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Note

Changes in dental wear and breakage in arctic foxes (*Vulpes lagopus*) across space and time: evidence for anthropogenic food subsidies?

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Abstract

Increased human presence in the Arctic may affect its vulnerable ecosystems. Effects on arctic and red foxes provide notable examples. Both have been documented to take anthropogenic subsidies when available, which can change diet and ranging patterns in complex ways that can either benefit or harm populations, depending on the situation. Understanding this complexity requires new tools to study impacts of increasing human presence on endemic mammals at high latitudes. We propose that dental ecology, specifically tooth wear and breakage, can offer important clues. Based on samples of arctic foxes (*Vulpes lagopus* (Linnaeus, 1758)) trapped prior to ($n = 78$) and following ($n = 57$) rapidly growing human presence on the Yamal Peninsula, Russia, we found that foxes trapped recently in proximity to human settlement had significantly less tooth wear and breakage. This is likely explained by a dietary shift from consumption of reindeer (*Rangifer tarandus* (Linnaeus, 1758)) carcasses including bone to softer human-derived foods, especially when preferred smaller prey (e.g., West Siberian lemmings, *Lemmus sibiricus* (Kerr, 1792), and arctic lemmings, *Dicrostonyx torquatus* (Pallas, 1778)) are unavailable. These results suggest that tooth wear and breakage can be a useful indicator of the consumption of anthropogenic foods by arctic foxes.

Key words: *Vulpes lagopus*, arctic fox, diet, dental ecology

Résumé

La présence humaine accrue dans l'Arctique pourrait avoir une incidence sur les écosystèmes vulnérables de cette région. Les effets sur les renards arctiques et roux en constituent des exemples notables. Il est documenté que ces deux espèces intègrent des subsides d'origine humaine quand ils sont disponibles, ce qui peut modifier leurs habitudes d'alimentation et de déplacement de manière complexe, au bénéfice ou au détriment des populations, selon la situation. La compréhension de cette complexité nécessite de nouveaux outils pour étudier les impacts de l'augmentation de la présence humaine sur les mammifères endémiques aux hautes latitudes. Nous proposons que l'écologie dentaire, plus précisément l'usure et la cassure des dents, peut fournir d'importants indices. À la lumière d'échantillons de renards arctiques (*Vulpes lagopus* (Linnaeus, 1758)) piégés avant ($n = 78$) et après ($n = 57$) l'établissement d'une présence humaine à croissance rapide dans la péninsule de Yamal (Russie), nous constatons que les dents de renards piégés récemment à proximité d'établissements humains présentent significativement moins d'usure et de cassure. Cela s'explique probablement par un changement d'alimentation, de la consommation de carcasses de rennes (*Rangifer tarandus* (Linnaeus, 1758)), dont des os, à des aliments d'origine humaine plus mous, particulièrement quand de plus petites proies de prédilection (p. ex. lemming brun, *Lemmus sibiricus* (Kerr, 1792), et lemming variable, *Dicrostonyx torquatus* (Pallas, 1778)) ne sont pas disponibles. Ces résultats indiqueraient que l'usure des dents peut être un indicateur utile de la consommation d'aliments d'origine humaine chez les renards arctiques. [Traduit par la Rédaction]

Mots-clés : *Vulpes lagopus*, renard arctique, régime alimentaire, écologie dentaire

Introduction

Intensification of human activity in the Arctic has in recent years presented an increasing threat to fragile high-latitude ecosystems. Because of extreme environments, food abundance in the Arctic can vary greatly and be unpredictable, so anthropogenic food subsidies may have an especially marked effect on individual animals and their interactions with others. One example that has received considerable attention involves the spread of red foxes (*Vulpes vulpes* (Linnaeus, 1758)) at the expense of their smaller congeners, arctic foxes (*Vulpes lagopus* (Linnaeus, 1758)). Conventional wisdom suggests that the northern limit of red foxes is determined by resource availability, whereas the southern limit of arctic foxes is dictated by competition with red foxes (Hersteinsson and Macdonald 1992). More people in the Arctic often means more human food refuse and hence anthropogenic subsidies that allow red foxes to expand into ever more northerly ranges than their "climate-imposed" distribution limit would otherwise allow (Elmhagen et al. 2017). This can benefit red fox populations, but it sidelines the endemic arctic foxes they compete with. The spread of red foxes can also impact prey species populations (e.g., Abbott 2011), and all these effects can be intensified by effects of climate change.

Consequences of increasing human activity in the Arctic are especially evident where there is development of large-scale infrastructure, such as for hydrocarbon extraction. Lehner (2012), for example, demonstrated that arctic foxes in the Prudhoe Bay oil fields of Alaska are more reliant on anthropogenic foods than are those in adjacent undeveloped areas. Human food refuse can comprise a significant proportion of arctic fox diets at Prudhoe Bay; and foxes that use human food refuse travel shorter distances, particularly in the winter, and avoid some resources consumed by foxes outside the developed area. There is little doubt that arctic foxes are attracted to anthropogenic subsidies. The species is well known to forage on human food waste — and will solicit food directly from people (Eberhardt 1977, 1982; Garrott et al. 1983). Given this, it is unsurprising that the Lappish name for "arctic fox" translates to "fearless" or "foolhardy" (Selås et al. 2010).

But anthropogenic subsidies are a mixed blessing for arctic foxes. A study in Fennoscandia (Angerbjörn et al. 2013) showed that supplemental feeding can increase the number of litters, resulting in substantial growth of breeding populations (up to 200%) in just 3–4 years. Built environments can also be a net positive for arctic fox populations because the predators that take cubs, wolverines (*Gulo gulo* (Linnaeus, 1758)) and eagles (e.g., Golden Eagle, *Aquila chrysaetos* (Linnaeus, 1758)) avoid human activity (May et al. 2006; Kaisanlahti-Jokimaki et al. 2008). On the negative side, however, the Prudhoe Bay oil fields also attract red foxes. Indeed, infrastructure development there in the 1970s may have fueled range expansion of red foxes onto the coastal plain of northern Alaska (Savory et al. 2014). At Prudhoe Bay, red foxes can consume even more human food waste than do arctic foxes (Savory et al. 2014). In some settings red fox diets include more than 50% anthropogenic foods (Iossa et al. 2010). And where the two fox species coexist, the larger, stronger red foxes usually displace their arctic fox congeners (Elmhagen et al. 2002, 2017; Killengreen et al. 2007; Selås et al. 2010).

To understand the effects of anthropogenic subsidies on foxes and indeed other taxa, we need a reliable way to monitor diets of these species that can detect consumption of human food refuse. Some have considered scats (e.g., Hersteinsson 1984; Eide et al. 2005) or stomach contents of individuals collected by hunters/trappers or from roadkill (e.g., Selås et al. 2010; Killengreen et al. 2011). Resulting data in such cases are limited to evidence from the last meal. Others have looked to stable isotopes of elements in bodily tissues; but these can only detect dietary differences reflected in chemical signatures specific to human food refuse, such as high δ^{13}C values associated with C_4 plants including maize and cane sugar (e.g., Newsome et al. 2010, 2015; Killengreen et al. 2011; Savory 2013, 2014; Scholz et al. 2020). And isotopes ratios reflect only the time interval during which the tissue sampled was formed. While scat samples, stomach contents, and isotope ratios are all valuable for inferring diet, additional approaches would be useful, particularly those that could offer more details and information on food preferences over longer time scales.

Here, we propose an additional tool for assessing impacts of anthropogenic foods — tooth wear and breakage. Studies of impacts of human activity on tooth wear and breakage in wild animals are an important part of dental ecology research today (Cuozzo and Sauther 2012). For example, Cuozzo et al. (2014) showed that anthropogenic disturbance of habitats in Madagascar has led lemurs to consume mechanically challenging introduced plants, resulting in excessive tooth wear that can reduce crowns to nubs. Furthermore, Van Valkenburgh et al. (2019) demonstrated that a declining prey-to-predator ratio related to the reintroduction of wolves (*Canis lupus* Linnaeus, 1758) at Yellowstone National Park in the USA has led to greater tooth wear and breakage in those canids, presumably because of the need to consume available carcasses more completely, including hard bone, as prey numbers have declined (Van Valkenburgh et al. 2019). And while tooth wear and breakage have yet to be considered as tools for assessing impacts of human activity in arctic foxes, a recent study did show variation among arctic foxes with access to different fallback foods (Ungar et al. 2021). Foxes in the northern part of the Yamal Peninsula, Russia, where they are reported to consume bones of reindeer (*Rangifer tarandus* (Linnaeus, 1758)) when preferred prey (e.g., West Siberian lemmings, *Lemmus sibiricus* (Kerr, 1792), and arctic lemmings, *Dicrostonyx torquatus* (Pallas, 1778)) are at low density or unavailable, had more tooth wear and breakage than southern Yamal foxes that have access to a richer diversity of small alternative prey taxa, including more species of rodents, two species of ptarmigan (Willow Ptarmigan, *Lagopus lagopus* (Linnaeus, 1758), and Rock Ptarmigan, *Lagopus muta* (Montin, 1781)), and the tundra hare (*Lepus timidus* Linnaeus, 1758).

We expect that the consumption of soft human food refuse in place of hard natural foods would likewise affect tooth wear and breakage in arctic foxes. A study of coyotes (*Canis latrans* Say, 1823) by Curtis et al. (2018) showed that wild individuals known to consume carcasses including bone have higher rates of both tooth wear and breakage than do captive individuals fed commercially produced wet food. We therefore hypothesize that arctic foxes that fall back on anthropogenic subsidies in lieu of reindeer carcasses (including bone) when sufficient preferred smaller game are unavailable would have less tooth wear and breakage because human foods tend to be calorically dense and mechanically soft and pliant. In contrast, those that consume more reindeer carcasses (including bone) should have more tooth wear and breakage. If these predictions hold, then dental ecology may have a role to play in monitoring long-term changes in arctic fox diet resulting from anthropogenic subsidies.

Materials and methods

This study considers arctic foxes of the Yamal Peninsula in western Siberia to assess the impact on dental ecology of increased human presence resulting from infrastructure development. The largest liquefied natural gas (LNG) plant above the Arctic Circle broke ground at Sabetta (71.2°N, 71.5°E) in northeastern Yamal in 2012 and was opened in 2017. Despite efforts by Yamal LNG to store and dispose of garbage, arctic foxes wander around the facilities to scavenge and are often fed by shift workers. We here compare tooth breakage and gross wear patterns for fox specimens collected in the vicinity during the 2019–2020 and 2020–2021 winter trapping seasons with those from samples gathered in Yamal (both in north Yamal and in the south) prior to establishment of large human settlements.

A total of $n = 135$ arctic fox specimens were included in this study. The sample comprises 57 newly collected individuals from Sabetta, and 78 specimens previously described in Ungar et al. (2021). All sampled individuals were caught in the wild in foothold traps or shot by trappers from the indigenous community of Yamal for fur harvesting (see Shtro 2009). No animal care protocol was required because we did not work with live animals. Carcasses that otherwise would have been discarded were purchased from trappers after fur removal. Foxes were identified based on their fur by trappers and based on size by researchers, and all skull specimens are archived and available for verification of species identification at the Arctic Research Station in Labytnangi, Russia.

The specimens from Sabetta were collected in December 2019 and February 2021 from the floodplain of the Sabetta River. These individuals were collected just outside of, but in close proximity to, the industrial workers' settlement and gas fields. This is referred to here as the 2019/2020 Sabetta sample. The earlier north Yamal sample ($n = 35$) is represented by individuals collected in the winter of 1981–1982 (Ust'-Yuribei, 68.9°N, 69.4°E; Seyakha, 70.1°N, 72.5°E) and the winter of 1983–1984 (Mordy-Yakha, 70.4°N, 67.3°E; Yaptik-Sale, 69.4°N, 72.5°E). This is referred to here as the 1981/1983 north sample. The south Yamal sample ($n = 43$) includes individuals collected in the winter of 1983–1984 (Labytnangi, 66.7°N, 66.4°E) and the winter of 2007–2008 (Erkuta, 68.2°N, 69.1°E). This is referred to here as the 1983/2007 south sample. For site locations see Fig. 1.

The earlier samples (collected between 1981 and 2007) precede the recent and marked increase in human presence on the Yamal Peninsula with the launch of numerous hydrocarbon industry projects over the past decade. These projects have led to road and railway construction and worker spread throughout the peninsula, resulting in dozens of industrial settlements, trading posts, and railroad stations (see Terekhina et al. 2021). In this sense, the 1981/1983 north sample provides a good contrast with the 2019/2020 Sabetta sample for a "before and after" comparison of foxes living around the boundary between low and high Arctic on Yamal. The southern sample represents foxes trapped in the low Arctic tundra and forest–tundra ecotone and provides a contrast in prey availability to those from the north. For example, the south has 10 rodent species, and ptarmigans and mountain hare are available in abundance year-round. The north, in contrast, has only five rodent species and much lower densities of ptarmigans and hare that decline significantly in the winter because snow cover limits availability of plant foods (Shtro 1995, 2006). In addition, semi-domesticated reindeer are available year-round throughout the peninsula as an alternative prey source.

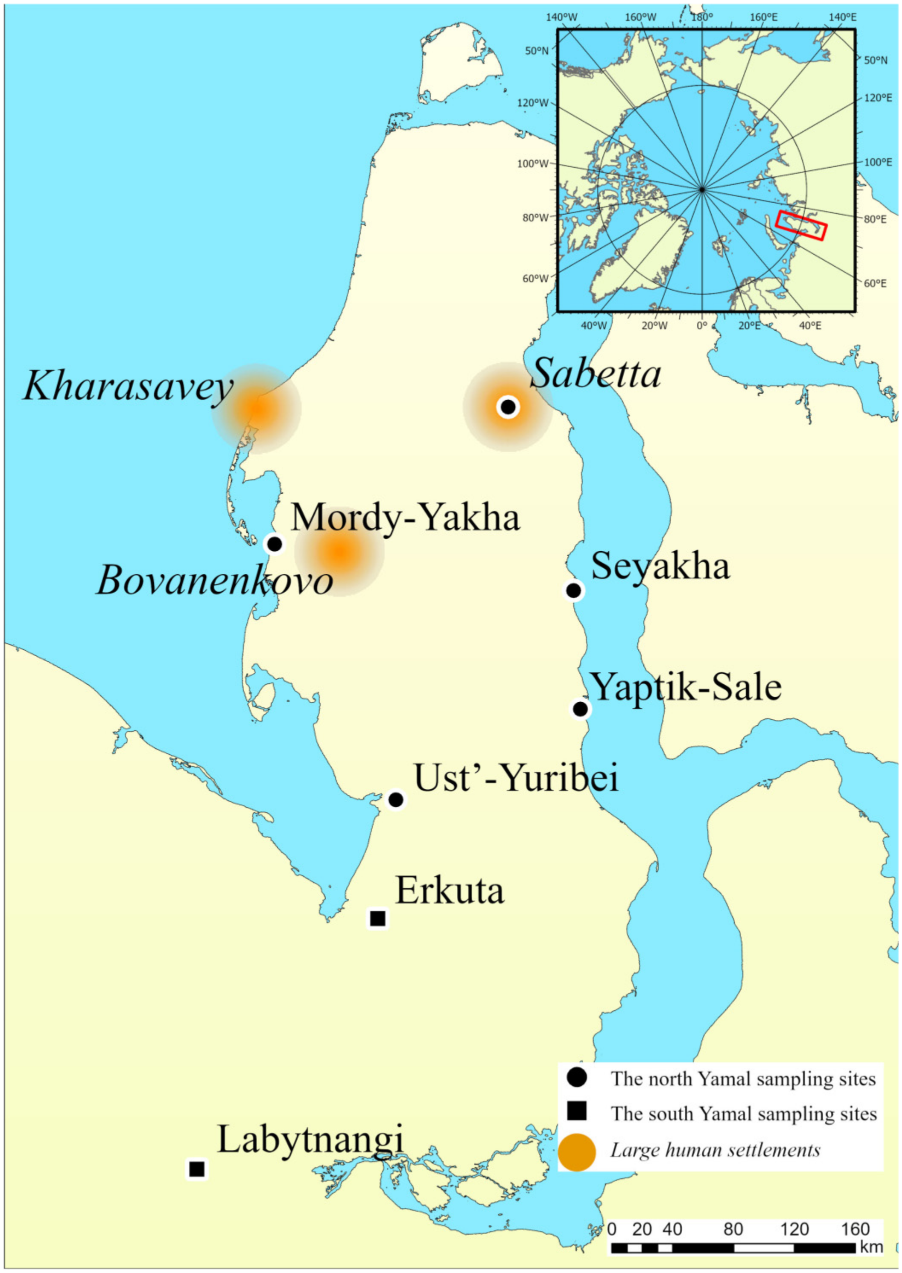
Heads of all specimens were detached and boiled to remove soft tissues, and metadata including sex of the individual and relative pulp cavity width of the lower right canine (RC_1) were collected during the process. Measurement of relative pulp cavity width followed Smirnov (1960). The RC_1 was extracted and sectioned, and the width of the pulp cavity was measured as a percentage of the root at its widest point. Relative pulp cavity width decreases with age. While the relationship between cavity diameter and age is not linear, cavity width can provide a proxy for relative age because odontoblasts continue to secrete dentin into the pulp cavity throughout life (Star et al. 2011; Couve et al. 2013).

Tooth gross wear and breakage data were collected and analyzed using the methods described in Ungar et al. (2021). Photographs of teeth were taken by PSU with a Nikon D7200 DLSR camera and an AF Micro Nikkor 60 mm macro lens (Nikon Corp., Tokyo, Japan) with an aperture value of f/32 and a field of view filled to maximize depth of focus and resolution of individual teeth. Eight views of each specimen were recorded: left and right upper and lower buccal, upper and lower occlusal, and upper and lower anterior.

Dental wear stage as well as number and identity of antemortem broken teeth were assessed and recorded by BVV. Wear staging was recorded for each individual as (*i*) slight, with little or no wear on shear facets and no blunting of cusps; (*ii*) slight-moderate, with slight wear on shear facets and minimal blunting of cusps; (*iii*) moderate, with shear facets apparent on carnassial teeth and cusps blunted on most teeth; (*iv*) moderate-heavy, with carnassial teeth moderately blunted and premolars and molars with well-rounded cusps; or (*v*) heavy, with carnassial teeth with strongly blunted cusps and premolars and molars with well-rounded cusps (see Supplementary Fig. S1).

Percent broken teeth was calculated using the quotient of the number of teeth with antemortem breakage and the number of teeth present for each specimen. Teeth were considered as broken antemortem only if there was clear evidence of fracture (e.g., broken cusps) and a fully blunted surface due to subsequent wear (following Binder and Van Valkenburgh 2010). If there was a sharp edge on the surface, then the tooth was not counted as broken given the chance that breakage was postmortem or just prior to death due to biting on traps. Likewise, missing teeth were not counted as broken given the possibility that that tooth loss was due to disease rather than trauma. Hence, the antemortem broken tooth estimate is probably an undercount — albeit underestimates are consistent across the study given fixed criteria for

Fig. 1. Map of the Yamal Peninsula with sampling locations for specimens used in this study. Sites where the southern and northern Yamal specimens were sampled are denoted by squares and circles, respectively. Large-scale human settlements are denoted in italic type and marked with the diffuse circles. Map data: Natural Earth (available from https://www.naturalearthdata.com/). Map projection: WGS 1984 UTM Zone 42 N. [Color online.]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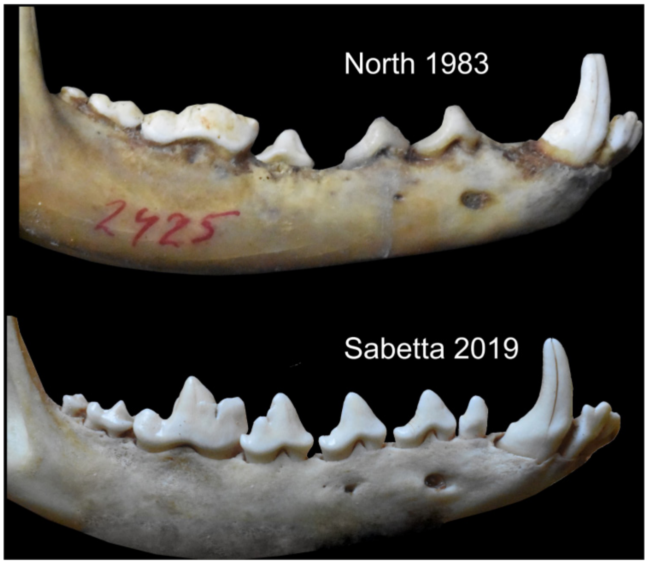
Sabetta
Mordy-Yakha
Bovanenkovo
Seyakha
Yaptik-Sale
Ust'-Yuribei
Erkuta
Labytnangi
● The north Yamal sampling sites
■ The south Yamal sampling sites
● *Large human settlements*
0 20 40 80 120 160
km

identification. Raw data can be found in Supplementary Table S1.

Two approaches were used for statistical analyses. First, we used a general linear model to compare wear stage and broken tooth percentages between the samples from Sabetta and those from earlier collections in the north and south of Yamal. Data were rank-transformed to mitigate violation of assumptions inherent to parametric statistical analyses (Conover and Iman 1981), and a MANOVA was used to determine whether samples differed in dental damage pattern. Individual ANOVAs were used to determine which factors (wear stage, broken tooth percentages) showed significant variation, and Tukey's honestly significant difference (HSD) pairwise comparisons tests were used to determine the sources of significant variation. This approach assumes no age-related bias differences between the samples given that wear and breakage can accumulate throughout life. This assumption was checked using an ANOVA on rank-transformed relative pulp cavity diameter data and Tukey's tests as needed to assess sources of significant variation.

A second method of analysis was designed to control for age to the extent possible. We used ANCOVA models to com-

Fig. 2. Comparison of mandibles of arctic foxes (*Vulpes lagopus*) sampled from northern Yamal in 1983 (top, #2425) and in 2019 (bottom, #270), before and after establishment of the Yamal LNG plant, respectively. These individuals have comparable relative pulp cavity diameters, suggesting similar ages at death. [Color online.]



pare regressions of percent broken teeth and gross wear score as dependent variables against relative pulp cavity width as the independent variable. As with the MANOVA model, all data were rank-transformed prior to analysis following Conover and Iman (1981). Separate tests were used to compare the Sabetta data with those of the 1981/1983 north and 1983/2007 south samples. Initial tests for homogeneity of regressions 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 evinced significantly different *y*-intercepts, indicating variation in percentages of broken teeth and (or) gross wear score for a given relative pulp cavity width (as a proxy for relative age).

Results

The results of this study are presented in Figs. 2–5 and Tables 1–3. The MANOVA test indicated significant variation in the model (Wilks' λ: $F = 5.98$; df = 4, 262; $p < 0.001$). Both ANOVAs for percent broken teeth ($F = 7.22$; df = 2, 132; $p = 0.001$) and wear score ($F = 11.96$; df = 2, 132; $p < 0.001$) showed significant variation between groups (see Fig. 3 and Table 2). Tukey's test results showed the sources of that variation. First, the Sabetta specimens had significantly lower percentages of broken teeth than either the 1981/1983 north ($p < 0.001$) or the 1983/2007 south ($p = 0.021$) sample. The south sample also had a lower percentage of broken teeth ($p < 0.001$) than the north sample as reported originally in Ungar et al. (2021). In addition, the Sabetta sample had significantly lower average wear scores than north ($p < 0.001$) but not south ($p = 0.593$) specimens. The south sample also had a lower wear score average ($p < 0.001$) than the north sample as reported originally in Ungar et al. (2021).

ANOVA results did show a difference in relative pulp cavity diameter and by implication age among the samples ($F = 3.39$; df = 2, 132; $p = 0.037$) (see Fig. 4 and Table 2). The Tukey's HSD test results indicated that the 1981/1983 north sample had significantly lower relative diameter values than the 1983/2007 south samples ($p = 0.026$), indicating a bias toward older aged individuals in the north relative to the south. There was no significant difference between the Sabetta sample and either the north ($p = 0.357$) or south ($p = 0.306$) in relative pulp cavity diameter, suggesting that differences in gross wear and tooth breakage between Sabetta and the other samples are not likely due to age-related biases.

The differences between groups were confirmed by the ANCOVA study (see Fig. 5 and Table 3). First, there were no differences in slope (homogeneity) between any pair of samples for the regression of either percent broken teeth on relative pulp cavity diameter (Sabetta vs. 1981/1983 north: $F = 1.03$; df = 1, 83; $p = 0.313$; Sabetta vs. 1983/2007 south: $F = 1.93$; df = 1, 96; $p = 0.168$; north vs. south: $F = 1.98$; df = 1, 74; $p = 0.164$) or for the regression of gross wear score on relative pulp cavity diameter (Sabetta vs. 1981/1983 north: $F = 0.65$; df = 1, 83; $p = 0.422$; Sabetta vs. 1983/2007 south: $F = 0.31$; df = 1, 96; $p = 0.579$; north vs. south: $F = 0.14$; df = 1, 74; $p = 0.709$). This indicates that slopes are comparable between samples for both broken teeth and gross wear regressions.

There were, however, significant differences between the samples in *y* intercepts. ANCOVA results indicate that all pairs of samples (Sabetta vs. 1981/1983 north: $F = 64.31$; df = 1, 84; $p < 0.001$; Sabetta vs. 1983/2007 south: $F = 13.85$; df = 1, 97; $p < 0.001$; 1981/1983 north vs. 1983/2007 south: $F = 11.72$; df = 1, 75; $p = 0.001$) differed in percent broken teeth. For a given relative pulp cavity diameter (again, a proxy for age), the Sabetta sample had the fewest broken teeth, the 1981/1983 north sample had the most, and the 1983/2007 south sample was intermediate. In addition, ANCOVA results for the gross tooth wear score data indicated that the Sabetta sample has significantly lower gross tooth wear scores than the 1981/1983 north sample ($F = 52.76$; df = 1, 84; $p < 0.001$) and that the 1983/2007 south sample has less gross wear than the 1981/2007 north sample ($F = 22.47$; df = 1, 75; $p < 0.001$). The Sabetta sample did not, however, differ from the 1983/2007 south sample in gross tooth wear score ($F = 1.50$; df = 1, 97; $p = 0.224$).

Discussion

A recent study by Ungar et al. (2021) suggested that differences in the dental ecology of southern and northern Yamal arctic foxes can be explained by variation in prey abundance across latitudes. In years when rodent densities are low, arctic foxes in the south consume ptarmigans and tundra hare because abundances are relatively high (Shtro 1995, 2006, 2009). In the north, these herbivores have been rare in the winter given limited availability of their food — the vegetation does not extend above the snowpack (Pavlinin 1971; Riabitsev 2001; Shtro 2006, 2009). On the other hand, reindeer calves have been available to hunt and carcasses available to scav-

Fig. 3. Comparisons of percent broken teeth (top) and wear stage (bottom) for northern Yamal 1981/1983 samples (left), southern Yamal 1983/2007 samples (middle), and Sabetta 2019/2020 samples (right).

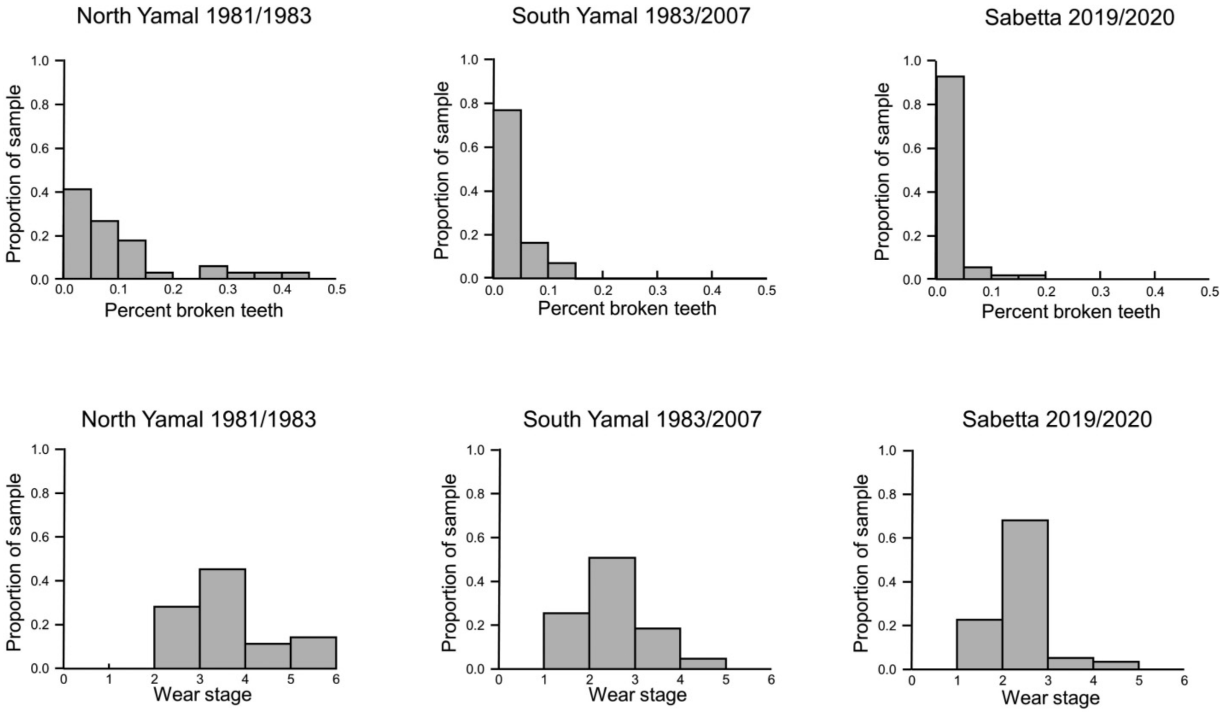
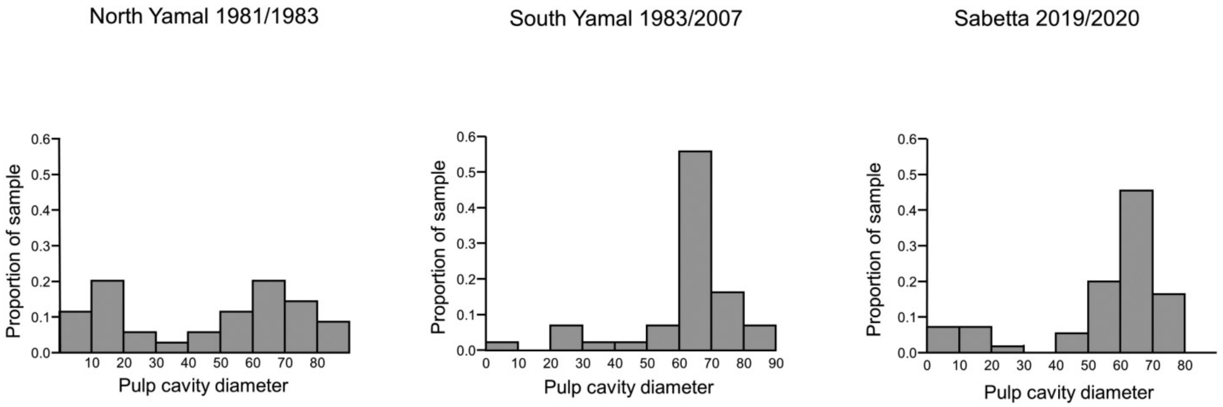


Fig. 4. Comparison of relative pulp cavity diameter distributions of Yamal 1981–2007 samples with 2019/2020 Sabetta sample.

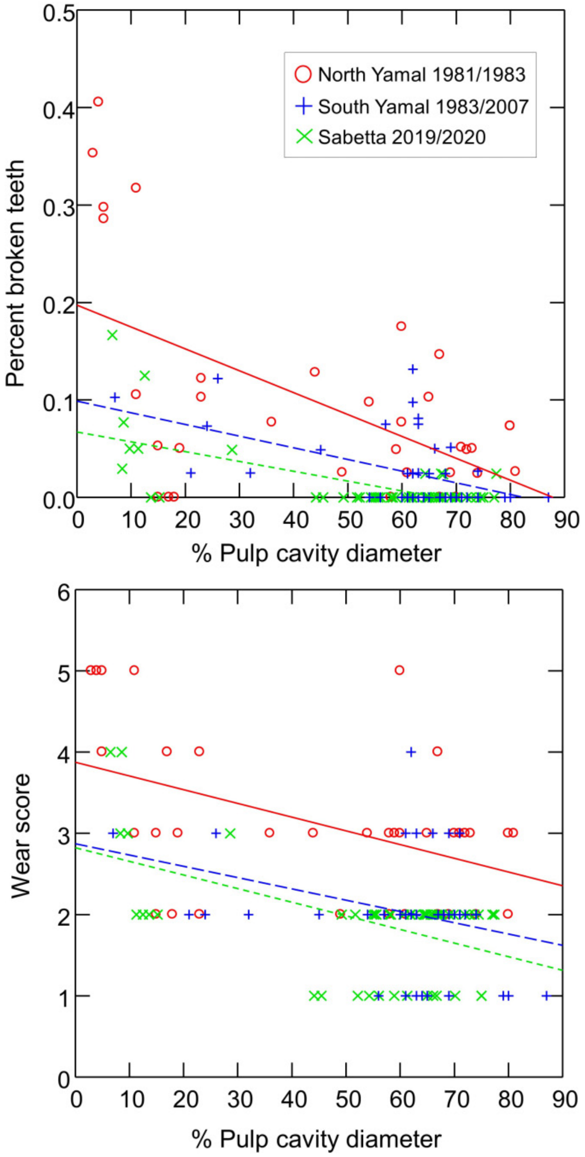


enge as alternative prey year-round across the peninsula. The more common consumption of reindeer, and their bones, as alternative prey in the north than the south was proposed as an explanation for the observation that northern Yamal arctic foxes had higher incidences of tooth breakage and more extreme gross wear than those in the south.

This proposed association between large vertebrate bone consumption and heavy tooth wear and breakage was based on previous observations that carnivoran species that often crush hard foods, such as bone or shell, have more gross wear and higher tooth breakage rates than those that consume mostly softer tissues (Van Valkenburgh 1988, 2009). Similar results have been found for comparisons of populations within species, such that individuals with more food stress and hence more complete carcass utilization — including bone — also have more gross tooth wear and higher breakage rates (Mann et al. 2017; Van Valkenburgh et al. 2019). And this is consistent with observations that wild coyotes known to consume bone have more worn and broken teeth than captive conspecifics fed soft commercial foods (Curtis et al. 2018).

Results presented here indicate that foxes collected during the 2019 and 2020 trapping seasons at Sabetta have less tooth wear and breakage, on average, than the 1981 and 1983 north Yamal individuals and less breakage, on average, than the 1983 and 2007 south Yamal individuals. The first possible explanation to consider is sampling bias by age. We would expect greater wear and more breakage of teeth in older samples, all else equal, given that tooth wear is cumulative over time and the probability of having at least one broken tooth is greater in older individuals. And indeed, our results in-

Fig. 5. Graphs of percent broken teeth (top) and wear score (bottom) of individuals compared with relative pulp cavity diameter. Red O symbols and solid lines represent north Yamal 1981/1983 samples, blue + symbols and large-dashed lines represent south Yamal 1983/2007 samples, and green × symbols and small-dashed lines represent Sabetta 2019/2020 samples. [Color online.]



dicate that the 1981/1983 north Yamal sample has a significantly smaller relative pulp cavity average than the south Yamal sample, indicating older individuals, on average (Fig. 4). There are also more individuals from Sabetta with relatively wide pulp cavities (likely juveniles) than in the older northern sample — though the difference in central tendencies is not statistically significant. This is unlikely to explain the differences in wear and breakage between the Sabetta and older northern samples though, because the ANCOVA results control for relative pulp cavity diameter and by extension for age to the extent possible. For a given relative pulp cavity diameter, the 2019/2020 Sabatta sample has less tooth wear and breakage than the 1981/1983 north sample (Fig. 5). Furthermore, there are actually more "old" individuals in the Sabetta sample (narrow pulp cavities) than the south Yamal sample, though again, relative pulp cavity diameter does not differ significantly between the two. All else equal, then, the Sabetta sample should have more tooth breakage than the south Yamal sample; but we find the opposite.

There are three alternative possible explanations for the low incidence of tooth breakage and minimal wear of the Sabetta fox teeth: (1) these foxes represent newcomers to Sabetta from areas with abundant preferred prey (lemmings); (2) softer alternative prey (e.g., ptarmigan and hare) have become more abundant in northern Yamal over the past few decades, perhaps due to climate change; or (3) arctic foxes in the area have incorporated more soft anthropogenic subsidies and consumed less reindeer bone as alternative food sources following settlement of a large number of people.

Hypothesis 1: 2019/2020 foxes arrived recently at Sabetta from areas with abundant preferred prey (lemmings)

Yamal is dominated by arctic foxes of the lemming ecotype, and its numbers depend on rodent population peaks and troughs — in particular, those of lemmings (Shtro 2009; Ehrich et al. 2015, 2017). For the lemming arctic fox ecotype, nomadic behavior is determined by intraspecific competition in response to high densities of individuals and low food availability, especially following strong lemming peaks (Roth 2002; Lai et al. 2015). As described by Soviet-era researchers, in the fall arctic foxes can "even move out of areas with the high lemming abundance" (Sdobnikov 1940). We consider the hypothesis that the individuals from Sabetta were immigrants from other areas with higher lemming densities, whereas those in the older northern Yamal sample were not, to be highly improbable. And indeed, our past study (Ungar et al. 2021) found no significant effect of lemming cycling within an area on tooth breakage or gross wear pattern (see Ungar et al. 2021), so sample bias based on local lemming abundance is also unlikely.

Hypothesis 2: more medium-sized alternative prey in the diet today than 40 years ago

Some parts of the Arctic have witnessed the appearance and growing abundance of medium-sized prey, such as hare and ptarmigans, over the past few decades (e.g., Tape et al. 2011, 2016). The northward expansion of these shrub herbivores can be explained by concomitant northward expansion of willow thickets (Mekonnen et al. 2021). Indeed, willow thickets are an important habitat for these species in Yamal (Ehrich et al. 2012). Unfortunately, there are no data available to compare densities of medium-sized prey in northern Yamal over the past 40 years. However, because the Sabetta sample has fewer broken teeth than our southern Yamal samples taken where these prey species are more abundant, it seems likely that Sabetta foxes had even softer diets than did older samples from lower latitudes at Yamal. More research is needed, however, to evaluate the hypothesis that there are

Table 1. Descriptive statistics for relative pulp cavity diameter, wear score, and percent broken teeth by sample analyzed in this study.

		Relative pulp cavity diameter		Wear score		Percent broken	
Sample	*n*	Mean	SD	Mean	SD	Mean	SD
North 1981/1983	35	45.057	26.941	3.114	0.993	0.096	0.109
South 1983/2007	43	61.023	16.348	2.023	0.801	0.026	0.038
Sabetta 2019/2020	57	55.399	20.160	1.895	0.646	0.011	0.031

Table 2. General linear model results comparing North 1981/1983, South 1983/2007, and Sabetta 2919 samples for both percent broken teeth and wear score (for details see the text).

MANOVA results (wear and percent broken)			
	df	*F*	*p*
Wilks' λ	4, 262	5.98	**<0.001**
ANOVA percent broken	2, 132	7.22	**0.001**
ANOVA wear score	2, 132	11.96	**<0.001**

	Tukey's percent broken		Tukey's wear score	
	Difference	*p*	Difference	*p*
North vs. Sabetta	47.346	**<0.001**	46.35	**<0.001**
South vs. Sabetta	16.101	**0.021**	5.98	0.593
North vs. South	31.245	**<0.001**	40.31	**<0.001**

Group comparisons of relative pulp cavity diameters			
	df	*F*	*p*
ANOVA	2, 132	3.39	**0.037**
Tukey's HSD test	Difference	*p*	
North vs. Sabetta	–11.298	0.357	
South vs. Sabetta	11.399	0.306	
North vs. South	–22.698	**0.026**	

Note: The *p* values in boldface type are statistically significant (defined by $p < 0.05$).

Table 3. ANCOVA results comparing North 1981/1983, South 1983/2007, and Sabetta 2019/2020 samples for both percent broken teeth and wear score controlling for age using C_1 relative pulp cavity diameter as a proxy (see text for details).

		Percent broken		Gross wear score	
	df	*F*	*p*	*F*	*p*
North vs. Sabetta					
ANCOVA	1, 84	**64.31**	**<0.001**	**52.76**	**<0.001**
Homogeneity	1, 83	1.03	0.313	0.65	0.422
South vs. Sabetta					
ANCOVA	1, 97	**13.85**	**<0.001**	1.50	0.224
Homogeneity	1, 96	1.93	0.168	0.31	0.579
North vs. South					
ANCOVA	1, 75	**11.72**	**0.001**	**22.47**	**<0.001**
Homogeneity	1, 74	1.98	0.164	0.14	0.709

Note: The *p* values in boldface type are statistically significant (defined by $p < 0.05$).

growing numbers of ptarmigans and hares in northern Yamal, and that these are important to arctic fox diets.

Hypothesis 3: replacement of reindeer bone as an alternative food with anthropogenic subsidies

This hypothesis seems the most plausible explanation for the results presented here given that an increase in human presence often results in availability of anthropogenic subsidies for arctic foxes (e.g., Eberhardt 1977, 1982; Garrott et al. 1983; Iossa et al. 2010; Lehner 2012; Savory et al. 2014; Elmhagen et al. 2017). Foxes seem to prefer softer, calorically dense human foods when they can get them. And while the Yamal LNG company takes measures to dispose of food waste to prevent its distribution into the surrounding ecosystem, foxes actively seek out anthropogenic subsidies, approaching and begging for food from shift workers. It remains possible that more timid arctic foxes in the area actively avoid settlements, but individuals considered in this study likely consumed anthropogenic subsidies. Highly processed and refined foods, such as bread and pasta, should lead to less tooth wear and breakage than would reindeer bone, a common alternative resource when preferred smaller prey are less available.

Growing human presence in the Arctic can have significant effects on fragile high-latitude ecosystems. The arctic fox provides a well-known example (e.g., Lehner 2012). Not only is arctic fox a flagship species for climate change in the Arctic (IUCN 2009), but it is emblematic of the effects of more direct anthropogenic disturbance. The effects of human activity are complex and multifactorial. On the one hand, such activity provides new opportunities for calorically dense, easy to obtain foods that can supplement the diet when preferred prey are less available; and arctic foxes are not shy about scavenging around human settlements (Eberhardt 1977, 1982; Garrott et al. 1983; Selås et al. 2010). Furthermore, because predators that take arctic fox cubs, such as wolverines and eagles, avoid humans (May et al. 2006; Kaisanlahti-Jokimaki et al. 2008), more anthropogenic subsidies and fewer predators can be a boon to arctic fox populations. Their teeth are certainly in better shape when they consume soft, nonabrasive human foods rather than falling back on reindeer bone, whether scavenging carcasses or taking calves (see above). In light of deleterious effects of climate change on foraging patterns and changes in availability of various prey species in some areas (e.g., Pamperin et al. 2008; Henden et al. 2010; Post et al. 2009; Ims et al. 2017), this can be a net positive. However, the arctic fox is a versatile generalist predator, so the impact may not be so clear in other places (Ehrich et al. 2017; Dudenhoeffer et al. 2021). And indeed, region-scale conservation efforts in Fennoscandia have even introduced artificial feeding by dog food pellets in an effort to recover the endemic arctic fox population there (Thierry et al. 2020).

On the other hand, intensification of human activity in the Arctic also brings challenges to arctic fox populations. As noted in the introduction for example, in some parts of the Arctic anthropogenic subsidies allow a northward spread of larger, competitively superior red foxes, which can take arctic fox dens, food, and cubs (Elmhagen et al. 2002, 2017; Killengreen et al. 2007; Selås et al. 2010; Rodnikova et al. 2011; Savory et al. 2014; Stickney et al. 2014). Finally, there are potentially other deleterious effects of anthropogenic subsidies on arctic foxes that have yet to be studied. What, for example, are the impacts of human food consumption on gut microbiomes? Recent studies of coyote and American black bear (*Ursus americanus* Pallas, 1780) microbiomes revealed marked changes in species composition and diversity in individuals that relied heavily on anthropogenic foods (Sugden et al. 2020; Gillman et al. 2022). The study by Sugden et al. (2020) even suggested that microbiome changes associated with consumption of human foods have a marked negative effect on the health of urban coyotes. In any case, much work remains to be done to assess both the extent and impacts of intensification of human activity on populations of arctic foxes and other endemic species in the Arctic. We believe that efforts to document effects of anthropogenic subsidies on dental ecology can contribute to this work.

In summary, this study suggests that dental ecology markers have the potential to serve as an indicator of human impact on arctic fox populations in developing areas of the Arctic. In this case, the presence of significantly lower than expected tooth wear and breakage patterns relative to foxes from regions with less human presence suggests a reliance on anthropogenic food sources that impose minimal wear of or breakage to teeth.

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Data availability

All original dental materials are archived at the Arctic Research Station of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Labytnangi, Yamalo-Nenets Autonomous District, Russia. All data analyzed in this paper are presented in Supplementary Table S1.

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The authors declare that there are no competing interests.

Supplementary material

Supplementary figure and table are available with the article at https://doi.org/10.1139/cjz-2022-0057.

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