Dental evidence for variation in diet over time and space in the Arctic fox, *Vulpes lagopus*.

by

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ABSTRACT

Studies of the effects of variation in resource availability are important for understanding the ecology of high-latitude mammals. This paper examines the potential of dental evidence (tooth wear and breakage) as a proxy for diet and food choice in *Vulpes lagopus*, the Arctic fox. It presents a preliminary study of dental microwear, gross wear score, and tooth breakage in a sample (n = 78 individuals) from the Yamal Peninsula of the Russian Arctic. While these measures have each been associated with feeding ecology in larger carnivorans (e.g., proportion of bone in the diet), they have yet to be combined in any study, and have rarely been applied to smaller species or those from high latitudes. Arctic foxes from the north and south of the peninsula, and those from rodent peak and trough density periods, are compared to assess impact of changes in food availability across space and time. Results indicate that microwear textures vary in dispersion, with more variation in texture complexity, including higher values (suggesting more consumption of bone), in the rodent-poor period in the north of Yamal. Gross wear scores and tooth breakage are also significantly higher for the north of Yamal than the south. These data together suggest that dental evidence can provide important insights into variation in the feeding ecology of Arctic foxes and potentially into the impacts of changes in food abundance across space and time.

KEYWORDS: Yamal Peninsula, microwear, tooth wear and breakage, feeding ecology

DECLARATIONS

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Authors' contributions. PSU, AAS, and NAS conceived of the project. NAS, VS, IF and AAS collected/processed specimens and generated metadata used in this paper. PSU, BVV, and ASP generated the dental data presented in this paper. PSU, DE, and BVV analyzed the data, and PSU, BVV, AAS, NAS, DE, OG, BVV, ASP, AT, and AV wrote the paper.

INTRODUCTION

Ongoing environmental changes in the Arctic underscore the importance of documenting and understanding impacts of variation in resource availability on the ecology of high-latitude mammals. Proxies designed to measure fine-scale ecological variation today, retrodict in the past, and monitor it in the future are especially valuable to this end. This paper investigates the combined potential of dental microwear, gross tooth wear scoring, and antemortem tooth breakage as a proxy for food choice in *Vulpes lagopus* (the Arctic fox), an emblematic high-latitude carnivore sensitive to variation in resources across space and time.

Dental evidence for carnivoran feeding ecology

Associations between diets of carnivorans and the wear and breakage of their teeth have been well-studied at both micro- and macro- scales. Analyses of carnivoran dental microwear have demonstrated consistent and predictable relationships between patterns of microscopic scratches and pits on molar surfaces and reported diets of numerous species. Bone-crunching hyaenas (*Crocuta crocuta*, *Hyaena hyaena*) for example, have more pits relative to scratches on the trigonid facets of their mandibular carnassials (M_1s) than do generalist lions (*Panthera leo*), whereas cheetahs (*Acinonyx jubatus*), known to avoid hard tissues, have the lowest pit-to-scratch ratios (Van Valkenburgh et al. 1990). The pits are explained as a result of crushing bone against the M_1 surface, whereas parallel scratches are inferred to result from slicing softer tissues (e.g. muscle) between opposing carnassial blades. In microwear texture analysis parlance, hyaenas have higher texture complexity (e.g., more pits of varying shapes and sizes), cheetahs have higher surface anisotropy (e.g., parallel scratches), and lions are intermediate (Schubert et al. 2010).

Similarly, at the macroscopic level, numerous studies have also shown clear associations between degree of gross dental wear and incidence of antemortem tooth breakage on the one hand, and reported diet of carnivoran species on the other. Carnivorans that crush hard foods, such as bone or shell, exhibit the most gross dental wear and highest rates of tooth fracture (Van Valkenburgh 1988; 2009). Differences are also reported within carnivoran species between populations with varying levels of food stress and, consequently, degree of carcass utilization (Mann et al. 2017; Van Valkenburgh et al. 2019). For example, a comparison of tooth fracture in gray wolves from localities or time periods that differed markedly in prey abundance revealed significantly higher numbers of broken teeth (more than double in some cases) in populations from low prey density areas or times given the need for more complete consumption of carcasses, including bone (Van Valkenburgh et al. 2019).

Because dental microwear and tooth breakage/gross wear operate at different time scales, the combination of these diet proxies holds particular potential to reveal details not discernable with one method alone. Dental microwear features wear away and surface texture is typically overwritten over the course of days or weeks -- the so-called “last supper” phenomenon (Grine 1986). On the other hand, gross tooth wear score and antemortem breakage accumulate over the lifetime of a tooth and, except for the very young, can reflect multiple seasons or years of diet. Comparison of results from these two methods may therefore allow us to use dental evidence as a proxy for food choice as it relates to changes in availability over time.

That said, there have been few dental ecology studies on smaller carnivorans or those from the Arctic, and none that we are aware of to combine dental microwear with gross tooth wear and breakage. Here we examine dental microwear, gross wear, and tooth fracture frequency in Arctic foxes of the Yamal Peninsula, Russia, from different bioclimatic zones and during years of high and low small rodent density to explore whether their teeth also record evidence of food stress and/or dietary shifts.

Arctic foxes of Yamal

Arctic foxes are an excellent target species for studying the impact of prey availability on feeding ecology at high latitudes. Not only is *V. lagopus* a climate change flagship species (IUCN 2009), but it is an apex predator, both affecting and affected by food web dynamics (e.g., Henden et al. 2009; Gharajehdaghipour et al. 2016; Ims et al. 2017). As such, documenting food choice in Arctic foxes is important for understanding high-latitude ecosystems as a whole.

The Yamal Peninsula is an excellent natural laboratory for studying the feeding ecology of Arctic foxes. The peninsula extends over 700 km south-north from the Polar Urals to the Kara Sea and presents a continuous biogeographic gradient from forest-tundra ecotone to the high Arctic (Figure 1). As a result, there is marked variation in availability of prey between the north and south. For example, the south has ten species of small rodent, among which in particular lemmings (*Lemmus sibiricus, Dicrostonyx torquatus*) are the preferred prey of Arctic foxes (Shtro 2009). Two ptarmigans (*Lagopus lagopus, La. muta*) and the mountain hare (*Lepus timidus*) serve as alternative prey. Ptarmigans and hares are abundant year round in the south, with individuals congregating in large numbers (up to hundreds of hares and a thousand ptarmigans), mostly in the wintertime (Shtro 1995; 2006). In contrast, the north has only five rodent species, and hares and ptarmigans are present only in the summer because wintertime snow cover limits availability of plant foods -- e.g., willows are taller and extend beyond the snowpack in the south (Pavlinin 1971; Riabitsev 2001; Shtro 2006; 2009). On the other hand, semi-domesticated and wild reindeer (*Rangifer tarandus*) and their carcasses are available throughout the peninsula year round.

This study set out to determine whether differences in prey availability across space and time on Yamal are reflected in Arctic fox teeth, specifically in patterns of dental microwear, gross wear score, and tooth breakage. If, as documented for other carnivorans, less availability of preferred prey results in more complete consumption of large animal carcasses (i.e., reindeer), including bone, we expect evidence of it in dental microwear, gross wear, and tooth breakage. More specifically, we expect to see such differences manifested when comparing individuals from the north and south and between rodent-rich and rodent-poor years. Differences between groups would suggest that Arctic fox teeth might be used to measure impacts of fine-scale variation in resource availability.

MATERIALS AND METHODS

A total of n =78 specimens were included in this study. All individuals were caught in foothold traps or shot by trappers from the indigenous community of Yamal to harvest fur. The current study represents a preliminary analysis focusing on three trapping periods: (1) 1981 (December 1981 - March 1982); (2) 1983 (November 1983 - March 1984); and (3) 2007 (October 2007 - March 2008). Foxes were selected to represent individuals from both northern and southern Yamal regions as well as both rodent-poor (1981/2007) and rodent-rich (1983) trapping periods (Shtro 2009; Sokolova et al. 2014). North Yamal is represented by individuals from 1981 (Ust'-Yuribei, 68.9° N, 69.4° E and Seyakha, 70.1° N, 72.5° E) and 1983 (Mordy-Yakha, 70.4 N, 67.3 E, and Yaptik-Sale, 69.4° N, 72.5° E), whereas the South Yamal sample includes individuals from 1983 (Labytnangi, 66.7°N, 66.4°E) and 2007 (Erkuta, 68.2°N, 69.1°E). This combination of samples from the north and south and from 1981/2007 and 1983 allows assessments of effects of both sampling location and trapping period on dental microwear, gross wear, and breakage.

Carcass processing and metadata collected

Skinless carcasses were purchased from indigenous fur trappers by the Arctic Research Station, Institute of Plant and Animal Ecology, Urals Branch of the Russian Academy of Sciences, in Labytnangi (IPAE). Heads of all specimens were detached and boiled for 1.5-2 hours prior to removal of soft tissues. Metadata including sex of the individual, relative pulp cavity width of a lower canine tooth (a proxy for age), and body fat score (a proxy for nutritional status) were collected during the process (see Online Resource 1).

The protocol for measurement of pulp cavity width followed Smirnov (1960). The lower right canine (C_1) was extracted and sectioned, and the width of the pulp cavity was measured as a percentage of the width of the root at its widest point (5 – 90%). While the relationship between cavity diameter and age is not linear, cavity width can provide a reasonable proxy for relative age because odontoblasts continue to secrete dentin, which decreases the volume of the pulp chamber, throughout life (Star et al. 2011; Couve et al. 2013).

The fat content of each individual was scored using the technique described by Pereleshin (1943). This measure combines information on muscle wasting and volume of body fat, with scores ranging from zero to four: (0) no measurable body fat and visibly wasted musculature; (1) no measurable fat and no visibly wasted musculature; (2) trace body fat in the groin and neck; (3) subcutaneous adipose tissue up to 1 cm thickness; and (4) large deposits of subcutaneous adipose tissue exceeding 1 cm in thickness. A score of zero suggests severe deficiency of caloric energy intake.

Dental microwear analysis

A total of *n* = 54 individuals were included in the microwear portion of this study (see Online Resource 1). Data acquisition and analysis followed usual microwear texture study protocols for carnivorans (Schubert et al. 2010). First, occlusal surfaces of the mandibular carnassial teeth (M_1s) of each individual were cleaned with alcohol-soaked cotton swabs and allowed to dry. Impressions were made using President's Jet Regular Body polyvinylsiloxane dental impression material (Coltène-Whaledent Corp., Cuyahoga Falls, OH, USA). High-resolution replicas were prepared using Epotek 301 cold-cure epoxy (Epoxy Technologies, Billerica, MA), centrifuged into the molds, and allowed to set before analysis. All replicas were subsequently screened by confocal profilometry at 100x, and those lacking unobscured antemortem microwear (see Teaford 1988 for criteria), were excluded from data collection and analysis (see Online Resource 1).

Microwear analysis focused on the M_1 trigonid shearing facet. Replicas were scanned using a Sensofar Plμ standard white-light scanning confocal profiler (Solarius Development Inc., Sunnyvale, CA). Four adjacent areas on the wear facet were scanned at 100x, each with a work envelope of 138 x 102 µm, for a total sampled area of 276 x 204 µm. The lateral point spacing for each scan was 0.18 µm, the vertical step was 0.2 µm, and the vertical resolution reported by the manufacturer is 0.005 µm. Resultant surfaces were processed and analyzed using SensoMap Premium Software (MountainsMap 8, Digital Surf Corp, Besançon, France). First, spikes and small artifacts were deleted with resultant missing data filled using a nearest-neighbor algorithm.

Second, area-scale fractal complexity (*Asfc*) and exact proportion length-scale anisotropy of relief (*epLsar*) were calculated for each surface. These attributes are described in detail by Scott et al. (2006). High complexity is typical for surfaces with pits of various shapes and sizes, and is often associated with crushing hard objects. High anisotropy is typical for surfaces dominated by aligned striations, and is often characteristic of facets used in shearing tough foods (see Calandra and Merceron 2016; DeSantis 2016; Ungar 2018 for review). Medians of values for the four scans of each tooth were calculated for each surface.

The principal statistical analyses of microwear data were divided into 1) comparisons of central tendencies and 2) comparisons of dispersion. A two-factor MANOVA was used to compare *Asfc* and *epLsar* central tendencies by year type (rodent-rich 1983 versus rodent-poor 1981/2007) and location (north versus south). Data were rank-transformed for the MANOVA to mitigate violation of assumptions inherent to parametric statistical analyses (Conover and Iman 1981). Bartlett's and Levene's (mean) tests were then used to assess variation in dispersion for *Asfc* and *epLsar*, comparing samples by year type for combined locations, and separately for the north and south samples. Levene's test results are more robust to departures from normality (Levene 1960).

We also tested the hypothesis that microwear texture complexity varies with fat content given the prediction that hungry or starving animals would more often consume bone from large prey or carcasses. The fact that microwear and fat content patterns likely reflect feeding behaviors over similar temporal scales of days to weeks (Teaford and Oyen 1988; Teaford et al. 2020) provides ample justification for such a comparison. In this case, we compared dispersion of *Asfc* values between samples parsed by fat score (score = 0 versus 1-4). This allowed us to compare the most nutritionally stressed animals with others, while providing sufficient sample sizes in each category for statistical analyses. Again, Bartlett's and Levene's tests were used to compare samples by combined locations and separately for north and south. Individuals with fat scores of zero for 1981/2007 were compared separately to those with scores of 1-4 from 1981/2007 and those with scores of 1-4 from all year samples. There were no 1983 (the rodent-rich year) specimens in the fat score = 0 category (see Online Resource 1 and Table 1).

Gross wear and breakage.

Data were collected from a total of n = 78 individuals for the gross tooth wear and breakage studies (see Online Resource 1). Whereas previous analyses of tooth fracture frequency in carnivorans relied on direct observation of specimens (e.g., Flower and Schreve 2014; Van Valkenburgh 1988; 2009), the present study was conducted using digital images of original dentitions. Photographs were taken using a Nikon D7200 DSLR camera and an AF Micro Nikkor 60 mm macro lens (Nikon Corp., Tokyo, Japan) with an aperture value = f32 and field of view filled to maximize depth of focus and resolution of individual teeth. Eight views of each specimen were recorded: maxillary and mandibular buccal (left and right), maxillary and mandibular occlusal, and maxillary and mandibular anterior to allow for assessment of gross dental wear and individual tooth breakage.

To prevent expectation bias in wear scoring or breakage assessment, specimens were scored blind to year of death, fat level, age, or location. Dental wear stage was assigned after examining all images for a given specimen as one of five stages: (1) 'slight', little or no wear on shear facets and no blunting of cusps; (2) 'slight-moderate', slight wear on shear facets and minimal blunting of cusps, (3) 'moderate', shear facets apparent on carnassial teeth and cusps blunted on most teeth; (4) 'moderate-heavy', carnassial teeth moderately blunted, premolars and molars with well-rounded cusps, or (5) 'heavy', carnassial teeth with strongly blunted cusps, premolars and molars with well-rounded cusps. Of these five wear categories, the 'slight' category was the most difficult to discern based on digital images (i.e., without being able to rotate or reposition the specimen to enhance visibility of shear facets). Consequently, it is likely that more individuals were assigned to the 'slight-moderate' category than would have been the case if assignments were made using the original specimens.

In addition to wear stage, the number and identity of all teeth broken antemortem were recorded. To avoid counting teeth that were broken postmortem or just prior to death due to biting on traps or other damage, teeth were recorded as broken only if there was clear evidence of fracture (e.g., partially or fully broken cusp) and a fully blunted surface due to subsequent wear (Binder and Van Valkenburgh 2010). If there was a suggestion of a sharp edge, then the tooth was not counted as broken. In addition, missing teeth were not counted as broken, even when alveolar resorption suggested tooth loss due to injury. Consequently, the total number of teeth broken prior to death are likely undercounted, though any underestimates are consistent across the study given consistent criteria of identification.

Because tooth wear score and breakage covary with age independent of other factors (see Van Valkenburgh et al. 2019 for discussion), our comparisons of samples by location and year type were designed to control for the age of each individual. We used relative pulp cavity width of the lower right canine as our proxy for age (Bradley et al. 1981; Smirnov 1960; Tumlison and McDaniel 1984; see above).

Two separate approaches were used for statistical analyses of tooth gross wear and breakage. We first used ANCOVA models to compare regressions of the dependent variable percent broken teeth (quotient of number of teeth with antemortem breakage to number of teeth present for each specimen) to the independent variable relative pulp cavity width. Both variables were rank-transformed before analysis to mitigate violation of assumptions inherent to parametric statistical analyses (Conover and Iman 1981).

Separate tests were used to compare specimens in the north and south, and specimens from the 1983 sample with those from the 1981 and 2007 trapping periods. Initial homogeneity of regressions tests were performed to demonstrate no significant differences in the slopes for each sample in each test. ANCOVA test results were then used to assess whether individuals in different samples had significantly different percentages of broken canines at a given pulp cavity width. The same ANCOVA model was used to compare regressions of wear score and pulp cavity width. In addition, Pearson's X^2 tests were used to determine whether there is a sex bias in canine breakage, e.g. resulting from combat associated with male-male competition. Tests were conducted to compare males and females for proportion of individuals with at least one broken canine present for the whole Yamal sample, and separately for those from the north and the south of the peninsula. We also compared percentages of teeth broken by tooth type (incisors, canines, etc.) between locations and years using Pearson's X^2 tests to assess the relative contribution of tooth type to overall fracture rates.

Gross tooth wear scores were analyzed further as categorical variables using cumulative link models (Christensen 2019; R Core Team 2020). In addition to location (north or south) and trapping period type (rodent-rich 1983 compared to rodent-poor 1981 and 2007), we included relative pulp cavity width and sex as possible covariates. Several candidate models with different combinations of variables were assembled (see Online Resource 2) and compared using Akaike's information criterion for small samples (AICc) following Hurvich and Tsai (1989). Models with a difference in AICc (ΔAICc) < 2 were considered to fit the data equally well and the simplest model was chosen. Equidistant thresholds were used. We used the same approach with a generalized linear model with a binomial error distribution for the proportion of broken teeth, and parameters were estimated from a quasibinomial model to take into account over-dispersion.

RESULTS

Results of this study indicate that groups parsed by location and year type differ significantly in aspects of tooth microwear, wear score, and breakage. While carnassial microwear texture complexity values do not differ in central tendencies among groups, dispersion is higher for the rodent-poor year (1981/2007) sample than for the rodent-rich year (1983) sample, specifically for those individuals from North Yamal. Furthermore, individuals from North Yamal have higher dental wear scores and more antemortem tooth breakage for a given pulp chamber width than those from South Yamal, independent of trapping period. All raw data can be found in Online Resource 1 and sample images are presented in Figure 2.

Microwear

Microwear statistics are provided in Tables 1-2 and illustrated in Figures 3-4. The MANOVA study found no significant variation in central tendency for microwear texture (*Asfc* and *epLsar*) by year type or location, and no significant interaction between the two factors (Table 2a). In other words, average texture complexity and anisotropy do not appear to differ between the rodent-poor 1981/2007 and rodent-rich 1983 trapping periods or between north and south samples. Furthermore, no significant differences in dispersion of anisotropy (*epLsar)* values were detected between samples parsed by location and year type.

On the other hand, 1983 and 1981/2007 samples do evince significant differences in dispersion of complexity (*Asfc*) values according to both Bartlett's ($X^{2\,1}$ = 10.587, p = 0.001) and Levene's ($F^{1,52}$ = 4.743, p = 0.034) tests (Table 2b, Figure 3). For tests where specimens were parsed by location, that difference is limited to the northern sample (Bartlett's test, $X^{2\,1}$ = 9.107, p = 0.003; Levene's test, $F^{1,23}$ = 10.948, p = 0.003). Complexity data for northern foxes collected during the rodent-poor 1981 trapping period include the highest values of this metric, with significantly greater variance than for those from this region collected during rodent-rich 1983. Dispersion of complexity does not vary within the southern sample, where individuals from both year types show modest variation compared with the northern specimens from 1981.

The analyses of dispersion of microwear texture complexity parsed by fat score also found significant variation for both Bartlett's and Levene's tests (Table 2c, Figure 4). *Asfc* dispersion for combined trapping periods varies significantly by fat score for northern (Bartlett's test, $X^{2\,1}$ = 12.29, p > 0.001; Levene's test, $F^{1,23}$= 26.379, p < 0.001) but not southern specimens, with fat score = 0 associated with higher complexity. The combined location sample for rodent-poor 1981/2007 specimens also differs significantly in texture complexity variation using both Bartlett's ($X^{2\,1}$ = 4.228, p = 0.040) and Levene's ($F^{1,24}$= 5.080, p = 0.034) tests. Considering the 1981 sample from the north alone, those with fat score = 0 have higher microwear texture complexity dispersion than those with fat scores 1-4 (Bartlett's test, $X^{2\,1}$ = 5.19, p > 0.023; Levene's test, $F^{1,8}$= 11.245, p < 0.010). The rodent-poor 2007 sample from the south does not differ in texture complexity dispersion by fat score. The dispersions of complexity values for both southern samples (fat score = 0 and fat score = 1-4) are modest compared with that for the northern fat score = 0 sample (Figure 4). These results have the caveat that the sample size for specimens with fat score = 0 is smaller than that for specimens with fat scores 1-4. This may limit interpretability, especially for the southern sample. On the other hand, the variance is actually higher in the fat score = 0 samples from the north and combined 1981/2007 sample, so significant differences in dispersion in these cases is not likely related to sample size differences.

Wear scores and tooth breakage

Summary and analytical statistics for wear scores and tooth breakage are presented in Tables 3-5 and Online Resource 2. Results are illustrated in Figures 5-7. The homogeneity of regressions tests for gross wear score and broken teeth against relative pulp chamber width found no significance when comparing samples by location and by year type. This suggests the slopes are comparable between locations and year types for both wear score and percent broken teeth.

The ANCOVA tests found significant differences between North and South Yamal samples in both wear score ($F^{1,75}$= 20.60, $p < 0.001$) and percent broken teeth ($F^{1,75}$= 11.72, $p = 0.001$) controlling for relative pulp chamber width. On the other hand, samples do not differ significantly by year type in either wear score or percent broken teeth (controlling for relative pulp chamber width) (Table 4a). While values are similar comparing 1983 and 1981/2007 samples, both wear score and percent broken teeth are higher in the north than in the south (Figure 6). This implies that Arctic foxes in North Yamal tend to wear and break their teeth more at a given age than do those in the South Yamal. Again, no significant differences were found for wear or breakage rates between rodent-rich and rodent-poor years.

In addition, Pearson's X^2 test results found no significant difference in incidence of canine breakage between males and females in the north, south, or overall combined sample (Tables 3b and 4b), suggesting that differences in tooth breakage between samples cannot be explained by sex specific behavior. Importantly, the greater rates of tooth breakage in the north are distributed across the tooth row, in teeth used for a variety of feeding modalities, including gnawing (incisors), killing (canines), and slicing and chewing (premolars, molars) (Tables 3c, 4c, and Figure 7).

The analysis of gross tooth wear with a cumulative link model confirms the above results. We selected the model with pulp chamber width and location based on AICc as the most parsimonious (ΔAICc = 2.19 to the next best model, see Online Resource 2). Models including sex or year type were not supported, nor was the model of an interaction between pulp chamber and location. The selected model shows lower tooth wear in younger foxes (those with relatively larger pulp chambers) and higher tooth wear for foxes from the north. The odds ratio for the tooth wear score of a fox to be in or above a certain category versus being below it is 6.75 (95 % confidence interval CI = 2.66 – 18.09; Table 5a).

Congruently, the model selected for the proportion of broken teeth includes also pulp chamber width and locality as variables. Two other models have small differences in AICc, but those include more parameters and are thus less parsimonious (see Online Resource 2). The selected model indicates that the foxes have more broken teeth in the north (odds ratio 2.35, CI = 1.35 – 4.24), and that older foxes have more broken teeth (Table 5b). In other words, like the ANCOVA model, the model selection approach indicates that northern foxes have significantly heavier tooth wear and more broken teeth when controlling for the age proxy than do southern foxes, and that year type and sex do not explain significant variation in these measurements. Further, older foxes (those with narrower pulp chambers) have more worn and more broken teeth all else being equal.

DISCUSSION

Results presented here suggest strongly that the combination of carnassial microwear, gross tooth wear score, and antemortem tooth breakage can provide important insights into variation in the diet and ecology of Arctic foxes across space and time. Because they operate at different time scales, the combination of these diet proxies holds particular potential to reveal details not discernable with one method alone. The fact that dispersion of microwear complexity varies with fat score in individual animals makes perfect sense in light of the fact that surface texture is overwritten over the course of days or weeks. On the other hand, gross tooth wear score and antemortem breakage accumulate over the lifetime of a tooth and, except for the very young, can reflect multiple seasons if not years of diet.

In this study, we found greater dispersion of microwear texture complexity in samples obtained from northern Yamal during the rodent-poor 1981 trapping period than in samples obtained in the north during the rodent-rich 1983 trapping period or in the south during either the 1983 or the rodent-poor 2007 period. The facts that the highest *Asfc* values were found in the northern 1981 sample and that high *Asfc* has been associated with consumption of bone in other carnivorans (Schubert et al. 2010) are consistent with the idea that at least some of these animals expanded their diets to include more bone in the days or weeks before trapping. The association between the high *Asfc* values and fat score = 0 (no measurable fat, wasted musculature) also suggests that hunger led these animals to more complete prey consumption, including more bone. Increased bone consumption does not seem to have happened in the south in 1983 or 2007, consistent with foxes in the south having more stable, consistent access to soft food resources than did their northern counterparts. The impact of hunger may actually be accentuated by the season of capture (fall/winter) for the individuals considered in this study, when preferred prey are scarce and arctic foxes are known to scavenge reindeer carcasses (Eide et al. 2012; Ehrich et al. 2017). Previous work on other taxa also found that microwear dispersion can be driven by occasional consumption of mechanically challenging fallback foods during lean times (Ungar 2009). Thus, microwear may be valuable as a proxy for shorter-term variation in food availability in Arctic foxes.

We found in addition that gross wear score and antemortem tooth breakage differ markedly between samples from North Yamal and South Yamal, regardless of the rodent conditions. Wear score is higher and there is more tooth breakage in the north than in the south for animals of a given relative pulp cavity width (and by implication, age). This is consistent with more consumption of bone by Arctic foxes inhabiting North Yamal than South Yamal, and could be augmented by factors that we could not assess here, such as greater food limitation due to increased competition or overall more limited resources in the north than the south. The lack of a difference in tooth wear score or fracture frequency between the rodent-rich 1983 and rodent-poor 1981/2007 trapping samples can be understood in the context of temporal scale of the signal. Because gross wear is aggregative and breakages accumulate over the lifetime of the dentition, we expect not to see a seasonal signal in these diet proxies – except perhaps for the youngest individuals.

The combination of microwear and gross wear score/breakage suggests that the differences between northern and southern Yamal are driven by year type (rodent-rich versus rodent-poor) and concomitant differences in food availability. The high wear and tooth fracture rate in the north likely relates to heavy consumption of bone during rodent-poor years. This makes sense if less bone is consumed in the north when rodents are plentiful in peak years (e.g.1983), and if less bone is consumed in the south regardless of year type given year-round availability of alternative prey, such as ptarmigans and hares.

Future directions

Results from this study suggest strongly that dental microwear, gross wear score, and antemortem breakage together reflect dietary ecology of Arctic foxes across space and time. That said, much work remains to be done to determine the potential of these proxies for measuring fine-scale ecological change today, inferring it for the past, and monitoring it in the future. We can consider, for example, the impact of rain-on-snow (ROS) extreme weather events occurring in some autumn and winter seasons. During ROS events, reindeer cannot break through ice encrusted pastures to feed (Forbes et al. 2016). Mass starvation and mortality of large numbers of reindeer follow, resulting in significant additional subsidies for all predators (Sokolov et al. 2016), including the Arctic fox (Ehrich et al. 2017). A larger-scale study including individuals trapped across a greater number of years with documented variation in autumn/winter icing might allow us to assess the impact of ROS extreme weather events on Arctic fox dental microwear and perhaps even gross wear score and breakage.

In addition, we hope in the future to consider microwear on other tooth surfaces, especially the M_2 talonid crushing facet analogous to Facet 9 typically used in studies of primate microwear (Krueger et al. 2008). While the carnassial trigonid facet is a standard surface for carnivoran microwear, canid M_1s are “only part of a dental armory, augmented…by the crushing molars behind them” (Van Valkenburgh 1989: 117). Indeed, the degree of dental differentiation in canids suggests that dental microwear on post-carnassials might be particularly valuable for assessing incidences of bone consumption in these carnivorans (Prassack et al. 2020; Tanis et al. 2018; Ungar et al. 2010).

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FIGURE LEGENDS

Fig. 1 The Yamal Peninsula. The sites from which specimens were sampled are as indicated on the map.

Fig. 2 Sample microwear photosimulations representing specimens from the north and south of Yamal during rodent-rich and rodent-poor sample periods. 1a) North, 1983; 1b) South, 1983; 1c) North, 1981; 1d) South 2007. Each montage represents an area 276 x 204 µm

Fig. 3 Box and whiskers plots for microwear texture complexity (*Asfc*) of specimens considered by location (north versus south) and sample period (rodent-rich years 1981/2007 versus rodent-poor year 1983). The hinges mark the first and third quantiles, the vertical lines between them are medians, each whisker represents a value 1.5 times the interquartile range. Boxes for southern specimens are blue (online version) and stippled. Sample sizes are presented in Table 1

Fig. 4 Box and whiskers plots for microwear texture complexity (*Asfc*) of specimens considered by fat score (0-4) and location (north versus south) for combined sample periods (2a) and rodent-poor sample periods (2b). The hinges mark the first and third quantiles, the vertical lines between them are medians, each whisker represents a value 1.5 times the interquartile range, and circles are far outliers. Boxes for southern specimens are in blue (online version) and stippled. Sample sizes are presented in Table 1

Fig. 5 Sample mandibles for North Yamal (4a) with heavy wear and South Yamal (4b) with slight/moderate wear.

Fig. 6 Regressions of wear stage (5a, 5b) and proportion of teeth broken (5c, 5d) per individual on relative pulp chamber area as a proxy for age (older individuals have smaller pulp chambers). North (indicated by red [online version] O) and South (indicated by blue [online version] X) Yamal (left) and rodent-rich (indicated by blue [online version] X) and rodent-poor (indicated by red [online version] O) sample periods (right) are considered separately. South and 1983 sample period regression lines are stippled

Fig. 7 Percentage of broken teeth by tooth type per sample (number broken/total number of teeth) for comparing north and south samples for rodent-rich (6a) and rodent-poor (6b) sample periods. Pms = pre-carnassial premolars, pc molars = post-carnassial molars. North and South Yamal sample represented by grey and white bars, respectively

TABLE LEGENDS

Table 1 Dental microwear summary statistics

Table 2 Dental microwear analytical statistics

Table 3 Gross wear and tooth breakage summary statistics

Table 4 Gross wear and tooth breakage analytical statistics: ANCOVA and X^2 test results

Table 5 Gross wear and tooth breakage analytical statistics: coefficients from the selected cumulative link model and the selected generalized linear model

Figure 1

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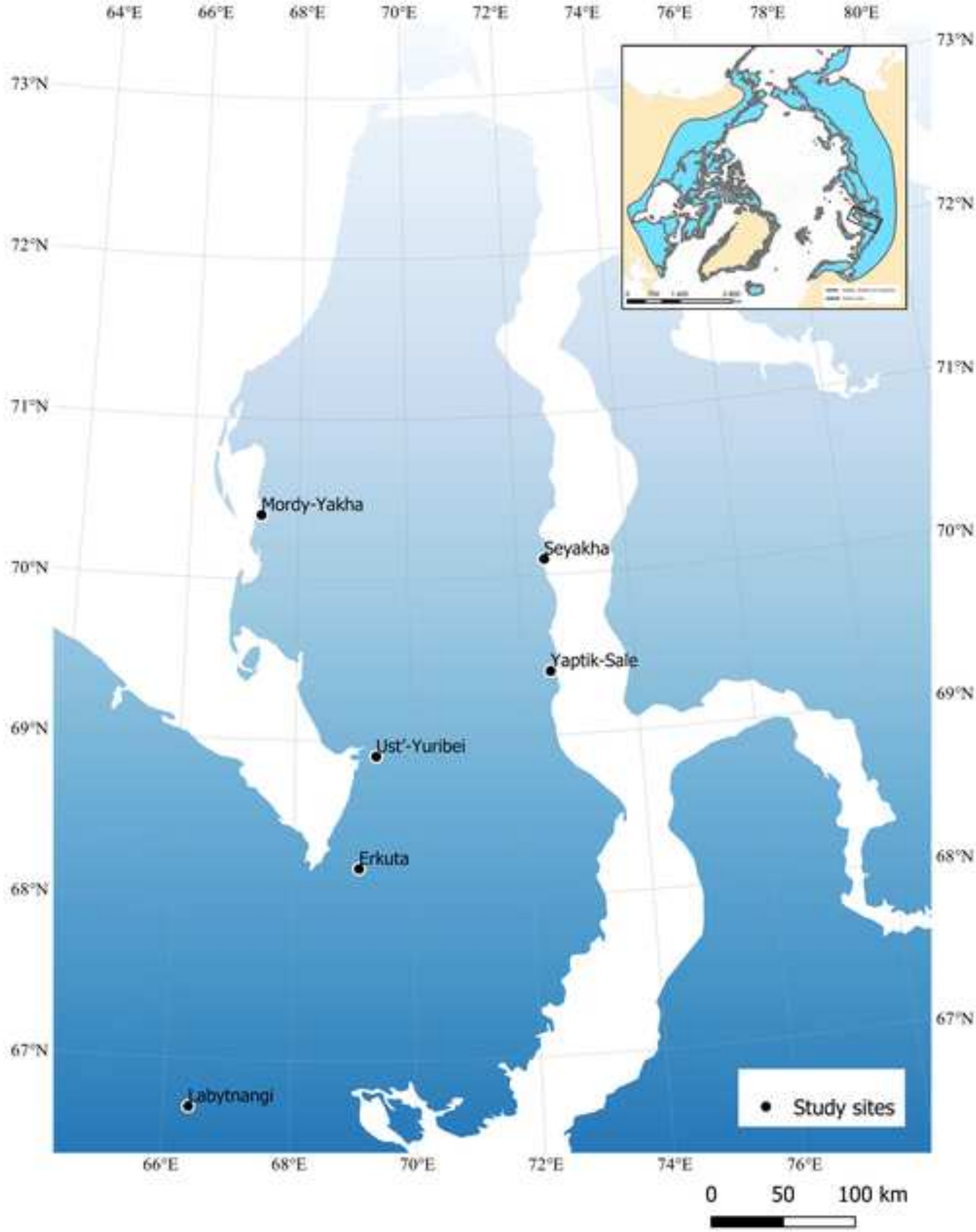

Figure 2

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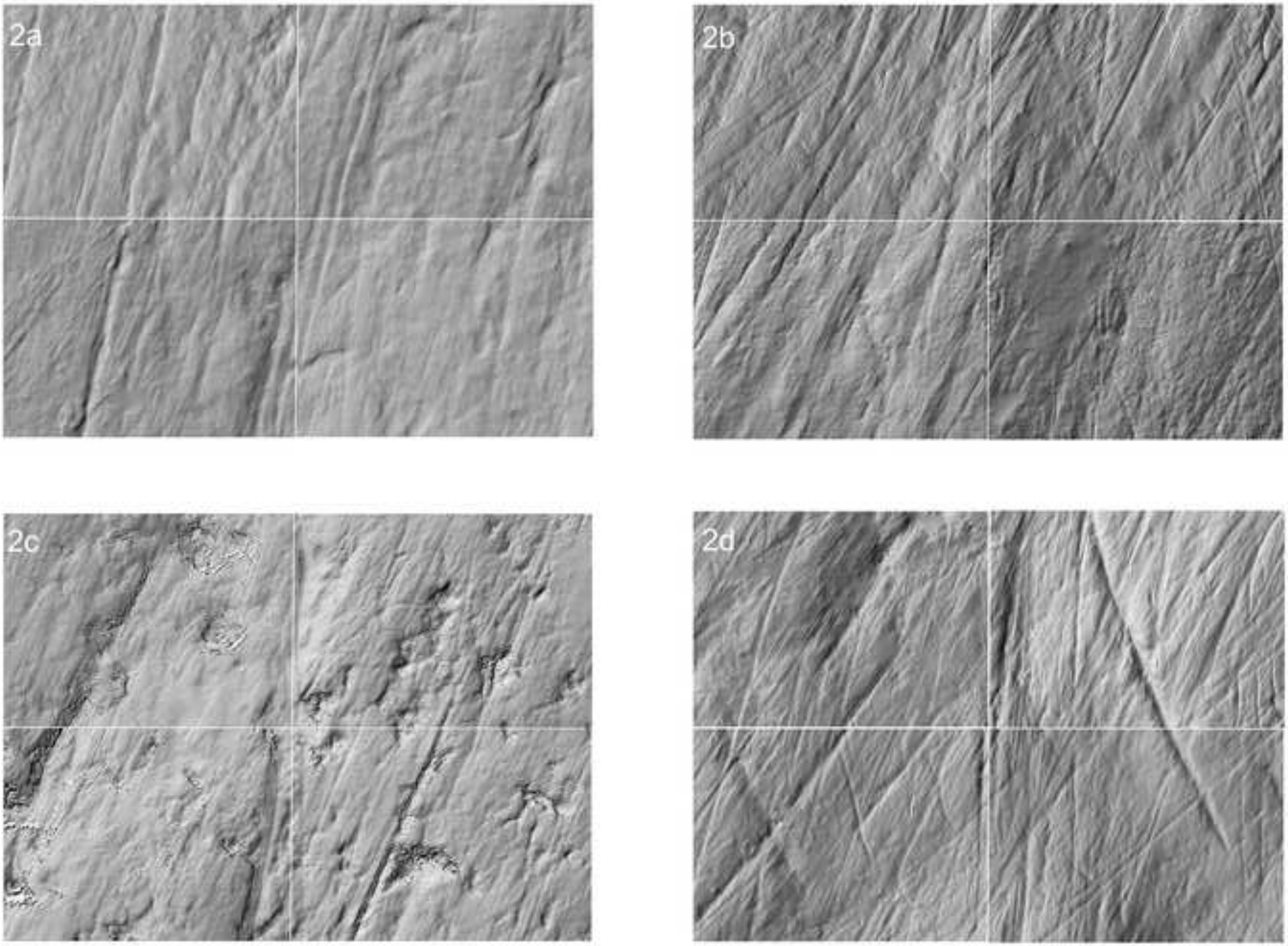
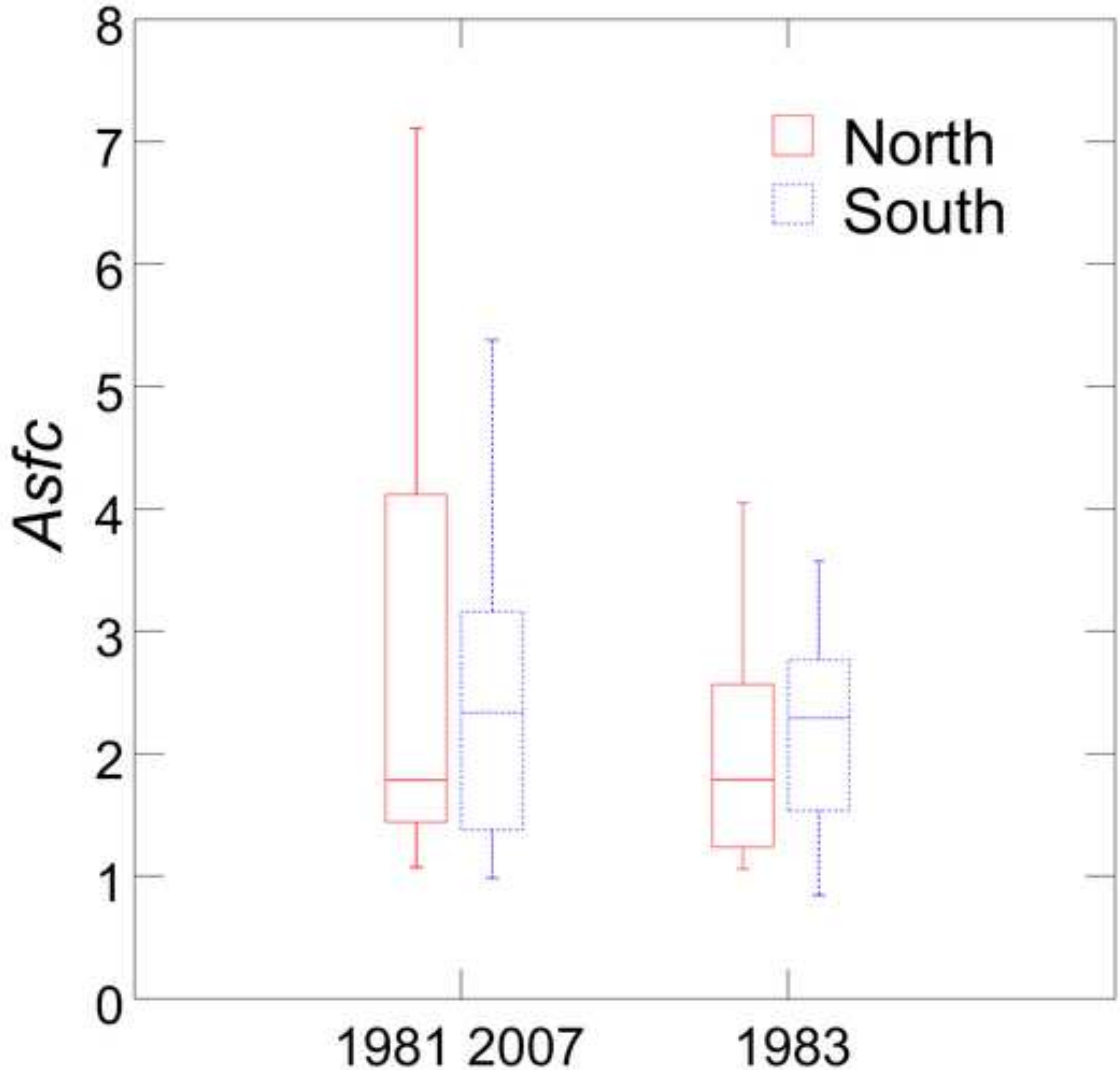


Figure 3



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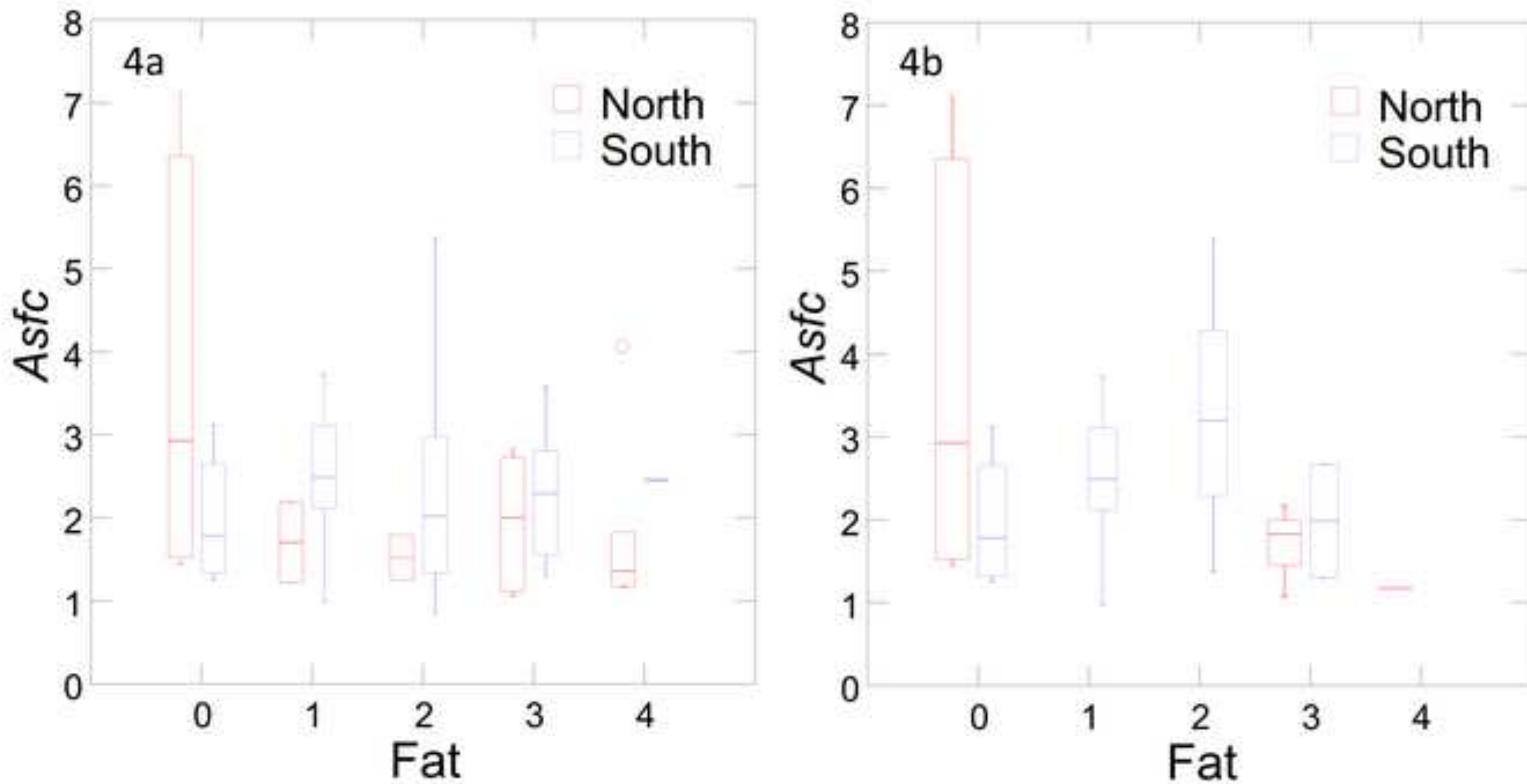

Figure 5

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Figure 6

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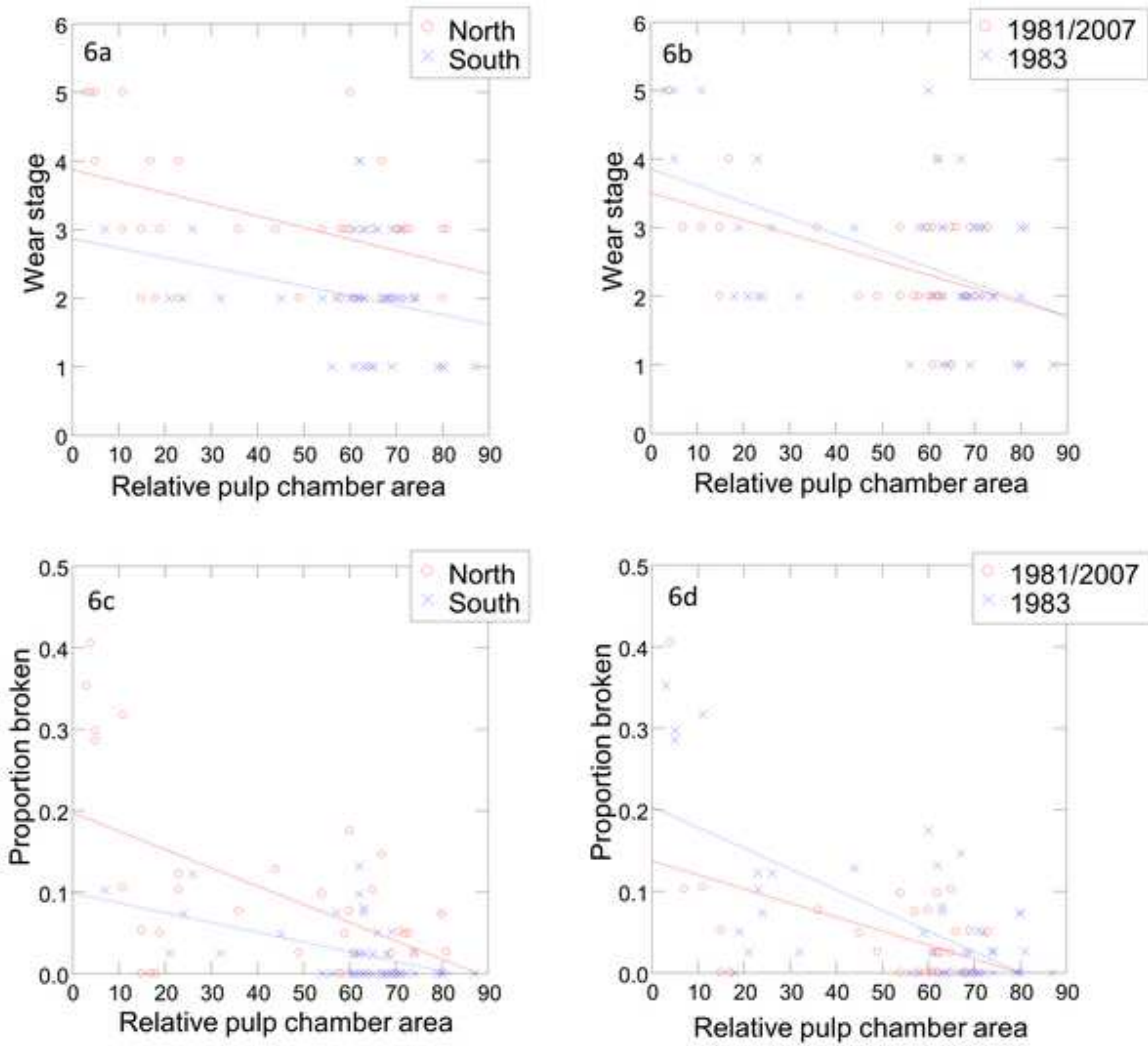

Figure 7

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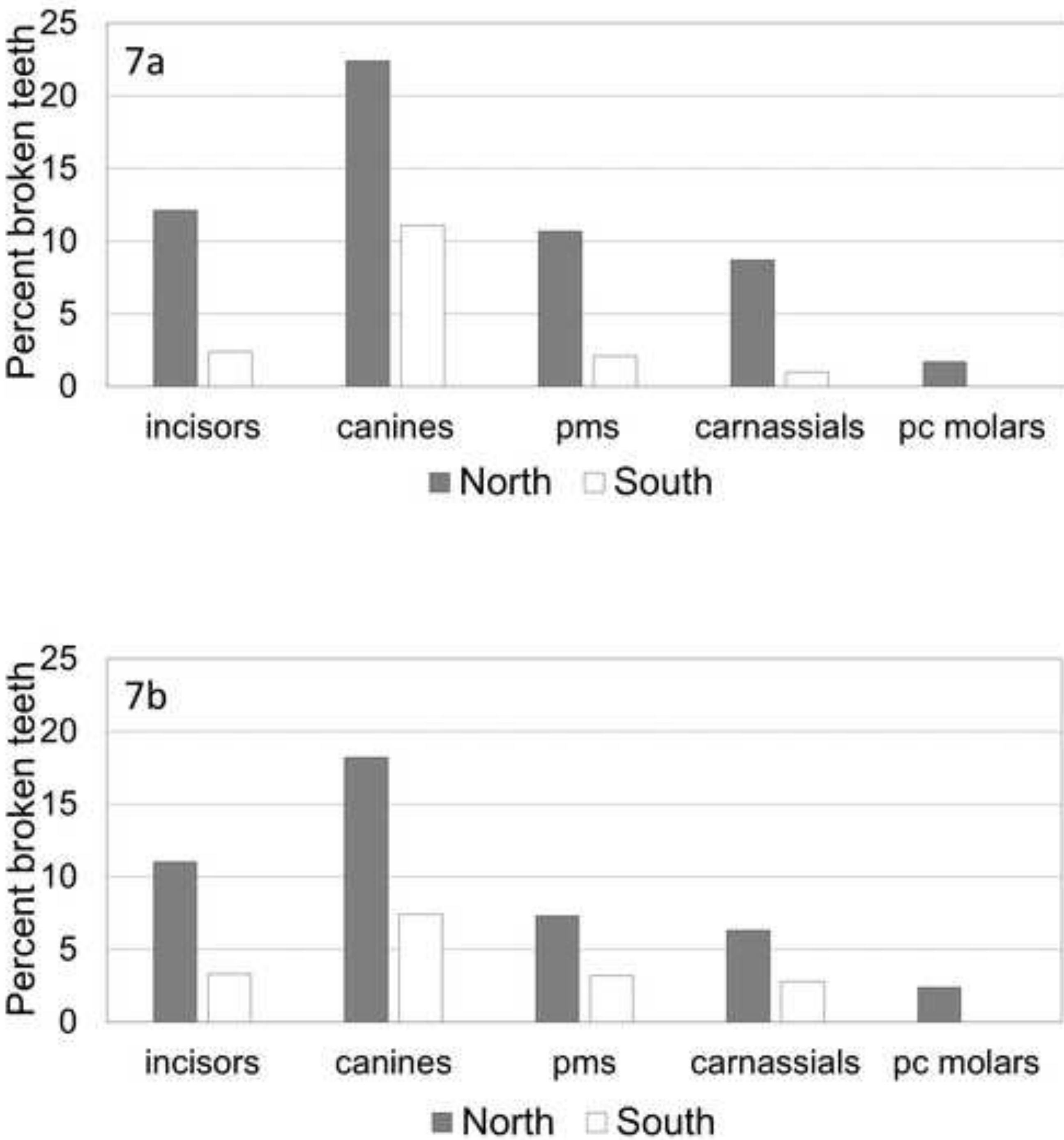

Table 1 Dental microwear summary statistics including means, standard deviations, and sample sizes.

A. Descriptive statistics for year, type and location

Asfc	1981/2007	1983
All	2.62 ± 1.613 (*n* = 26)	2.03 ± 0.832 (*n* = 28)
North	2.85 ± 2.223 (*n* = 10)	1.94 ± 0.873 (*n* = 15)
South	2.47 ± 1.145 (*n* = 16)	2.13 ± 0.806 (*n* = 13)
epLsar		
All	0.00644 ± 0.018166 (*n* = 26)	0.00676 ± 0.014491 (*n* = 28)
North	0.00608 ± 0.022136 (*n* = 10)	0.00663 ± 0.015166 (*n* = 15)
South	0.00666 ± 0.015492 (*n* = 16)	0.00691 ± 0.014142 (*n* = 13)

B. Descriptive statistics for fat versus no-fat individuals (*Asfc*)

		No fat	Fat present
All years	**North**	3.72 ± 2.55 (*n* = 6)	1.86 ± 0.815 (*n* = 19)
	South	1.99 ± 0.861 (*n* = 4)	2.37 ± 1.032 (*n* = 25)
1981/2017	**All**	3.02 ± 2.158 (*n* = 10)	2.36 ± 1.168 (*n* = 16)
	North	3.72 ± 2.550 (*n* = 6)	1.56 ± 0.527 (*n* = 4)
	South	1.99 ± 0.861 (*n* = 4)	2.63 ± 1.214 (*n* = 12)

Table 2 Dental microwear analytical statistics

A. Tests of central tendency

	Wilk's Λ	*F*	*df*	*p*
Year type	0.982	0.446	2, 49	0.643
Location	0.95	1.300	2, 49	0.282
Interaction	0.998	0.047	2, 49	0.954

B. Tests of dispersion

	Bartlett's Test			Levene (mean)		
	X^2	*df*	*p*	*F*	*df*	*p*
Asfc						
All	**10.587**	**1**	**0.001**	**4.743**	**1, 52**	**0.034**
North	**9.107**	**1**	**0.003**	**10.948**	**1, 23**	**0.003**
South	1.519	1	0.218	0.774	1, 27	0.387
epLsar						
All	1.232	1	0.267	0.61	1, 52	0.438
North	1.501	1	0.220	1.911	1, 23	0.180
South	0.106	1	0.744	0.074	1, 27	0.787

C. Fat versus non-fat tests of dispersion for *Asfc*

		Bartlett's Test			Levene (mean)		
		X^2	*df*	*p*	*F*	*df*	*p*
	Asfc						
All years	**North**	**12.29**	**1**	**<0.001**	**26.379**	**1, 23**	**< 0.001**
	South	0.144	1	0.704	0.163	1, 27	0.690
1981/2007	**All locations**	**4.228**	**1**	**0.040**	**5.08**	**1, 24**	**0.034**
	North	**5.19**	**1**	**0.023**	**11.245**	**1, 8**	**0.010**
	South	0.434	1	0.510	0.335	1, 14	0.572

Table 3 Gross wear and tooth breakage summary statistics

A. Summary statistics for wear score and percent present teeth broken

Wear score	1981/2007	1983
All	2.5 ± 0.9 (*n* = 30)	2.5 ± 1.1 (*n* = 48)
North	3.0 ± 0.9 (*n* = 12)	3.2 ± 1.1 (*n* = 23)
South	2.2 ± 0.8 (*n* = 18)	1.9 ± 0.8 (*n* = 25)
Percent broken		
All	5.1 ± 7.7 (*n* = 30)	6.2 ± 9.0 (*n* = 48)
North	8.3 ± 10.9 (*n* = 12)	10.3 ± 11.0 (*n* = 23)
South	2.9 ± 3.5 (*n* = 18)	2.3 ± 4.0 (*n* = 25)

All locations

	Wear score	Percent broken
1981/2007	2.5 ± 0.9 (*n* = 30)	5.1 ± 7.7 (*n* = 30)
1983	2.5 ± 1.1 (*n* = 48)	6.2 ± 9.0 (*n* = 48)

B. Incidence of at least one broken canine (1+) in samples by location.

	South		North		All	
	0	1+	0	1+	0	1+
Female	15	4	9	10	24	14
Male	18	6	10	6	28	12

C. Summary statistics for percent broken by tooth position.

		Incisors	Canines	Premolars	Carnassials	Post-carnassials
1981/2007	North	11.0	18.0	7.3	6.2	2.4
	South	3.3	7.4	3.2	2.8	0.0
1983	North	12.1	22.4	10.7	8.7	1.7
	South	2.3	11.4	2.1	1.0	0.0

Table 4 Gross wear and tooth breakage analytical statistics: ANCOVA and Chi-squared results

A. ANCOVA Results controlling for age

Wear score		North vs. South		1981/2007 vs. 1983	
	df	*F*	*p*	*F*	*p*
ANCOVA	1,75	20.60	**0.000**	1.49	0.226
Homogeneity	1,74	0.14	0.709	0.26	0.612

Percent broken		North vs. South		1981/2007 vs. 1983	
	df	*F*	*p*	*F*	*p*
ANCOVA	1,75	11.72	**0.001**	1.31	0.256
Homogeneity	1,74	1.99	0.164	0.70	0.406

B. Proportion of specimens with at least one broken canine.

	X^2	*df*	*p*
All locations	0.411	1	0.522
North	0.801	1	0.371
South	0.093	1	0.761

C. Percent tooth fracture by tooth position in north versus south.

	1981/2007			**1983**		
	X^2	*df*	*p*	X^2	*df*	*p*
incisors	8.354	1	**0.004**	20.482	1	< **0.001**
canines	2.337	1	0.126	2.943	1	0.086
premolars	3.651	1	0.056	19.948	1	< **0.001**
carnassials	0.87	1	0.351	6.352	1	**0.012**
post-carnassials	3.363	1	0.670	3.276	1	0.070

Table 5 Gross wear and tooth breakage analytical statistics: coefficients from the selected cumulative link model and the selected generalized linear model

A) Coefficients from the selected cumulative link model to explain gross tooth wear are presented with standard errors and *p* values

	Coefficient (logit scale)	Standard error	*p*
Age	-0.037	0.011	< **0.001**
North compared to south	1.909	0.487	< **0.001**
Threshold 1	-3.246	-4.292	
Spacing	2.173	0.251	

B) Coefficients from the selected generalized linear model (binomial error) to explain the proportion of broken teeth.

	Coefficient (logit scale)	Standard error	*p*
Intercept	-2.083	0.348	
Age	-0.027	0.005	< **0.001**
North compared to south	0.856	0.291	**0.004**