Mobility and season of death of the Arctic foxes killed by Gravettian hunters at Kraków Spadzista, Poland

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Abstract
The Late Gravettian site of Kraków Spadzista is important for understanding human behaviour and adaptation in cold, northern and marginal landscapes approaching the coldest part of the last glacial cycle. This paper focuses on the large assemblage of Arctic fox (*Vulpes lagopus* L.) remains found at the site, and presents new data on the mobility patterns and season of death of the animals killed by Gravettian hunters. Laser ablation strontium isotope analysis of teeth from five individuals indicates that each analysed fox was born and grew up in a different and isotopically distinct location, and had migrated tens or hundreds of kilometres into the vicinity of Kraków Spadzista before being killed by Gravettian hunters. Season of death data gathered from the dental cementum of at least 10 fox individuals demonstrate that the majority were killed in a window between late winter and late spring. Given the predictable nature of seasonal changes in Arctic fox hide quality and bodily fat reserves, we argue that the foxes were most likely killed at the start of this window, i.e. in late winter. The results are interesting for reconstructing the context to human hunting strategies in the Late Gravettian, revealing the choices made by hunters about where and when to procure these small prey.

Highlights

3 to 5 bullet points (maximum 85 characters, including spaces, per bullet point).

- Arctic foxes at Kraków Spadzista were killed mostly in late winter
- Each analysed fox was born and grew up in an isotopically distinct location
- Arctic foxes were highly mobile travelling tens or hundreds of km
- Foxes were trapped in large numbers and possibly attracted by rotting mammoth meat
- Fox hunting was part of an integrated economic subsistence strategy

1. Introduction

Kraków Spadzista is one of the largest Upper Palaeolithic sites in Central Europe. It is located in southern Poland at the edge of the North European Plains, and contains extensive deposits dating to the Late Gravettian between approximately 24,500-23,000 ^{14}C years BP (Wilczyński *et al.*, 2020). The site is important for understanding human behaviour and adaptation in cold, northern and marginal landscapes approaching the coldest part of the last glacial cycle.

Kraków Spadzista is best-known for the vast and dense accumulations of woolly mammoth bones discovered there (trenches B and B1), together with clear evidence that at least some of these individuals were killed and butchered by humans (Kufel-Diakowska *et al.*, 2016). More than 100 individual mammoths were found, together with lithic scatters and other occupation debris (Wojtal *et al.*, 2019). A large campsite area (trenches C and D) and a workshop zone (trenches E, E1 and F) have also been defined at the site (Wilczyński *et al.*, 2012b).

This paper focuses on the second-most abundant prey species at Kraków Spadzista, Arctic fox (*Vulpes lagopus* L.), which is represented by more than 2400 elements and a minimum number of individuals (MNI) of 29. The majority of Arctic fox remains were found in the workshop zone, located approximately 30 m south of the main accumulation of woolly mammoth, in an area used for the production of lithic tools and the processing of prey animals other than woolly mammoth (Wilczyński *et al.*, 2012b). The Arctic fox assemblage has been widely interpreted as evidence for autumn-winter season hunting to obtain thick furs for use as clothing (e.g. Lipecki & Wojtal, 2015; West, 1996b). However, this interpretation has relied on inconclusive evidence from osteological analyses and tentative results of dental cementum analysis of two fox teeth that were never verified or confirmed (West, 1996a).

Here, we present new data on the season of death of the Arctic foxes killed at Kraków Spadzista by Gravettian hunters and the first direct evidence describing mobility patterns of Arctic fox in a mammoth steppe ecosystem. Season of death is determined via analysis of dental cementum, a well-established technique for investigating age and season of death in mammals (Lieberman, 1993, 1994; Lieberman & Meadow, 1992; Rendu *et al.*, 2010), which has been widely applied to animal teeth of Palaeolithic age (Burke & Castanet, 1995; Niven *et al.*, 2012; Rendu, 2010). Mobility patterns of the foxes were investigated using strontium isotope analysis of tooth enamel by laser ablation. Strontium isotope analysis distinguishes mobility and migration across different geologies during the period of tooth formation (Bentley, 2006; Ericson, 1985). Recent developments in the laser ablation technique have confirmed and improved the accuracy of the measurements (Gerling & Lewis, 2017; Irrgeher *et al.*, 2016; Muller & Anczkiewicz, 2016; Willmes *et al.*, 2016). The technique has also been applied previously to enamel samples of Palaeolithic and younger ages (Kowalik *et al.*, 2020; Lugli *et al.*, 2019; Pryor *et al.*, 2016a; Pryor *et al.*, 2016b).

The new information on mobility and season of death is used to address the following questions:

1. Is an autumn-winter kill pattern — and, by extension, season of human occupation at the site — supported by a greatly-expanded sample of Arctic fox teeth?
2. Do Arctic fox mobility patterns in the mammoth steppe palaeoenvironment conform to predictions from modern ecology and what do the results suggest about Arctic fox behaviour in the unique mammoth steppe ecosystem?
3. What do the data reveal about the ecological context and seasonal prey selection strategies of Late Gravettian hunters at Kraków Spadzista?

2. Background

2.1 Kraków Spadzista

The Kraków Spadzista site complex lies on a promontory of the Saint Bronisława hill at the eastern end of Sowiniec horst at a height of 50 m above the floodplain of the Rudawa River in southern Poland

(Figure 1). Excavations between 1967 and 2017 have revealed substantial quantities of lithics and faunal material deposited across an area of almost 2 ha associated with a weakly developed and periglacially deformed soil (Łanczont *et al.*, 2015; Wilczyński *et al.*, 2012b). The southern and north-eastern sides of the horst where the site is located are high and descend steeply, or sometimes vertically, into the Vistula and Rudawa river valleys below (Łanczont 2015). It is suggested that the large accumulations of woolly mammoth bones found at the site formed as Upper Palaeolithic hunters took advantage of this natural morphology to trap woolly mammoth prey at the top of the slopes (Wojtal *et al.*, 2019).

FIGURE 1 around here

The Arctic fox remains were excavated in two main phases. The first phase comprised two trenches, E and F, excavated in 1987 and 1989 respectively. The second phase, in 2012, focused on trench E1, which was located in between the two previous trenches and formed a connection between them. The collective deposits belong to one of two "workshop zones" for flint working and processing of prey animals other than woolly mammoth (Wilczyński *et al.*, 2012b). Radiocarbon dates for the zone cluster around 23,000-25,000 ^{14}C years BP, the same date range obtained for the woolly mammoth accumulation in parts B and B1 of the site nearby (Wojtal & Wilczyński, 2015). The deposit is interpreted as a palimpsest resulting from separate visits made to the same hillside (Wilczyński, 2015).

The 1980s excavations discovered 214 bones of Arctic fox and a MNI of 14 (West 1996). The bones were recovered by hand and no sieving system was used. The resulting faunal assemblages contained an abundance of cranial bones and axial elements but very few smaller bones including those from the feet, leading to the suggestion that foxes were skinned and pelts removed with the feet still attached (West, 1996b). West (1996b) also noted that the fox bones were from young animals about 1.5 years old. Unfortunately, many of these bones were lost or destroyed and only 69 elements from the original assemblage survive today (Wilczyński *et al.*, 2012b).

New excavations in 2012 in trench E1 connected trenches E and F together and coincided with a reanalysis of all materials from the site (Wojtal *et al.*, 2015). All sediments from trench E1 were wet sieved, and the excavations produced 2014 bones of Arctic fox representing all parts of the skeleton including foot bones, bringing the MNI for areas E, E1 and F to 23, including the surviving remains from the 1980s excavations (Wojtal & Wilczyński, 2015). Remains of a further six individuals are known from other parts of the site, including four in the camp zone (trenches C, C2 and D), and two from the mammoth bone accumulation (trenches B and B1). This brings the total MNI of Arctic Fox at the site so far to 29. The combined faunal evidence unambiguously indicates that whole-carcasses of animals were brought back to the site for processing, a refinement of West's (1996b) earlier interpretations (Lipecki & Wojtal, 2015). Further single remains of Arctic fox were excavated from a new trench G in 2017 – these are currently being studied and are not included in the figures mentioned here (Wojtal *et al.* in prep.).

The Arctic fox remains are heavily fragmented and no cutmarks have been found, however, many bones were covered in calcite precipitation which obscured the surface, making it difficult to detect such features (Lipecki & Wojtal, 2015). No deciduous teeth were found, but adult teeth in various stages of wear are present, suggesting the hunted animals span a wide range of ages from sub-adult to very old individuals (Lipecki & Wojtal, 2015).

2.1.1 Previous seasonality studies

An absence of deciduous teeth and unfused epiphyseal bones of Arctic fox has been interpreted as indicating an autumn-winter kill pattern by hunters obtaining fox hides during the season of their highest quality (Lipecki & Wojtal, 2015; West, 1996b). However, if Gravettian hunters deliberately selected adult Arctic foxes and actively avoided the younger animals, the logic behind this inference ceases to be valid. Direct estimates for the season of death are available from dental cementum in two Arctic fox teeth, which tentatively suggest individuals approximately 18 months old were killed in

the "mid autumn" (West, 1996a), however these results are described as preliminary and have never been substantiated or verified. Dental cementum of two reindeer teeth from area F have also been described as showing a late summer or early autumn kill pattern (Nývltová Fišáková, 2013).

3. Arctic fox
3.1 Palaeoecology
Today, Arctic fox has a circumpolar distribution and is found mainly in coastal or Arctic tundra environments and mountainous regions above the treeline (Grue & Jensen, 1976; Hofreiter & Stewart, 2009). Cubs are born in late spring (May-June) and remain close to the den where they were born until becoming independent at 12-14 weeks, reaching full adult body size at 14-28 weeks (Audet *et al.*, 2002). Arctic foxes are an opportunistic predator and scavenger, focusing mostly on small mammals like voles and lemmings but will also consume birds, eggs, some plant foods including berries, and occasionally large mammals such as reindeer (Audet *et al.*, 2002). They are vulnerable to natural fluctuations in food supplies and many foxes can die of winter starvation in bad years (Prestrud, 1991).

Arctic fox distribution and mobility patterns vary seasonally, being communal and territorial during spring-summer and solitary and highly mobile during autumn-winter. The territorial phase begins at the start of the breeding season in early spring, coinciding with the period when young are born and raised in family units. Pups remain near the den within a range of 3.7 + 1.7 km^2 and are reliant on food brought back by the parents (Audet *et al.*, 2002; Eberhardt *et al.*, 1982). Territorial size of adults varies greatly depending on food availability and can be as small as 4 km^2 in areas with high density, high quality food sources but as large as 60 km^2 in marginal areas (Anthony, 1997; Audet *et al.*, 2002). This arrangement persists until adult males abandon the family group around mid-summer, followed by the females who leave a few weeks later. Dispersal of young occurs a few weeks later in early autumn.

From early autumn until the start of the next breeding season in early spring, Arctic foxes are highly mobile and mostly solitary (Audet *et al.* 2002), other than when congregating to scavenge carrion from large animal carcasses. The scale of mobility depends greatly on the distribution and availability of food and the impact of seasonal food shortages. While Arctic foxes will remain close to their summer territories when possible, long distance movements covering hundreds or thousands of kilometres may also occur in late summer/early autumn in search of food, followed by a return trip in the spring.

Arctic fox abundance varies considerably year-to-year in modern habitats with peaks every 3-5 years that are thought to relate to rodent abundance (Audet *et al.* 2002). Local fluctuations depend on reproduction by local animals, survival rates of young and immigration (Audet *et al.* 2002). Arctic foxes in the wild today typically live for 3-4 years, but may reach up to 10 years (Audet *et al.*, 2002).

3.2 Tooth growth and cementum formation
Permanent molars in Arctic fox, similar to the red fox (*Vulpes vulpes* L.), begin to form at or around birth. Enamel mineralises progressively from crown to root and virtually simultaneously in all teeth. Tooth eruption begins in mid-late summer of the first year of life and is complete by the start of the autumn at approximately six months of age (Audet *et al.*, 2002; Lloyd, 1980). Enamel strontium isotope ratios therefore reflect the isotopic composition (source location) of food provided by the parents from their summer territory, near the den where the individual was born. The latest-forming enamel close to the enamel-root junction may also include the late summer period, as the foxes begin to move and hunt independently. Canine teeth continue to erupt throughout life as the cusp wears, but no further enamel formation occurs (MacPherson, 1969).

Arctic fox dental cementum starts to form as soon as the permanent tooth roots appear. The first dark cementum band is deposited after approximately one year of life in February-May, visible under crossed polarised light (Grue & Jensen, 1976). Further dark cementum bands occur annually thereafter, forming in the late winter-early spring season (February-May). Foxes killed in the summer,

autumn and early- to mid-winter period therefore show a light-coloured band at the outer cementum edge.

4. Geology and strontium isotope basemap
4.1 Geology
The geology of Poland may be divided into two main territories. North and central areas comprise the Polish part of the North European Plains, a geological region of low-lying ground which stretches west-east from the North Sea to the Ural Mountains. These more or less flat plains were levelled by successive Quaternary-era glacial advances that left behind deep glacial deposits over most of Poland including areas of moraine, coversands and glacial gravels (Marks *et al.*, 2016). This material was transported within ice sheets from Scandinavia and is derived from Precambrian magmatic and metamorphic rocks as well as Paleozoic carbonates (Zieliński *et al.*, 2016). Patches of Quaternary-era loess are also present across this northern plains region.

The second main territory comprises southern Poland, including the upland regions of the Kraków-Częstochowa Upland (also known as the Polish Jura Chain), the Świętokrzyskie Mountains (also known as the Holy Cross Mountains) which are among the geologically oldest in Europe, the Sudetes in the south west (part of the Bohemian Massif) and the Carpathians in the south and south east. These upland areas are geologically heterogeneous and include a mix of limestones, granites and more recent volcanic basalts (Marks *et al.*, 2006).

Kraków Spadzista lies in the southern geological zone within a geological formation known as the Carpathian Foredeep, a large basin at the northern edge of the Carpathian mountains filled by thick Miocene argillaceous sediments, known as the Kraków iec Beds (Oszczypko, 1998). These Miocene deposits are mostly overlain by Pleistocene loess, glacial tills and fluvioglacial sands although erosion has exposed the underlying Miocene deposits in places (Szczepanek *et al.*, 2018). Sowiniec horst, where Kraków Spadzista is located, comprises an area of raised ground composed of Jurassic (Oxfordian) karstic limestone. The cultural materials lie within Quaternary loess and gley sediments belonging to the Central European loess belt (Haase *et al.*, 2007), underlain by the Miocene marine clays and limestone bedrock that are typical for the region (Kalicki *et al.*, 2007; Łanczont *et al.*, 2015).

FIGURE 2 AROUND HERE

4.2 Bioavailable strontium isotope basemap
Estimates of bioavailable strontium quoted here are derived primarily from measurements of archaeological bone, which is porous to water-soluble strontium in the burial environment, and tooth enamel of archaeological fauna judged to reflect local signatures in the studies reporting the data. Human enamel data is only used where migration can be confidently ruled out.

Tooth enamel from eleven Pleistocene rodents discovered at Kraków Spadzista span a wide range of ^{87}Sr/^{86}Sr values from 0.7095 to 0.7116 (Kowalik *et al.*, 2020). This range is virtually identical to that observed throughout the broader Vistula valley and Carpathian Foredeep region combined (see below), and hints at a potentially complex situation whereby at least some of the analysed rodents did not grow up locally near the site. The density of rodents at Kraków Spadzista is very high for an open air site (MNI= >100 from three trenches dug in 2011-2013 alone), and it is not yet known how such large numbers of rodents came to be incorporated into the assemblage. One possibility is that rodents lived at the site around the time of human occupation or after it was abandoned (see Frank *et al.*, 2020 for information on rodent behaviour near mass death assemblages), however it is not clear whether this could have produced the high isotopic diversity observed within the assemblage. Fox dentine ^{87}Sr/^{86}Sr values reported in this article cover a much smaller isotopic range suggesting a relatively homogenous local isotopic context, and it is possible that local rodents may have been influenced by strontium derived from the rotting mammoth carcasses that was recycled back into the food chain. Alternative possibilities include that rodent remains were brought to the site by owls or other birds of prey roosting at the site after it was abandoned by humans, that rodent

remains were brought inside the stomachs of the foxes hunted by humans and thus represent a wide geographic range, or even that humans directly hunted the rodents themselves. Each of these possibilities require further investigation. Regardless of how the rodent data is interpreted, the isotopic overlap with the broader Vistula valley and Carpathian Foredeep suggests that this region, and the Kraków Spadzista site which sits within it, should be treated as a single isotopic zone when mobility assessments are made (Figure 5).

Estimates of bioavailable strontium in the Vistula valley and broader Carpathian Foredeep are provided by Late Neolithic human tooth enamel from seven individuals buried approximately 50 km northeast of Kraków in the Małopolska Upland (Figure 2), a loess plateau on the edge of the Vistula River valley and bordering the Kraków-Częstochowa Upland, which ranged from 0.7095 to 0.7104 (Szczepanek *et al.*, 2018). The internal consistency among these individuals suggests they are a group of locals, averaging bioavailable strontium from the Pleistocene loess, glacio-fluvial deposits and outcropping Miocene clays that comprise the Vistula valley floor and broader Carpathian Foredeep basin. The observed range is similar to values measured for local rainwater (0.7093), and to river water from the upper reaches of the Warta River (0.7100-0.7103) which rises in the Kraków-Częstochowa Upland approximately 60 km northwest of Kraków Spadzista (Zieliński *et al.*, 2017). This implies a degree of equifinality in the expected $^{87}Sr/^{86}Sr$ range for the Częstochowa Upland and Vistula valley near Kraków Spadzista.

Elsewhere in the Carpathian Foredeep, Late Neolithic samples from loessic sites in south-east Poland produced a slightly more radiogenic range between 0.7098-0.7114 while soluble strontium in loess at the Magdalenian site of Klementowice 210 km north-east of Kraków Spadzista was measured at 0.71193 (Figure 2; Belka *et al.*, 2018; Pryor *et al.*, 2016b; Szczepanek *et al.*, 2018). Combined, these data suggest a bioavailable strontium isotope range of 0.7095-0.7120 for the Vistula valley as it passes through the Carpathian Foredeep and for loess environments more generally in south-east Poland, but also make clear that different locations have distinct isotopic signatures within this range (Figure 5). Loess deposits in south-western Poland south of Wroclaw have higher $^{87}Sr/^{86}Sr$, from 0.7115-0.7147 (Pokutta & Frei, 2011; Pospieszny & Bełka, 2015).

Turning to the North European Plains, groundwaters from aquifers in this region show a wide range of $^{87}Sr/^{86}Sr$ values varying between 0.708 and 0.714 (Grabowski *et al.*, 2014; Voerkelius *et al.*, 2010; Zieliński *et al.*, 2017). This reflects the particular geological stratigraphy of the northern plains whereby surficial highly radiogenic quaternary deposits of glaciogenic origin (values above 0.7118) overlie deeper carbonate deposits dating to the Late Jurassic and Late Cretaceous eras, which have much lower $^{87}Sr/^{86}Sr$ values in the range 0.7080-0.7086 (see Zielinski *et al.* 2017 for a detailed analysis). By comparison, modern day surface waters in three major Polish rivers — the Vistula, Warta and Oder — show a consistent range of values between 0.7090 and 0.7106 reflecting mixed waters from atmospheric and groundwater sources, and input from modern contaminants including fertilisers, sewage and industrial activities (Löfvendahl *et al.*, 1990; Zieliński *et al.*, 2017). Two groundwaters (points 11 and 12 in Figure 2) also reflect either modern contamination (Grabowski *et al.*, 2014), or subterranean mixing of waters from the two lithological units. Meanwhile, waters draining the upper catchment of the smaller River Notec in Central Poland are in the range 0.7127-0.7128, which agrees well with data from archaeological bones recovered in the region (see below) and confirm the influence of highly radiogenic near-surface sediments on bioavailable strontium values in the North European Plains (Zieliński *et al.*, 2016).

As expected, the small number of datapoints describing bioavailable strontium composition in the northern plains region reflect the quaternary glaciogenic surficial deposits, being mostly above 0.7120 and all >0.7117 (Figure 2; Table A.1). This includes bone and enamel data, from both wild and domestic fauna, found at sites across the central plains region and dating from the Neolithic to the Medieval era (Buko *et al.*, 2013; Marciniak *et al.*, 2017; Pospieszny *et al.*, 2015). Modern fauna contaminated with fertiliser-derived strontium and some archaeological human enamel isotope data reported in these studies were not used here as it remains unclear which individuals are local and which are migrants (e.g. Buko *et al.* 2013). Birch and oak leaves from the south plains region also show

^{87}Sr/^{86}Sr values above 0.7125 (Zieliński *et al.*, 2017). The post-medieval cemetery at Drawsko in west Poland is an exception in showing much lower values, where bones from wild fauna and tooth enamel from 56 human individuals produced values between 0.7097 and 0.7130 (Gregoricka *et al.*, 2014). However, as Drawsko lies more than 100 km behind the Fennoscandian ice sheet margin in an area inaccessible at the time Kraków Spadzista was occupied, this site is not included further in the basemap modelling. Groundwaters with ^{87}Sr/^{86}Sr values corresponding to carbonate aquifers are included for reference in Table A.1 and Figure 2, but as these geologies are sub-surface and appear to have negligible effects on plant and animal ^{87}Sr/^{86}Sr values they were not used to assess mobility of the Kraków Spadzista foxes.

Strontium data from two rodent assemblages from Borsuka Cave and Żarska Cave, located in the Kraków-Częstochowa Upland approximately 21 km north-west from Kraków Spadzista, span wide ranges between 0.7095 – 0.7132 and 0.7112 - 0.7122 respectively (Kowalik *et al.*, 2020), overlapping with data from both the Carpathian Foredeep and North European Plains. Similarly to the Kraków Spadzista rodent data, the large isotopic range indicates that these rodents were sourced from geologically varied substrates, again raising the question of whether this reflects local rodents living on highly varied geologies or a more mixed assemblage that includes rodent remains carried in over longer distances by birds of prey and other animals that used the cave. Two leeched loess samples from Borsuka Cave suggest a much narrower range for sediments at the site itself of 0.7116-0.7117, well within the range identified for loess in the Carpathian Foredeep and Vistula valley more generally.

Bioavailable strontium isotope ratios have not yet been characterised for the upland regions of southern Poland. Estimates based on the strontium isotope marine curve suggest marine-derived rocks in the Holy Cross Mountains, the Sudetes and the flysch deposits in the Outer Carpathians will have initial values between 0.7068-0.7092 (McArthur *et al.*, 2012), while whole-rock measurements on tertiary basaltic volcanics within the Sudetes range produced very low values between 0.70317-0.70369 (Blusztajn & Hart, 1989). Whole-rock values are unlikely to be directly representative of bioavailable Sr, due to differential erosion/dissolution of different mineral components, inputs from atmospheric sources, and/or movement of groundwaters and other factors (Price *et al.*, 2002). However, the data clearly suggest that bioavailable strontium will be substantially lower in the upland environments of southern Poland than are found in most of the rest of the study region. This conjecture is supported by measurements on five groundwaters derived from the Carpathians ranging between 0.7086-0.7096 (Voerkelius *et al.*, 2010).

5. Materials and methods

5.1 Age and season of death

Dental cement is deposited annually around the roots of teeth in seasonal bands which distinguish periods of fast and slow growth, correlating with summer and winter seasons respectively (Goodwin & Ballard, 1985; Lieberman, 1994). These bands are visible under transmitted cross-polarised light passing through thin-sections approximately 30-100 µm thick (Lieberman, 1994). Eighteen loose fox teeth excavated in 2012 from trench E1, all lower canines and premolars, were selected for dental cementum analysis to study age and season of death. Additionally, four mandibles containing teeth were selected and two teeth were sampled from each jaw (Table 1). The 26 selected teeth came from various grid squares around the site, showed generally good levels of preservation and displayed no obvious damage to the tooth roots.

The sampled teeth comprised 10 right canines (including three from mandibles), and seven left canines (including one from a mandible). Unfortunately, it was not possible to determine which side the premolars came from, unless they were extracted from a mandible. Therefore, we conservatively estimate the MNI studied for dental cementum as ten, based on the number of right canines, although differences in tooth wear and scattering of teeth around the site suggest the actual number is almost certainly higher.

Between one and five sections of dentine with adhering cementum were cut from each root using equipment housed in the Department of Archaeology, University of Exeter, and the Institute of

Systematics and Evolution of Animals in Kraków. A mix of longitudinal and horizontal cross-sections were used. Sections from nine teeth (individuals 1-9) were divided between researchers based in Exeter and Kraków and analysed independently to check for consistency and repeatability of results (Table 1). The remaining teeth were analysed only in Kraków.

In Exeter, thin sections were prepared by embedding the tooth pieces in Epofix© epoxy resin. Once hardened, the samples were ground using 35 μm and 15.3 μm grits to create a fresh cross-section through the cementum layers and then mounted on glass slides using the adhesive Loctite 358, which was cured by exposure to ultra violet light for 60 seconds. Thin sections were cut to approximately 90 μm thick using a Kemet Geoform thin section machine, then polished by hand using a 15.3 μm grit and 1 μm alumina oxide powder until the cementum structures were clearly visible.

The second set of samples was processed in Sample Preparation Laboratory (GeoPrep) of the Kraków Research Centre, Institute of Geological Sciences, Polish Academy of Sciences. Tooth pieces were embedded in Araldite 2020 resin and cut with a low-speed Struers Minitom saw equipped with diamond cutting disc to expose the desired section. In the case of smaller teeth, samples were carefully ground by hand to expose the section instead. Samples were then mounted onto glass slides using Araldite 2020 resin and ground manually using 35 μm, 15.3 μm, 10.3 μm and 5 μm grits to 80-100 μm thickness. Sections were finished by polishing with 0.3 μm alumina oxide powder using a Logitech automatic polishing machine.

Thin sections were analysed in Exeter and Kraków under cross-polarised transmitted light at x25, x50, x100, x200 and x500 magnification to study the cementum banding. A λ filter was used to aid identification of diagenetic contamination of the cementum structures (Rendu *et al.*, 2010; Stutz, 2002). Sections were discarded when diagenetic interference was suspected or cementum growth structures were unreadable. Age and season of death assessments made independently in Exeter and Kraków were then compared to check for consistency and repeatability of results, corroborating the findings in all cases.

5.2 Mobility

Arctic fox mobility patterns were investigated using further teeth extracted from the four mandibles analysed for season of death (KSF100-KSF103) and one loose tooth (KSF104)(MNI = 5). Enamel-dentine strips approximately 3-5mm wide were cut parallel to the axis of growth, in each case retaining some of the dentine core of the tooth that was also used for analysis (see below). The untreated tooth fragments were embedded on edge in Epofix© epoxy resin and then sanded using 90 and 30 μm grits to create a flat surface ready for analysis. Strontium isotope ratios were measured along the centre-line of the enamel cross-sections by Laser Ablation Multi-Collector Inductively Coupled Plasma Mass Spectrometry (LA-MC-ICPMS), using a New Wave Research 193nm excimer laser ablation system (NWR193) coupled to a Thermo Scientific Neptune multi collector ICP-MS located in the National Oceanography Centre, University of Southampton. The enamel to be analysed was pre-ablated to remove surface contaminants. The laser, with a spot size of 150 μm, was set to pulse at 15 Hz while traversing the sample at 10 μms^{-1}. The ablated sample was swept from the laser cell using helium gas, which was then mixed with argon and nitrogen gas flows before entering the plasma ion source. ^{87}Sr/^{86}Sr was measured in static collection mode with an integration time of 1.05 seconds using a tuned mass spectrometer setup designed to reduce oxide production, which was monitored as ^{254}(UO)$^{+}$/^{238}U^{+} (Lewis *et al.*, 2014). Mass bias was corrected as normal using an ^{86}Sr/^{88}Sr ratio of 0.1194 according to an exponential mass fractionation law, after which further corrections were made to correct for isobaric interferences when calculating the strontium isotope ratio (Horstwood *et al.*, 2008; Lewis *et al.*, 2014). Rare earth element contamination was monitored using ^{89}Y as a proxy, and data showing significant concentrations were rejected as diagenetic (Woodhead *et al.*, 2005). A small positive offset from known ^{87}Sr/^{86}Sr values of in-house standards is usually observed due to molecular interference on ^{87}Sr of ^{40}Ca^{31}P^{16}O^{+} which is the primary constituent of the enamel matrix, but this is within the precision of a typical measurement. Repeat analysis bracketing the archaeological samples of an in-house enamel standard prepared from a pig fed exclusively marine foods and measured with Thermal

Ionisation Mass Spectrometry (TIMS) to 0.709078 showed an offset of +79 ± 81 parts per million (ppm; 1σ) for the laser ablation analyses over the TIMS values. This is well within the precision of individual measurements of 200-600 ppm and the total variation within the teeth of >5500 ppm, and is therefore considered insignificant to our interpretation of the isotopes.

Bioavailable strontium at the burial location in Kraków Spadzista was characterised using measurements of tooth dentine from the five analysed teeth. Like bone, dentine becomes contaminated with diagenetic strontium absorbed from the environment after burial (Hoppe *et al.*, 2003), which is useful for determining the $^{87}Sr/^{86}Sr$ of sediments in the vicinity of the buried tooth.

6. Results

FIGURE 3 AROUND HERE

6.1 Age and season of death
Thin section analyses revealed varying degrees of weathering affecting all studied teeth, with the exception of two canines which preserved no cementum layer (Table 1). Cementum banding in nine teeth was unreadable due to extensive recrystallization and contamination of the cementum structure, plainly visible under both polarised light and when using the Lambda filter. Sections from 12 teeth showed weathered but still readable cementum banding (Figure 3), revealing that most of these (n=10) died during formation of the dark, slow-growth band which develops between February and May in modern Arctic fox populations (Grue & Jensen, 1976). This includes two foxes that died just as the slow growth band was starting to form, indicating a mid-late winter season of death. Two further foxes were killed during formation of the fast-growth band, which forms between June and January in modern populations. Age at death based on counting of cementum bands suggested almost all the hunted foxes were aged between 1-2 years, apart from one fox aged 4 years. Overall, these results indicate a strong seasonal bias towards kills made within the late winter to early spring period. The results clearly do not support a model of habitual year-round kills, or kills focused on the autumn to early-winter period as has previously been suggested (West, 1996a, 1996b).

FIGURE 4 AROUND HERE

6.2 Mobility
Dentine strontium isotope ratios of the analysed foxes had a median of 0.71060 and indicate a 'local' range for Kraków Spadzista loess of 0.71028 – 0.71092, defined as the median ± the interquartile range (0.00032). This is well within the typical $^{87}Sr/^{86}Sr$ range for other loess sites in Central Europe and is in good agreement with $^{87}Sr/^{86}Sr$ values recorded in Neolithic human tooth enamel samples from loessic sites in south-east Poland and slightly more radiogenic than those observed from loessic sites in the Małopolska Upland (Belka *et al.*, 2018; Szczepanek *et al.*, 2018). The dentine data fall in the middle of the range observed in tooth enamel of rodents from the site (Kowalik et al., 2020), and show much greater internal consistency, lending support to the argument that at least some of the rodents grew up away from the site.

Fox enamel $^{87}Sr/^{86}Sr$ varied over a much wider range than the tooth dentines, from 0.70933 to 0.71331 (Figure 4, Table 2). Variability within each individual tooth was low, with a maximum intra-individual range of 0.00073 (1020 ppm) compared to overall variability of 0.00398 (5610 ppm). Foxes KSF101 and KSF103 both show evidence for small fluctuations in enamel $^{87}Sr/^{86}Sr$ during the period of tooth growth, ranging between 0.7116 and 0.7120, and between 0.7093 and 0.7100 respectively (Figure 4). This variability may be related to direct mobility of the fox cubs with their parents across different geologies or, perhaps more likely given the young age at which Arctic fox teeth form, to variability in the strontium isotopic content of food brought to the fox cub by its parents, reflecting hunting trips to different geological substrates. Overall, however, enamel strontium isotope ratios for

each of the five investigated foxes remained largely consistent during the period of tooth growth, with no evidence for substantial mobility during the early parts of their lives.

A more intriguing result is the clear separation in $^{87}Sr/^{86}Sr$ values measured for each individual, with each fox displaying a distinct strontium isotope range that is significantly different from all other individuals (Kruskal-Wallis with Bonferroni post-hoc correction; all p-values = <0.001). KSF103 occupies the least radiogenic range at 0.7093-0.7100; three individuals KSF100, KSF101 and KSF102 show distinct isotopic signatures within a mid-range of values between 0.7108-0.7122; while KSF104 produced a highly radiogenic range of 0.7125-0.7133. This demonstrates that the food and water consumed by each fox during tooth growth was derived from five isotopically unique and distinct geologies, indicating that the five foxes grew up in five different locations.

FIGURE 5 AROUND HERE

The fox enamel data show almost no overlap with the 'local' range defined from the tooth dentines. Additionally, although three foxes show some overlap with the rodents from Kraków Spadzista, this overlap occurs at either end of the rodent range rather than in the middle, as would be expected if the foxes consumed large numbers of rodents averaging the full isotopic range. Meanwhile, two foxes (KSF101 and KSF104) show more radiogenic values than both the dentine and rodent enamel data. These facts rule out a very local origin for the foxes from the loess environments adjacent to the Saint Bronisława hill. The least radiogenic individual, KSF103, matches closely with Neolithic humans buried in the Małopolska Upland (Figure 5), whose strontium isotope values reflect the mix of loess, Pleistocene glacio-fluvial sediments and Miocene bedrock which characterises this region (Szczepanek *et al.*, 2018). Located around 50 km north-east from Kraków Spadzista on the margins of the Vistula River valley, this Małopolska Upland region seems a very likely point of origin for KSF103. Alternatively, this individual also overlaps with the lowest end of the range for Neolithic humans who lived on loess deposits in south-east Poland near the Carpathian foothills, which therefore constitutes another less likely and more distant potential source location. In any case, the data firmly rule out the North European Plains and loess regions in SW Poland as possible source locations for KSF103.

Three foxes, individuals KSF100, 101 and 102, show most similarity with values measured in loess environments in the Carpathian Foredeep and Vistula river valley, and with the loess samples from Borsuka Cave in the Kraków-Częstochowa Upland (~0.7116) (Kowalik et al. 2020). Unfortunately due to the overlap in ranges from different regions, it is not possible to further define specific source regions for these individuals with the presently available data. For example, all three foxes fall in the middle of the range defined by the rodent assemblages from Borsuka/Żarska Caves located 21km NW of Kraków Spadzista meaning a relatively local origin in the Kraków-Częstochowa Upland is possible for these individuals if the rodents lived locally. However, KSF100 and KSF102 also match closely with the range observed in tooth enamel of a Magdalenian horse killed at Klementowice in eastern Poland c.215 km north-east of Kraków Spadzista (Pryor *et al.*, 2016b), while individual KSF101 overlaps with loess deposits in SW Poland up to 300 km west of Kraków Spadzista as well as values seen across the North European Plains. Longer-distance migrations can therefore not be ruled out for these individuals.

Meanwhile, the most radiogenic individual KSF104 also overlaps with the upper end of the range observed in the Borsuka/Żarska Caves rodent assemblages, but as only two of 17 rodents measured had $^{87}Sr/^{86}Sr$ ratios above 0.712, a local derivation from here seems unlikely. Rather, KSF104 coincides with strontium isotope ranges of both the SW Polish loess around 250 km west of Kraków Spadzista, and the Polish North European Plains at distances of between 100 and 450 km from the site including regions immediately adjacent to the Fennoscandian ice sheet at its maximum extent (Figure 2). Alternatively, other more distant locations with bioavailable strontium ratios >0.713 occur on granitic bedrocks in the upland environments of the eastern Bohemian Massif at various places, approximately 300 km southwest from Kraków Spadzista (Pryor et al. *in prep.*). However, sources in

this region are considered less likely due to palaeoenvironmental and site distribution data suggesting the eastern Bohemian Massif was uninhabitable and abandoned by both fauna and humans during the Gravettian (Musil, 2010).

In summary, it is clear from the enamel data that each fox individual was born and grew up in a different and isotopically distinct location and had travelled tens or hundreds of kilometres to reach the vicinity of Kraków Spadzista before being killed by Gravettian hunters, probably somewhere near the site given that carcasses were transported in whole (Lipecki & Wojtal, 2015). The isotopic data is consistent with three of the five foxes (KSF100, 102 and 103) having been born and raised in the environs of the Kraków-Częstochowa Upland, the Vistula River valley or the broader Carpathian Foredeep region 20-220km distant from Kraków Spadzista, up to the northern limit of loess distribution marked by the site of Klementowice. KSF101 may also have been born in this region but could instead have come from the north European plains or south-west of Poland. KSF104 can only have come from a highly radiogenic region such as the north European Plains or south-west Poland, involving travelling distances of 100-450 km. Mobility over distances of this magnitude is well within the normal annual mobility of Arctic fox populations observed today (Audet *et al.*, 2002).

7. Discussion and Conclusions
7.1 Ecology and behaviour
Arctic fox is one of several carnivorous species belonging to the unique mammoth steppe faunal suite which colonised central and eastern Europe during the last ice age (Musil, 2010; Wojtal, 2007). This also includes the red fox, which in modern environments is a direct competitor to the Arctic fox such that Arctic fox is excluded via interspecific competition wherever the red fox occurs in numbers (Hersteinsson & MacDonald, 1992). Meanwhile, the geographic range of red fox is limited by resource availability, as its larger body size is too expensive to upkeep in areas of low productivity (Hersteinsson & MacDonald, 1992). During the Gravettian, the red fox occurred alongside the Arctic fox throughout Moravia and the adjacent Carpathian Basin, as evidenced at sites including at Pavlov I, Dolni Vestonice and Moravany-Lopata II (Vlačiky, 2009; Wilczyński *et al.*, 2015; Wojtal *et al.*, 2012). It is not known how these species may have adapted their ecological niches to form a sympatric relationship in these regions. Conversely, the red fox was almost absent from the modern territory of Poland during the mid-Upper Paleolithic, almost certainly indicating that there was too little food there for the red fox to survive (Cyrek *et al.*, 2000; Lipecki & Wojtal, 2015; Wilczyński *et al.*, 2012a; Wojtal, 2007).

Our new data suggest that habitual seasonal mobility, sometimes over long distances, was a characteristic feature of Arctic fox colonisation of the north European Plains, just as mobility is key to its colonisation of more marginal Arctic territories today. Modern Arctic foxes remain near their summer territory throughout the year when food supply permits, particularly in resource-rich areas where foods may include plentiful birds eggs, marine foods or large numbers of rodents (Anthony, 1997). However, migrations in autumn/early winter are widely attested when concentrated food supplies are not available, followed by a return journey in spring back to their breeding territory (Audet *et al.*, 2002). Bulk collagen δ^{34}S ratios of fauna from the nearby Gravettian site of Předmostí, located in north Moravia, have previously suggested that Arctic fox occupied territories that were isotopically distinct from those of an array of other fauna found at the site (including mammoth, reindeer, bovids, wolf, wolverine and cave lion), consistent with long distance mobility of Arctic foxes to territories not visited by the other analysed fauna (Bocherens *et al.*, 2015). The strontium isotope data reported here confirms and strengthens this finding, indicating that long-distance seasonal mobility was sometimes necessary for survival among Arctic foxes living on the north European Plains in the Late Pleistocene, while the absence of the competitor red fox indicates this was driven by the need to find food rather than interspecific competition.

7.2 Seasonality of fox hunting
The majority of Arctic foxes at Kraków Spadzista were killed in the interval between late winter and late spring. Although this may be a simple consequence of short-duration seasonal presence/absence

of humans at the site, it may instead reflect deliberate choices about when to hunt, process and consume fox prey. Arctic fox provided both food and hides to Palaeolithic hunters and both are seasonally variable resources. Arctic foxes develop thick winter fur coats which begin to form in the autumn and reach full length around the beginning of December; this winter fur usually begins shedding by early spring (Bockstoce, 2018:18). Similarly, foxes lay down substantial stores of body fats seasonally that are greatest from late autumn throughout the winter season and do not start to become seriously depleted until early spring, triggered by the high-energy demands of reproduction (Audet *et al.*, 2002; West, 1997). Considering these seasonal changes alongside the dental cementum data, we argue that hunters most likely targeted the foxes in the first half of the interval indicated by the cementum data – the late winter period – before the onset of fur shedding and loss of critical fat supplies; an all-important priority in Upper Palaeolithic human diets (Pryor, 2008). Arctic fox hides are thin and warm, and have traditionally been used for baby clothes, undergarments, or trim for parkas (Bockstoce, 2018; Monchot & Gendron, 2011).

7.3 Fox trapping
At least 29 Arctic fox individuals have already been identified from Kraków Spadzista and further recently excavated materials are currently being analysed (Wojtal *et al.* in prep.). Given that a large portion of the site remains unexcavated, the total number of Arctic foxes killed at Kraków Spadzista is almost certainly higher than presently documented. This goes beyond simple, incidental hunting and suggests a more deliberate, organised procurement strategy. The strontium isotope data indicate that these foxes were not obtained by hunters targeting local dens and killing many foxes from the same family. Rather, hunters engaged in large-scale winter hunting of solitary Arctic foxes that were ranging widely across the landscape.

Hunting large numbers of foxes was most likely accomplished using trapping technology (West, 1997). The basic concepts of trapping are simple, yet ethnographic records and documentation relating to the 19th-20th century fur trade note that becoming a successful trapper requires "skill, study and endurance", building experience over a period of decades (Bockstoce, 2018:20-24). Hunters must have intimate knowledge of a landscape and fox behaviour within it to predict patterns of fox movement and select appropriate locations to place traps. Annual variations in fox abundance must be understood and accounted for. Bait must be carefully positioned to lure the fox. Trap design is also important, especially when the furs are to be used. Potential trapping methods include dead falls, simple snares and other leg-hold traps, as well as more sophisticated and complex designs (Bockstoce, 2018; Monchot & Gendron, 2011). If the foxes do not die immediately they will perish over a period of time from starvation and/or hypothermia. Prey killed during the winter season will probably be frozen when collected, and must be thawed out at campsite prior to processing (Bockstoce, 2018:31).

Organised trapping typically requires establishing a network of many traps that may be spread quite widely across a landscape. The traps must be checked at regular intervals to collect captured prey and re-set. Rodent faunas documented at cave sites in the Kraków-Częstochowa Upland and the Carpathian foothills north and south of Kraków Spadzista respectively indicate the availability of food for Arctic foxes in these hilly environments (Socha, 2014; Valde-Nowak, 1991). Food sources would also have been available across the Vistula river valley, and it is possible that foxes followed specific seasonal migration routes through these river valley corridors seeking game (West, 1997). Hunters at Kraków Spadzista may thus have trapped foxes throughout the Vistula valley landscape and neighbouring uplands, using the site as a base camp for ranging visits to maintain trapping lines and for processing hides.

An alternative possibility is that foxes were attracted directly to Kraków Spadzista by partially decayed carcasses of woolly mammoth. Today, foxes can be attracted in great numbers to a single whale carcass in the arctic, where they can be trapped easily (Audet *et al.*, 2002; Bockstoce, 2018:18). Rotting mammoth carcasses at Kraków Spadzista may have offered a similarly inviting food source and made it easier for hunters to kill large numbers of foxes without long treks to retrieve prey from traps scattered across the landscape. Evidence that Arctic foxes were attracted to Gravettian campsites in

Central Europe has previously been observed in the form of gnawed bones at Dolní Věstonice II (Wojtal *et al.*, 2018), and indirectly through carbon and nitrogen isotopic data measured on Arctic foxes killed at Předmostí. In the latter case, Arctic foxes killed at Předmostí regularly consumed mammoth meat as a core dietary component, while one individual was heavily reliant upon it (Bocherens *et al.* 2015). Arctic foxes could not have hunted large fauna such as mammoth themselves, meaning this dietary component must have been sourced by scavenging. Human kill-butchery sites would therefore have been attractive to Arctic fox living in the Central European mammoth steppe.

At Kraków Spadzista, carnivore gnaw marks are present on approximately 4% of the mammoth bones (Wilczyński *et al.*, 2012b). This evidence is still being assessed, but preliminary data shows that gnawed bones were found mostly in trench B+B1, while gnaw marks are located particularly on long bone diaphysis and epiphyses, and to a lesser extent on other elements including metapodials, tarsals and carpals. The shape and dimensions of the gnaw marks are consistent with those made by wolves (*Canis lupus*) or cave hyenas (*Crocuta crocuta*), but as cave hyenas went extinct several thousand years prior to the occupation of Kraków Spadzista (Stuart & lister, 2014) and no cave hyena remains have been discovered at the site, it can be assumed that the gnaw marks identified so far were made by wolves. Further investigation will determine whether Arctic foxes also left gnaw marks on the Kraków Spadzista remains.

7.4 Understanding prey behaviour and the context of hunting strategies in the Late Gravettian

Seasonal variations in resources have profound effects on hunter-gatherer societies and the choices they make (Binford, 1980; Bird & Bird, 2005), and prey mobility and predictability is an important example of this. Establishing patterns of prey mobility and season of capture, as we have done here, is therefore an effective proxy for reconstructing human subsistence strategies in a seasonally changing landscape, revealing the choices made by hunters as they planned ahead, strategized and scheduled visits to particular locations to target seasonally-available resources that varied in quality and abundance (Pike-Tay *et al.*, 2008).

Kraków Spadzista was one of the most northerly sites in central Europe during the Late Gravettian when much of the northern plains region had already been abandoned (Verpoorte, 2009). Bayesian modelling of radiocarbon dates indicates that Kraków Spadzista was occupied between 27.9 and 27.6 cal kya BP (Wilczyński *et al.*, 2020), only a few thousand years prior to the Fennoscandian ice sheet reaching its maximum extent in Poland at about 24.0 cal kya BP (Marks *et al.*, 2016). Mean annual temperature was between -1.0°C and +4.3°C, based on oxygen isotope analysis of woolly mammoth tooth enamel from the site (Pryor *et al.*, 2013). Further evidence for a cold and harsh climate on the north European Plains is provided by ice wedge casts and coleopteran remains (Jary, 2009; Kasse *et al.*, 1998).

The seasonality of death data demonstrates human presence at Kraków Spadzista during the coldest point of the seasonal cycle, refuting any possibility that the site formed as a result of northward migrations during summer followed by winter abandonment. No evidence for dwellings has been found, suggesting that hunters stayed for short visits and possibly used temporary shelters, such as tents, which left no archaeologically-recognisable signs (Wilczyński *et al.*, 2012b). It is still unclear whether human occupation related to the hunting of Arctic fox was contemporaneous to mammoth hunting, or whether the fox hunting was conducted 'independently' – perhaps carried out by small task groups that visited the site for that explicit purpose. In either case, the close physical association of cultural materials, including bones of mammoth and foxes, and stratigraphic data, suggest the site formed relatively quickly over a few years or decades but not hundreds or thousands of years (Wilczyński *et al.*, 2012b). This is consistent with the hypothesis that scavenging foxes may have been attracted to rotting mammoth carcasses, and suggests that fox hunting took place at a time when mammoth meat and fat resources were available to humans, either freshly hunted or as stored foods prepared earlier in the year. Arctic fox hunting at Kraków Spadzista should therefore be understood as part of an integrated economic strategy, contributing important fats, protein, hides, and potentially other raw materials such as bones and teeth for tools and personal ornaments respectively.

Reconstructing the seasonal mobility of the mammoth killed at Kraków Spadzista would help clarify when mammoth were present near the site, and therefore whether fox hunting could have occurred simultaneously with mammoth hunting, or necessarily reflects a separate, specific activity.

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Figure 1
Topographic map of southern Poland showing the location of Kraków Spadzista with respect to key landscape features including mountains, hills and river valleys.

Figure 2
Geological map of Poland and the Czech Republic at 1:1,000,000 (EGDI, accessed 1st March 2020), annotated with datapoints numbered 1-30 used to infer spatial variability in bioavailable strontium isotope ratios or otherwise mentioned in the text. Further information on the bioavailable strontium isotope data including references is given in Table A.1. The Fennoscandian icesheet is shown according to Ehlers *et al.* (2011), and loess cover according to Haase *et al.* (2007). A topographic map of area marked by a rectangle is shown in Figure 1.

Figure 3

Thin sections of dental cementum. Fast growth increments are marked with numbers, slow growth increments are marked with arrows. The section through KSF 6 was studied at the University of Exeter and shows a fox which died during deposition of the slow-growth increment. The section through KSF 8 was studied at the Institute of Geological Sciences in Kraków and shows a fox which died during deposition of the fast-growth increment.

Figure 4
Strontium isotope profiles and summary boxplots of the five investigated Arctic fox teeth. Profiles are based on a moving 10-point mean average of the individual laser ablation measurements. Dark grey shading around the lines indicates measurement error, calculated as the standard mean error. Strontium isotope ratio of the loess at Kraków Spadzista is indicated by the light grey shaded bar, based on measurements of dentine in the five investigated teeth. Arrows indicate periods of potential mobility in individuals KSF101 and KSF103.

Figure 5
Summary of strontium isotope data from the five investigated foxes alongside bioavailable strontium data listed by region (Table A.1; Figure 2).
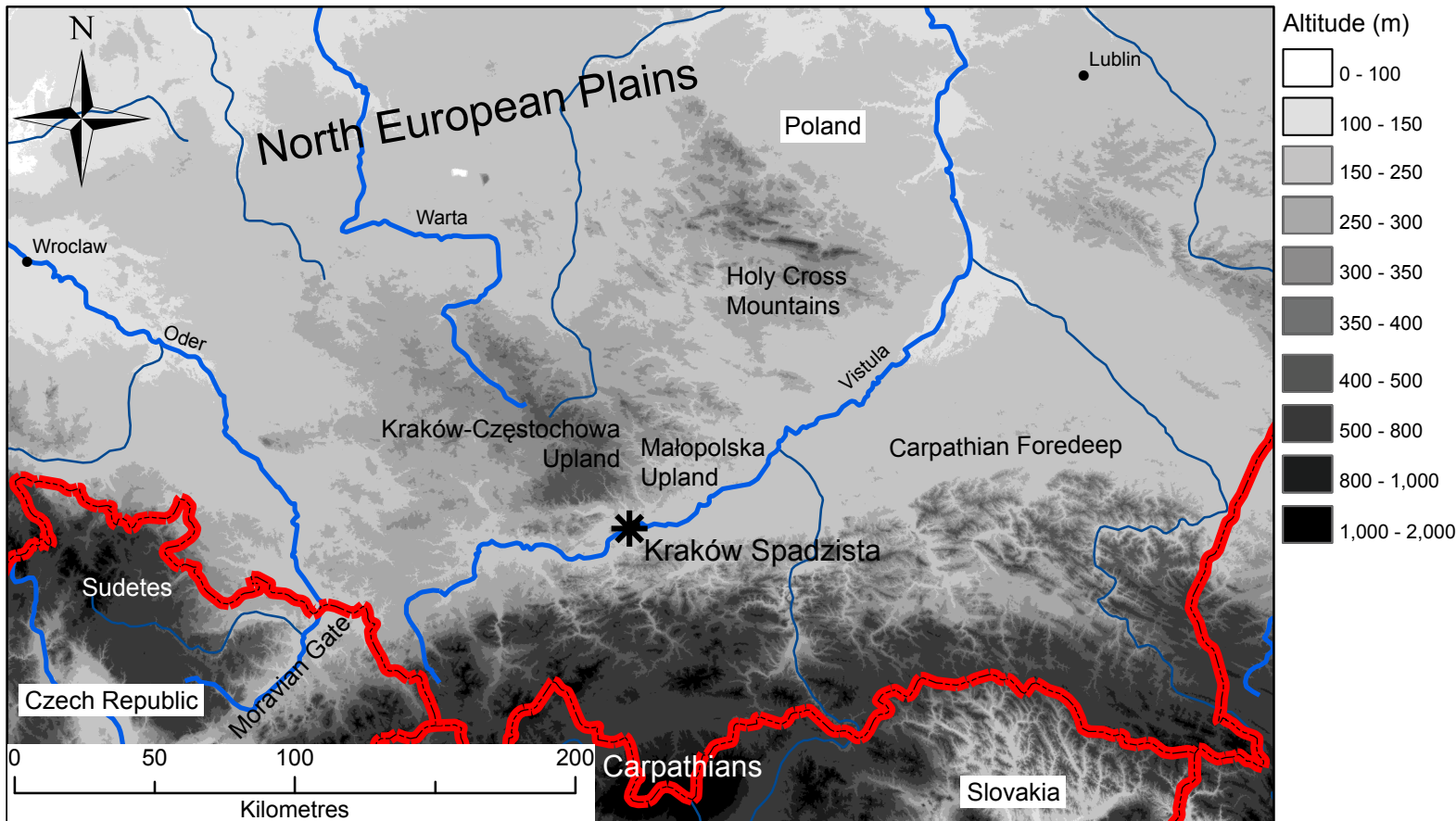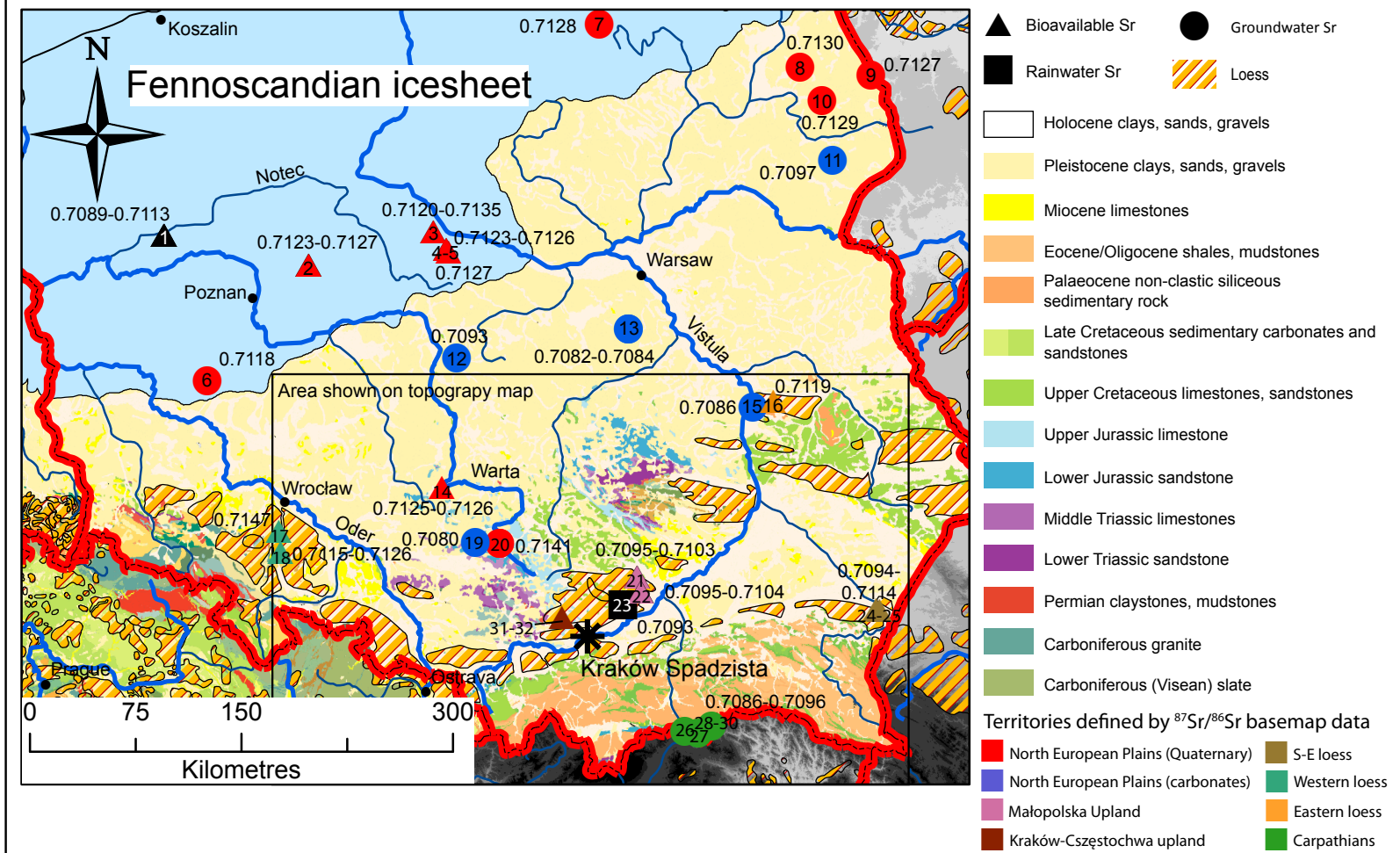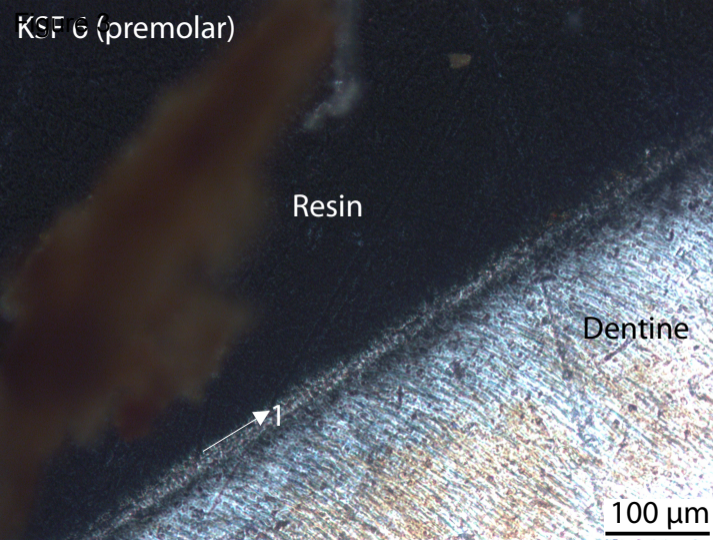
Figure 1

Figure 2

KSF 6 (premolar)

Resin

Dentine

1

100 µm

KSF 8 (premolar)

Resin

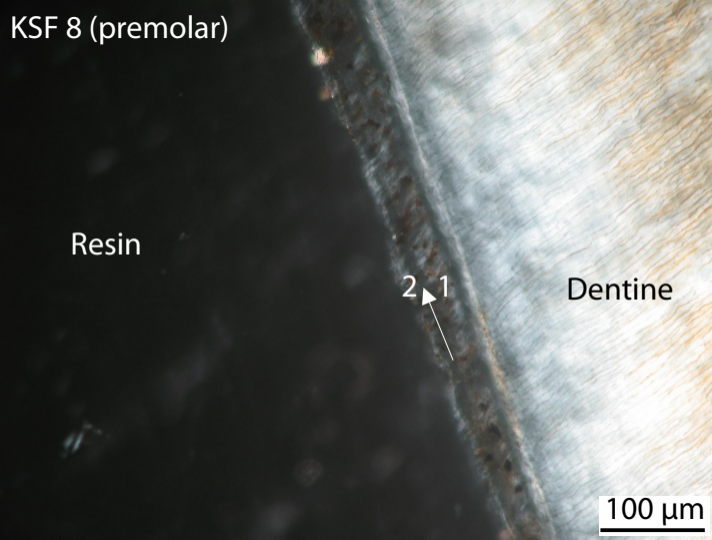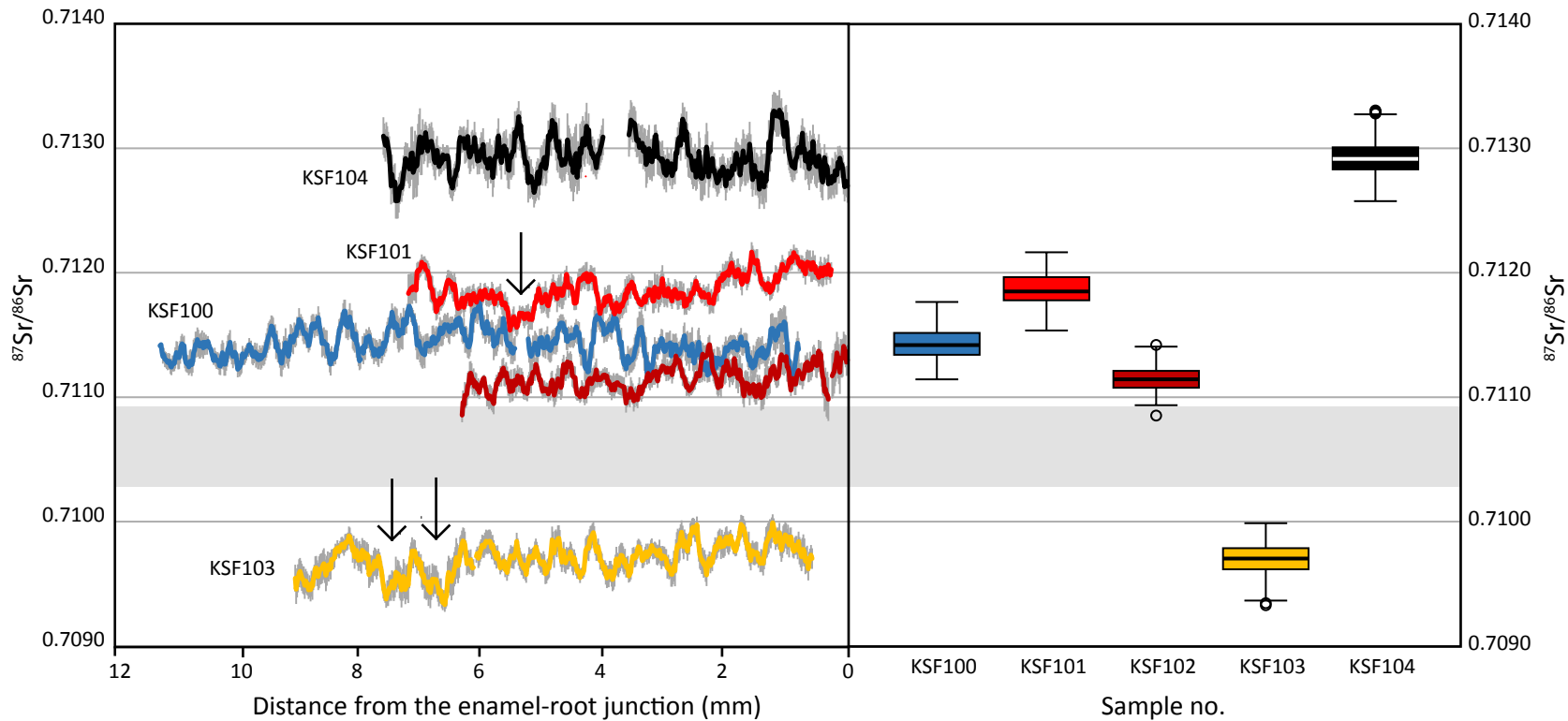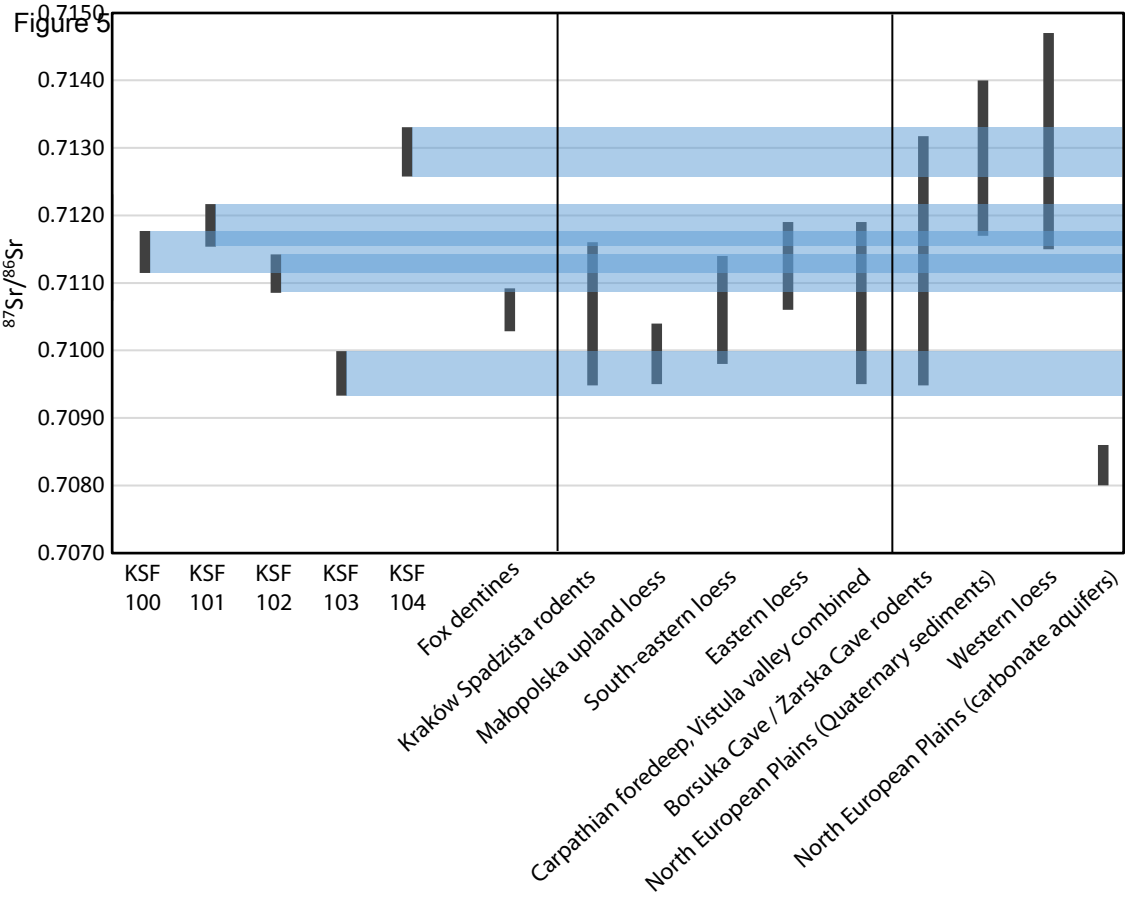Dentine

2 1

100 µm

Figure 4

Figure 5

1   Table 1: Dental cementum results.
2   * - L = Longitudinal section; CS = cross section
3

Individual	Field catalogue number	Element	Loose tooth or from a jaw?	Sections studied in Exeter (n)	Sections studied in Kraków (n)	Section orientation *	Cementum condition	Annual cementum bands (n)	Final cementum band	Season of death	Sr analysis	Sr element
27	B3 197M	canine	Loose tooth	-	-						KSF104	Canine
1	F4 3278	premolar	Loose tooth	1	2	L / CS	Recrystallised	-		Indeterminate		
2	F4 2894	premolar	Loose tooth	1	2	L / CS	Recrystallised	-		Indeterminate		
4	E1 4033	premolar	Loose tooth	2	3	L / CS	Recrystallised	-		Indeterminate		
3	F2 3231	premolar	Loose tooth	2	3	L / CS	Weathered	1	Slow growth increment just started	Winter		
5	E3 450	premolar	Loose tooth	3	1	CS	Weathered	2	Slow growth increment	Late winter-early spring		
6	F3 4361	premolar	Mandible	1	1	L	Weathered	1	Slow growth increment	Late winter-early spring	KSF101	M1
6	F3 4361	canine	Mandible		1		None present			--		
7	F1 4241	premolar	Mandible	1	2	L / CS	Weathered	1 or 2	Slow growth increment just started	Winter	KSF102	Premolar
7	F1 4241	canine	Mandible		1		Recrystallised			Indeterminate		
8	E1 4297	premolar	Mandible	2	2	L / CS	Weathered	2	Fast growth increment	mid summer-mid winter	KSF103	Canine
8	E1 4297	canine	Mandible		1		Recrystallised			Indeterminate		
9	E3 581	premolar	Mandible	1	2	L / CS	Weathered	2	Slow growth increment	Late winter-early spring	KSF100	Canine
9	E3 581	canine	Mandible		1		Recrystallised			Indeterminate		
10	F4 3278	canine	Loose tooth		1		Weathered	2	Slow growth increment	Late winter-early spring		
11	F3 3538	canine	Loose tooth		1		Weathered	2	Slow growth increment	Late winter-early spring		
12	F1 3841	canine	Loose tooth		1		Weathered	2	Slow growth increment	Late winter-early spring		
13	F2 3231	canine	Loose tooth		1		Weathered	4?	Slow growth increment	Late winter-early spring		
14	A2 454	canine	Loose tooth		1		Weathered	2	Slow growth increment	Late winter-early spring		
17	C2 2949	canine	Loose tooth		1		Weathered	1	Fast growth increment	mid summer-mid winter		
15	F3 3538	canine	Loose tooth		1		Recrystallised			Indeterminate		
16	F2 3231	canine	Loose tooth		1		Recrystallised			Indeterminate		

18	F3 3538	canine	Loose tooth	1	Recrystallised	Indeterminate
19	F2 3231	canine	Loose tooth	1	Recrystallised	Indeterminate
20	F4 3278	canine	Loose tooth	1	Recrystallised	Indeterminate
21	F2 3833	canine	Loose tooth	1	Recrystallised	Indeterminate
25	E4 407	canine	Loose tooth	1	None present	--

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13   Table 2: Strontium isotope results.
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| Sample | Enamel | | | | | | | Dentine |
	Mean	Median	Std. Deviation	Minimum	Maximum	Range	Interquartile Range	Median
KSF100	0.71143	0.71142	0.00012	0.71115	0.71177	0.00062	0.00018	0.71053
KSF101	0.71187	0.71185	0.00012	0.71154	0.71217	0.00063	0.00019	0.71040
KSF102	0.71115	0.71115	0.00010	0.71086	0.71142	0.00057	0.00014	0.71065
KSF103	0.70970	0.70971	0.00012	0.70933	0.70999	0.00066	0.00017	0.71089
KSF104	0.71293	0.71292	0.00014	0.71258	0.71331	0.00073	0.00018	0.71060

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18   Table A.1: Strontium isotope basemap data shown in Figure 2.

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Map No.	Site	Sr value	Material	Region	Reference
1	Drawsko 1	0.71130-0.71133	Mouse bones	Drawsko	Gregoricka et al 2014
1	Drawsko 1	0.70974	Fox bone	Drawsko	Gregoricka et al 2014
1	Drawsko 1	0.70885-0.70984	Hare bones	Drawsko	Gregoricka et al 2014
2	Kopydlowo	0.71232-0.71274	Bones (unident)	North European Plains	Marciniak et al 2017
3	Bodzia	0.7120-0.7135	Human tooth enamel and bones	North European Plains	Buko et al 2013
3	Bodzia	0.7131	Red deer long bone	North European Plains	Pospieszny et al 2015
4	Kruszyn	0.7123-0.7126	Pig enamel and bone	North European Plains	Buko et al 2013
5	Ludwinowo	0.7127	Roe deer long bone	North European Plains	Pospieszny et al 2015
6	6	0.71175	Groundwater	North European Plains	Voerkelius et al 2010
7	7	0.712794	Groundwater	North European Plains	Voerkelius et al 2010
8	8	0.712971	Groundwater	North European Plains	Voerkelius et al 2010
9	9	0.71269	Groundwater	North European Plains	Voerkelius et al 2010
10	10	0.712882	Groundwater	North European Plains	Voerkelius et al 2010
11	11	0.709665	Groundwater		Voerkelius et al 2010
12	Poddebice	0.709120-0.709575	Groundwater (sub-surface) (fertiliser contamintation)		Grabowski et al 2015
12	Poddebice	0.708877-0.710344	Ner River water (surface water) (fertiliser contamination)		Grabowski et al 2015
13	13	0.708162-0.708383	Groundwater	North Plains (carbonate aquifers)	Voerkelius et al 2010
14	Załęcze Landscape Reserve	0.712534 -0.712614	Birch and oak leaves	North European Plains	Zielinski et al 2017
15	15	0.70859	Groundwater	North Plains (carbonate aquifers)	Voerkelius et al 2010
16	Klementowice	0.711926	Tooth dentine	Eastern loess	Pryor et al 2016
17	Szczepankowice, Wroclaw	0.7147	Rodent bone	Western loess	Pokutta and Frei 2011
18	Karczyn	0.7115-0.7126	Animal bone and tooth enamel	Western loess	Pospieszny and Belka 2015
19	19	0.70801	Groundwater	North Plains (carbonate aquifers)	Voerkelius et al 2010
20	Korwinow	0.714149	Groundwater	North European Plains	Zielinski et al 2017

21	Malżyce, site 30	0.70954-0.71028	Human tooth enamel	Loess Małopolska upland	Szczepanek et al 2018
22	Gabułtow, site 1	0.70956-0.71039	Human tooth enamel	Loess Małopolska upland	Szczepanek et al 2018
23	Odonow	0.70929	Rainwater		Szczepanek et al 2018
24	Neolithic site cluster	0.7104-0.7114	Neolithic human tooth enamel and fauna	South-eastern loess	Szczepanek et al 2018
25	Święte	0.7094-0.7109	Neolithic human tooth enamel	South-eastern loess	Belka et al 2018
26	26	0.70964	Groundwater	Carpathians	Voerkelius et al 2010
27	27	0.70876	Groundwater	Carpathians	Voerkelius et al 2010
28	28	0.708919	Groundwater	Carpathians	Voerkelius et al 2010
29	29	0.708592	Groundwater	Carpathians	Voerkelius et al 2010
30	30	0.70898	Groundwater	Carpathians	Voerkelius et al 2010
31	Borsuka Cave (rodents)	0.70948-0.71317	Rodent tooth enamel		Kowalik et al. 2020
31	Borsuka Cave (loess leechates)	0.71157-0.71166	Loess leechates		Kowalik et al. 2020
32	Żarska Cave	0.71124-0.71249	Rodent tooth enamel		Kowalik et al. 2020

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Author statement

Declarations of interest: none'.