and herding district as a random effect. SHG = dwarf shrub, hay, and grass pasture. Model predictor estimates (from Gaussian models with an "identity" link), confidence intervals (CI) and p-values (p) are reported. ICC is the intraclass correlation coefficient, and τ_{00} is the random effect intercept variance.

	log(*Asfc*)			*epLsar* (× 1000)		
	Estimates	CI	*p*	Estimates	CI	*p*
(Intercept)	1.19	1.09–1.28	< 0.001	3.61	3.27–3.95	< 0.001
SHG ha	-0.05	-0.29–0.20	0.710	0.35	-0.50–1.20	0.420
Ground lichen ha	-0.23	-0.41– -0.05	0.014	0.26	-0.39–0.91	0.428
Maximum reindeer	0.26	-0.07–0.59	0.125	-0.25	-1.41–0.91	0.675

Random effects		
σ^2	0.326	3.041
τ_{00}	0.005 $_{District}$	0.116 $_{District}$
ICC	0.015	0.037
N	9 $_{District}$	9 $_{District}$
Observations	179	179
Marginal R^2 / Conditional R^2	0.058 / 0.072	0.028 / 0.064
AIC	822.358	724.123

deer and caribou microwear studies identified the species as a mixed feeder and feeding ecological studies report the same (*see* Rivals & Solounias 2007, Merceron & Madelaine 2006, Bignon-Lau *et al*. 2017, below), this result makes sense.

Concerning variation within the sample, at least some of it can be explained by differences in the availability of food types in the districts (*see* Fig. 4). Specifically, a significant portion of the observed variation in complexity is related to the abundance of ground lichen. Lower *Asfc* values are associated with more lichen. Two explanations can be considered. First, more lichen means less mechanically challenging and abrasive foods, thereby diluting the wear signal that would otherwise have been left by such foods. Second, mastication of soft and pliant lichen is expected to cause light attrition from direct tooth-to-tooth contact, further masking the pits and scratches left by more demanding foods still consumed alongside the lichen. The lack of variation in *epLsar* with lichen availability is not surprising in this light either. We find no reason why lichen consumption should affect the directionality of microwear features on the tooth surface which most likely relates to material properties of the foods that cause the microwear features (e.g., grass, hay and dwarf shrubs).

While previous microwear studies have proven valuable for separating ruminants by proportions of graze and browse in the diet (*see* Scott 2012), it was not possible to assess impacts of differential availability of each food type on diet in these samples because the available pasture inventory data did not separate grass and hay from dwarf shrubs. Furthermore, these food types are all commonly consumed in the autumn by reindeer. Indeed, the lack of difference in either microwear attribute by dwarf shrub, hay and grass pasture (ha) is consistent with consumption of grass/hay and browse to similar degrees in these districts independent of the number of available hectares of this pasture type.

The feeding ecology of *Rangifer tarandus* in Lapland and the role of lichen

Reindeer in Finnish Lapland frequently graze pine bogs and open mires, both with large amounts of edible grasses and sedges, in the spring and early summer. They prefer grasses and leaves of deciduous trees and shrubs in logged/felled areas later in the summer and autumn and, when cratering in the snow during early winter, they consume lichen as well as available grass, hay and dwarf shrubs. Dry (oligotrophic) pine forests, especially old growth ones, are used mainly as ground lichen pastures in the winter, while old growth mesic and submesic spruce/pine forests are arboreal lichen pastures used especially later in the winter. Thus, around the time of slaughter reindeer are transitioning toward their lichen-dominated winter diet but still also consume grass, hay, dwarf shrubs and other available items (Kumpula 2001, Kumpula *et al*. 2007, 2008, Bezard *et al*. 2015 and references therein).

That said*, R. tarandus* is unusual among ruminants in its ability to digest lichens, and these algal-fungal symbionts can make up more than half of the winter diets of reindeer and caribou (*e.g.*, Boertje 1984, Gaare & Skogland 1978, Scotter 1965, Steen 1968). This winter food source is therefore an important key to the success of reindeer at high latitudes. However, as climate and land use patterns change and intensive long-term reindeer grazing and summer trampling (*cf*. Forbes 2006) continue, substantive lichen cover is declining across the Arctic in general and northern Finland specifically (Joly *et al*. 2009, Kumpula *et al*. 2014). There is value, therefore, in developing proxies like tooth wear for tracking diet variation of these important livestock over time and space, particularly as concerns consumption of lichen and alternative winter foods.

The role of tooth wear as a proxy for lichen consumption

Skogland (1988) found that wild female reindeer in Hardangervidda, Norway (with high population density and low lichen availability), wore their teeth much more rapidly than those in the Knutshø area (with more lichen and fewer reindeer to eat them). As ground lichen availability dropped in the wintertime, he reasoned, more foods of lower nutritional value were consumed and grit-covered short lichens and rock lichens were exploited. The resulting tooth wear was said to have a "multiplier effect", wherein decreased masticatory efficiency affects nutrient absorption, further limiting energy assimilation and resulting in leaner cows with increased offspring loss and lowered reproductive success. Such observations have led others, such as Kojola *et al*. (1998), to look to gross tooth wear as a proxy for lichen availability — or lack thereof (*see* above).

But microwear has also been used to infer diets of *R. tarandus*. Rivals and Solounias (2007) conducted a low-magnification feature-based microwear analysis of wild caribou molars from eastern Canada. Microwear feature numbers were moderate and fell between dedicated grazers with more scratches and browsers with more pits, consistent with a mixed feeder diet, just as suggested for reindeer by Merceron and Madelaine (2006). Rivals and Solounias' (2007) samples also showed remarkable variation between seasons. More pits were reported for individuals collected in April and November, but more scratches were recorded for those from June to September. Rivals and Solounias attributed the difference to the cyclic migration of the population, from tundra in the summertime where/when they consumed more willows and graminoids, to boreal forest in the winter where/when they preferred lichens and mushrooms.

In a more recent study, Bignon-Lau *et al*. (2017) compared microwear textures between the reindeer populations from Knutshø and Hardangervidda. Their results also indicated that *R. tarandus* samples had microwear complexity and anisotropy values within the range of dietary generalists, but in this case the Hardangervidda sample had higher complexity and lower anisotropy than Knutshø, suggesting more browse for the former and more graze for the latter. They relate these differences to higher population density and concomitant lesser abundance of preferred grasses, sedges and lichens for the Hardangervidda individuals, leading to a more restricted, browse-dominated diet. In contrast, greater availability of graminoids and lichens was suggested to explain the lower complexity and higher anisotropy signature for the Knutshø sample.

These studies employed very different techniques and reported on microwear at very different scales; and each had its assumptions about lichen availability and consumption. Further, Rivals and Semprebon's (2016) observation of an increase in pits in winter caribou, when lichen consumption peaks, contrasts with Bignon-Lau *et al*.'s (2017) finding of lower complexity (and presumably fewer pits) in their sample with greater access to lichens. The current study might help shed further light on the microwear patterning associated with lichen consumption. First, nine samples (not just two) with varying lichen availability were considered. Further, rather than inferring lichen availability from reindeer density (assumed to be inversely correlated), this study reports results for districts with estimated reindeer numbers and actual measured terrestrial lichen pasture sizes in hectares. In this case, results are consistent with Bignon-Lau *et al*.'s (2017) suggestion that higher lichen availability leads to more consumption and lower microwear texture complexity values. It should be noted, however, that Bignon-Lau *et al*. (2017) used the now defunct ToothFrax/SFrax software packages (Surfract Corp., Worchester, MA) rather than MountainsMap to generate texture data so results for that study should not be compared directly with those presented here (*see* Calandra *et al*. 2022).

Other factors that might affect (or effect) variation in microwear textures

There remains substantial variation in microwear texture complexity and anisotropy that cannot be explained by lichen availability in a district. It cannot be explained by supplementary feed either, as this is not given to reindeer during autumn in the weeks leading up to slaughter. Individuals sampled for this study likely received no feed in autumn when gathered from natural pastures during the roundup either. While it is possible that some silage or dry hay was offered once the animals were in the gathering enclosures in the latest round-ups (after the snow had already come), they were kept there no more than a few days prior to slaughter, so while this might have introduced some noise to the diet signal, it would not likely have swamped texture signatures given that whole surface patterns can take weeks to turnover with diet change (Winkler *et al*. 2020).

Concerning feeding in natural pastures, there is no reason to expect a one-to-one correspondence between relative abundances of different food types and what reindeer select to eat. The summaries of Lönnberg (1909) and Skuncke (1958) suggest that semi-domestic reindeer generally consume a wide variety of plants, in addition to lichen and mushrooms, but we know little about the details in the Finnish herding districts in the mid-1990s. Reindeer are likely to eat a preferred species when available even if its biomass is less than lower-ranked fallback food taxa. Further, given reindeer movement within these large herding districts, some even highly nutritious resources may become (and are recorded as) abundant precisely because reindeer avoid the areas where they grow for other reasons, such as insect harassment, anthropogenic disturbance or traditional migration paths (*e.g.*, Helle *et al*. 2012, Myrrvoll *et al*. 2011, Skarin *et al*. 2015, Vistnes *et al*. 2004).

There is also the issue of seasonality and resource availability when the microwear was produced. Slaughter occurred in the late autumn and early winter, before the transition to a lichen-dominated winter diet was complete. While lichen certainly played a role, mushrooms are consumed from August until October where available, and grasses such as *Dechampsia flexuosa* are often still available up to early winter when snows come and reindeer crater until December.

As a final note, we reiterate that lichens themselves cause little microwear, as they are soft and lack intrinsic abrasives. The microwear surface observed would then reflect other, less commonly consumed items — particularly any mechanically challenging and abrasive foods. We would nevertheless expect that a minor component of shrubs, grasses and other items in the diet would leave a different microwear signature than a major amount of the same foods, since the number of occlusal events per unit time would be lower. Relatively fewer deep scratches and pits should be observed. When combined with attritional wear due to tooth-to-tooth movements, high consumption of lichen might in this way result in lower complexity and/or anisotropy depending on the nature of whatever else was consumed.

Conclusions

While there is considerable variation in microwear texture complexity within and among the districts for reindeer analyzed here, a significant portion of the variation seems to track lichen availability. The story is, however, a complex one and much work remains to be done, including studies of reindeer with better control over diet in the days and weeks prior to death to better understand the etiology of microwear patterns and their relationships with consumption of lichens and other food types. Tracking relationships between food choice and availability in the past through microwear is an important key to understanding paleoecology, but this study suggests that it might also play a role in neontological studies of impacts of environmental variation on feeding behaviors today.

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