

1 Collagen stable isotopes provide insights into the end of the mammoth steppe in the central East
2 European plains during the Epigravettian

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17

18 **Abstract**

19 Higher $\delta^{15}\text{N}$ values in bone collagen of mammoth (*Mammuthus primigenius*) compared with coeval
20 large herbivores is a classic trait of the mammoth steppe. An exception applies to the Epigravettian
21 site of Mezhyrich (ca. 18-17.4 ka cal BP) in the central East European plains, where mammoth
22 bones have $\delta^{15}\text{N}$ values equivalent to or in a lower range than those of horse specimens (*Equus* sp.).
23 We expanded our preliminary dataset to a larger sampling size of mammoth, other large herbivores
24 and carnivores from contemporaneous and nearby sites of Buzhanka 2, Eliseevichi and Yudinovo.
25 The unusual low mammoth $\delta^{15}\text{N}$ values were confirmed at Buzhanka 2 and for some specimens
26 from Eliseevichi, while most individuals from Yudinovo displayed the expected high $\delta^{15}\text{N}$ values,

27 meaning similar to those of the large canids. The possibility of a contrast in migration pattern is not
28 supported since the $\delta^{34}\text{S}$ values, a marker of mobility, do not correlate with the $\delta^{15}\text{N}$ values of
29 mammoth bone collagen. No clear chronological tendency could be revealed, at least not at the
30 scale of radiocarbon dating. The low range in $\delta^{15}\text{N}$ values is likely to reflect a change in the specific
31 niche of the mammoth in the southern part of its distribution.

32

33 **Keywords:** bone collagen, carbon-13, Central Europe, Epigravettian, mammoth, nitrogen-15,
34 sulphur-34

35

36 **Introduction**

37 The central East European plains are famous for their Epigravettian sites that date to around 15-12
38 ^{14}C ka BP (ca. 18.2-13.8 cal ka BP) and display impressive large structures made from the bones of
39 woolly mammoth (*Mammuthus primigenius*) (e.g. Gladkih et al., 1984; Soffer, 1985; Hoffecker,
40 2002). The origin of the large accumulations of mammoth remains is still a matter of debate, with
41 the main hypotheses being the collection of natural occurrences *versus* active hunting (e.g. Soffer,
42 1985; Haynes 1989; Svoboda et al., 2005). In favour of this second scenario, studies of the
43 mammoth remains of Yudinovo (Germonpré et al., 2008) concluded that the mammoths were
44 hunted and, at Mezhyrich, mammoths were obtained by combined procurement via collection of
45 carcasses and active hunting (Péan, 2015). Hunting practices were observed in older sites of the
46 Gravettian culture in the Dnieper and Desna valleys (Demay et al., 2016).

47 Between ca. 22 and 12 ^{14}C ka BP (ca. 26.2-13.8 ka cal BP), the Dnieper and Desna basins
48 correspond to the southern part of the geographical distribution of the woolly mammoth (Markova
49 et al., 2013; Kahlke, 2014). Over time their distribution shifted northwards, while the density of the
50 mammoth population decreased (Markova et al., 2013). According to Markova et al. (2013), the
51 combined effect of gradual warming and growing human pressure is most likely to have had a

52 negative impact on the mammoths, resulting in their local extinction in the Russian and Ukrainian
53 plains around 14-12 ¹⁴C ka BP (ca. 17.0-13.8 ka cal BP) (Stuart et al., 2005).

54 Through investigating the diet and habitat of mammoth specimens collected by Epigravettian
55 human groups, it may be possible to detect signals of ecological stress. For decades stable isotopes
56 have been applied as ecological trackers of animal species typical of the Upper Palaeolithic
57 ecosystem (review in Bocherens, 2015). Studies considering carbon and nitrogen stable isotopes
58 ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in bone collagen have revealed a typical isotopic pattern reflecting niche
59 partitioning among the herbivore and carnivore species of the so-called “mammoth steppe”.

60 Typically, horse and mammoth were among the most ¹³C depleted of the herbivore species of the
61 mammoth steppe ecosystems with a typically enriched ¹⁵N signature for the mammoth. The
62 enrichment on average collagen $\delta^{15}\text{N}$ values of the woolly mammoth compared with those of horse
63 and reindeer ranges from ca. +3 to +6 ‰, which places the mammoth in a similar range as a
64 carnivore such as the wolf (e.g. Bocherens et al., 1994; Iacumin et al., 2000; Fox-Dobbs et al.,
65 2008; Szpak et al., 2010). The cause of the ¹⁵N enrichment in mammoth collagen has been debated,
66 with physiological adaptation to aridity and niche specificity being postulated (Bocherens et al.,
67 1994; Bocherens, 2003). The first of these hypotheses can be reasonably ruled out because 1) the
68 effect of aridity has been demonstrated to impact directly on plants rather than animals, and should
69 thus affect all the herbivores (e.g. Murphy et al., 2006; Hartman et al., 2011), 2) modern elephant,
70 rhinoceros and zebra fed with the same food in term of isotopic signature display the same
71 enrichment (Kuitens et al., 2015), 3) the trophic position of the mammoth calculated from the $\delta^{15}\text{N}$
72 values of glutamic acid (Glu) and phenylalanine (Phe) amino acids is equivalent to that of other
73 herbivores (TP=2) (Schwartz-Narbonne et al., 2015; Naito et al., 2016b). Hence, dietary
74 specialization, such as the consumption of mature grasses in disturbed areas (Bocherens, 2003),
75 explains the specific isotopic position of the mammoth. As a result, a degradation of the habitat,
76 when the species has no possibility to shift its distribution, should lead to a change in its isotopic
77 signature.

78 The results of the isotopic analyses of the mammoths from Mezhyrich seem to confirm a scenario
79 of a population subject to environmental stress and thus being especially vulnerable to human
80 predation (Drucker et al., 2014). Indeed, these specimens have unusually low $\delta^{15}\text{N}$ values making
81 them equivalent to or even lower in range of values than the associated horses. A change in the
82 environment may have led to the loss of the ecological niche specific to the mammoth and thus, to
83 the possible direct competition for forage between mammoths and horses. Interestingly, data
84 published by Iacumin et al. (2000) for the contemporaneous sites of Yudinovo and Eliseevichi,
85 about 400 km north of Mezhyrich, yielded $\delta^{15}\text{N}$ values on average higher than at Mezhyrich.
86 However, the lack of comparable data on other animal species did not allow us to evaluate if the
87 higher ^{15}N content of the mammoth of Yudinovo and some of Eliseevichi specimens corresponds to
88 those expected from a “classic” mammoth steppe isotopic pattern.

89 In this paper, we undertook a more complete analysis of samples from Yudinovo and Eliseevichi,
90 including specimens from herbivore species other than mammoth and carnivores. Unpublished data
91 from Buzhanka 2, that delivered a lithic industry comparable to that from the site of Mezhyrich,
92 were also added. We aim to determine the extent to which the isotopic position and thus ecological
93 niche of the mammoth specimens has shifted at Yudinovo and Eliseevichi, and how this compares
94 to the results from Mezhyrich. In addition to difference in diet, possible contrasts in mobility of the
95 mammoths found in the mentioned sites is addressed by using bone collagen sulphur isotopes ($\delta^{34}\text{S}$)
96 to explore how some individuals may have been able to maintain access to their specific niche.

97

98 **Material and methods**

99 The Epigravettian Yudinovo site is located on the right bank of the Sudost' River, a
100 tributary of the Desna (Fig. 1). Here several mammoth-bone complexes were discovered. In
101 addition to the numerous mammoth bones, the site yielded huge quantities of ivory hunting tools
102 and ivory ornaments. Several production areas were revealed: for flint processing, ivory processing,
103 and polar-fox skinning and butchering (Khlopachev, 2006; Khlopachev et al., 2006). The faunal

104 assemblage is dominated by remains from arctic fox (*Alopex lagopus*) and mammoth. The
105 Yudinovo mammoths were hunted to obtain large quantities of bones, meat, fat, organs, and brain
106 (Germonpré et al., 2008). The skeletal remains of the adult mammoths were used to build the
107 complexes (Soffer, 1985; Germonpré et al., 2008, Germonpré and Sablin, 2017). A recent ancient
108 DNA study produced new radiocarbon dates obtained on mammoth teeth from the site
109 (Palkopoulou et al., 2013: Table 1).

110 The Epigravettian Eliseevichi site is located on the right bank of the Sudost' River about 65 km
111 northeast of Yudinovo (Fig. 1). The site is characterised by a specific lithic industry including
112 backed microliths and portable art. Remains of several pits with mammoth skulls and large
113 quantities of worked ivory were discovered here. The faunal assemblage is dominated by remains of
114 arctic fox, mammoth and large canids (Demay et al., 2017). Eliseevichi is also famous for the
115 discovery of two complete skulls of Palaeolithic dogs (Sablin and Khlopachev, 2002, 2003).
116 Radiocarbon dates on mammoth correspond to the Epigravettian period (Table 1).

117 The site of Mezhyrich is located 15 km west of the Dnieper River in Central Ukraine (Fig. 1). This
118 Epigravettian site provided four mammoth bone dwelling structures surrounded by several large
119 pits (e.g. Kornietz et al., 1981; Soffer et al., 1997; Pidoplichko, 1998; Péan, 2015). The site has
120 yielded more than 15,000 artefacts, attributed to the Epigravettian, made of flint, bone, mammoth
121 ivory and antler: tools, weapons, portable art and body ornaments. Ongoing field works have aimed
122 to determine the function of the pits and activity areas in relation to the bone dwelling structures
123 nos. 1, 2 and 4 (Nuzhnyi, 2002, 2008; Péan et al., 2015, Shydlovskiy et al., 2015). Mammoth is the
124 most represented species through the remains of a minimum of 149 individuals, associated with
125 hares (*Lepus* sp.) and carnivores (wolf, fox, bear...) and other herbivores (mainly reindeer, bison
126 and horse) (Kornietz et al., 1981; Soffer, 1985). A recent study of the site of Mezhyrich, that
127 included a detailed examination of the faunal remains of pit 7 related to dwelling 1, concluded to
128 that mammoth was used as a food resource in addition to provide raw and fuel material (Péan,

129 2017). AMS dating on mammoth and carnivores suggest three settlement phases during the
130 Epigravettian period (Table 1; Haesaerts et al., 2015).

131 The site of Buzhanka 2 is an Epigravettian site discovered in 2003 on the right bank of the Middle
132 Desna valley (Fig. 1). The archaeological excavation in 2003 and 2006 under the direction of D.
133 Stupak revealed three archaeological layers in loessic sediments, notably a pit filled with mammoth
134 tusks, mandibles and ribs, and many lithic artefacts (Stupak, 2005; Stupak, 2014). The tool industry
135 presents a striking similarity with the one found at Mezhyrich (Stupak, 2014). Beside mammoth
136 remains, large canid (cf wolf), fox (*Alopex lagopus/Vulpes vulpes*), bear (*Ursus* sp.) and reindeer
137 (*Rangifer tarandus*) were identified. Two AMS dating results confirmed the Epigravettian
138 attribution based on the tool industry (Table 1).

139 We compiled previously published carbon and nitrogen stable isotope data of mammoth and
140 associated fauna from Mezhyrich (Iacumin et al., 2000; Drucker et al., 2014), and of mammoth
141 from Yudinovo and Eliseevichi (Iacumin et al., 2000). We expanded the data set with 18 new
142 specimens, including mammoth (n=1) and large canid (n=1) from Buzhanka 2, large canids (*Canis*
143 sp.) and arctic fox (*Alopex lagopus*) from Eliseevichi (n=3), and mammoth (n=6) with associated
144 herbivores (n=2), namely reindeer (*Rangifer tarandus*) and muskox (*Ovibos moschatus*), carnivores
145 (n=5), namely large canid, arctic fox and brown bear (*Ursus arctos*), from Yudinovo. We measured
146 $\delta^{34}\text{S}$ when the quantity of collagen left after the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses allowed (n=35).

147 The collagen was purified in the Department of Geosciences at the University of Tübingen for the
148 samples of Buzhanka 2 (Bocherens et al., 1997) and at the University of Oxford for the Yudinovo
149 and Eliseevichi samples (Stevens and Hedges, 2004). In both cases, the extraction procedure is
150 based on an acid-base-acid method inspired from Longin (1971), which includes a first step of
151 demineralization with HCl (1M in Tübingen, 0.5M in Oxford), a second step in NaOH to remove
152 humic acids and lipids (0.125M in Tübingen), and a final step of gelatinization at a low pH (2 in
153 Tübingen, 3 in Oxford) several hours at high temperature (17h at 100°C in Tübingen, 48h at 75°C
154 in Oxford).

155 The elemental and isotopic measurements were performed at the Geochemical unit of the
156 Department of Geosciences at the University of Tübingen (Germany), using an elemental analyser
157 NC 2500 connected to a Thermo Quest Delta+XL mass spectrometer. Only $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses
158 on the new Eliseevichi and Yudinovo samples were conducted at the Research Laboratory for
159 Archaeology and the History of Art at the University of Oxford. The $\delta^{34}\text{S}$ analyses of the extracted
160 collagen of these specimens were carried out at the University of Tübingen. Samples analysed at
161 Oxford were processed using a Carlo Erba elemental analyser coupled to a PDZ Europa Geo 20/20
162 mass spectrometer.

163 The elemental ratios C:N, C:S and N:S were calculated as atomic ratios. The isotopic ratios are
164 expressed using the “ δ ” (delta) value as follows: $\delta^{13}\text{C} = [({}^{13}\text{C}/{}^{12}\text{C})_{\text{sample}}/({}^{13}\text{C}/{}^{12}\text{C})_{\text{reference}} - 1] \times 1000$
165 ‰ , $\delta^{15}\text{N} = [({}^{15}\text{N}/{}^{14}\text{N})_{\text{sample}}/({}^{15}\text{N}/{}^{14}\text{N})_{\text{reference}} - 1] \times 1000 \text{ ‰}$, and $\delta^{34}\text{S} = [({}^{34}\text{S}/{}^{32}\text{S})_{\text{sample}}/({}^{34}\text{S}/{}^{32}\text{S})_{\text{reference}}$
166 $- 1] \times 1000 \text{ ‰}$. The international references are V-PDB for $\delta^{13}\text{C}$ values, atmospheric nitrogen
167 (AIR) for $\delta^{15}\text{N}$ values, and CDT for $\delta^{34}\text{S}$ values. At Oxford, measurements were made relative to
168 in-house reference standards Nylon (Nylon 66, BDH, UK) and Alanine (L-Alanine, Fluka, UK),
169 whose isotopic ratios are calibrated against IAEA standards. At Tübingen, measurements were
170 normalized to $\delta^{13}\text{C}$ values of USGS24 ($\delta^{13}\text{C} = -16.00 \text{ ‰}$) and to $\delta^{15}\text{N}$ values of IAEA 305A ($\delta^{15}\text{N}$
171 $= +39.80 \text{ ‰}$). The reproducibility was $\pm 0.1 \text{ ‰}$ for $\delta^{13}\text{C}$ measurements and $\pm 0.2 \text{ ‰}$ for $\delta^{15}\text{N}$
172 measurements, based on one standard-deviation of the mean of multiple analyses of purified
173 collagen from modern bones and international standards (Tübingen) and in-house standards
174 (Oxford).

175 Samples were calibrated to $\delta^{34}\text{S}$ values relative to CDT of NBS 123 ($\delta^{34}\text{S} = +17.10 \text{ ‰}$), NBS 127
176 ($\delta^{34}\text{S} = +20.31 \text{ ‰}$), IAEA-S-1 ($\delta^{34}\text{S} = -0.30 \text{ ‰}$) and IAEA-S-3 ($\delta^{34}\text{S} = +21.70 \text{ ‰}$). The
177 reproducibility is $\pm 0.4 \text{ ‰}$ for $\delta^{34}\text{S}$ measurements, and the error on amount of S measurement is 5 %.
178 Reliability of the collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values can be established by measuring the chemical
179 composition of collagen, with C:N ranging from 2.9 to 3.6 (DeNiro, 1985), percentage of C and N
180 above 8% and 3%, respectively (Ambrose, 1990). We retained $\delta^{34}\text{S}$ values of samples for which the

181 atomic C:S and N:S in collagen were included in the range of 300-900 and 100-300, respectively
182 (Nehlich and Richard, 2009).

183

184 **Results and discussion**

185 **Tracking diet and habitat using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$**

186 Based on the compiled data from Iacumin et al. (2000) and Drucker et al. (2014), the mammoth of
187 Mezhyrich displayed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values spanning from -20.6 to -19.7 ‰ and $+2.9$ to $+5.3$ ‰,
188 respectively (Fig. 2). The isotopic values of horse (-19.9 ‰ for $\delta^{13}\text{C}$, $+4.6$ and $+4.9$ ‰ for $\delta^{15}\text{N}$)
189 overlap with the highest values provided by the mammoth. Such a pattern is very unusual for the
190 mammoth steppe ecosystem where typically mammoth $\delta^{15}\text{N}$ values are systematically higher than
191 those of associated ungulates, such as horse, reindeer and large bovids (see review in Bocherens,
192 2015). The classic isotopic pattern of the mammoth steppe implies comparable $\delta^{15}\text{N}$ values between
193 mammoth and large predators (e.g. Bocherens et al., 1994, 1996, 1997, 2011, 2015; Fox-Dobbs et
194 al., 2008; Bocherens, 2015). At Mezhyrich, large canids showed higher $\delta^{15}\text{N}$ values ($+5.9$ to $+8.4$
195 ‰) than both horse and mammoth, and higher $\delta^{13}\text{C}$ values (-19.3 to -18.7 ‰), which are consistent
196 with carnivore's trophic enrichment. Interestingly, the fox analysed at Mezhyrich showed lower
197 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values compared with the large canids (Fig. 2). This indicates that they are likely to
198 have consumed small mammals such as hare, which have low $\delta^{15}\text{N}$ values (Mezhyrich hare: -21.0
199 and -19.7 ‰ for $\delta^{13}\text{C}$, $+1.6$ and $+2.0$ ‰ for $\delta^{15}\text{N}$), which is consistent with other contexts where
200 small game were targeted by small canids (e.g. Drucker et al., 2017). Two additional data from
201 Buzhanka 2 from one mammoth ($\delta^{13}\text{C} = -20.6$ ‰, $\delta^{15}\text{N} = +5.2$ ‰) and one large canid ($\delta^{13}\text{C} = -$
202 18.7 ‰, $\delta^{15}\text{N} = +7.8$ ‰) were consistent with the results obtained at Mezhyrich.

203 The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the Yudinovo mammoths varied from -20.8 to -19.5 ‰ and from $+5.0$
204 to $+8.9$ ‰, respectively (Fig. 3). The range of $\delta^{13}\text{C}$ (-20.6 to -20.1 ‰) and $\delta^{15}\text{N}$ ($+4.8$ to $+6.7$ ‰)
205 values of the Eliseevichi mammoths overlapped with the isotopic range of the Yudinovo

206 mammoths, however this is mainly due to one individual from Yudinovo with significantly lower
207 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than its counterparts from the same site. But even the lowest Yudinovo
208 mammoth $\delta^{15}\text{N}$ value (+5.0 ‰) was clearly higher than the reindeer and muskox $\delta^{15}\text{N}$ values
209 obtained from this site (+3.3 and +2.9 ‰ respectively). Both reindeer and muskox provided the
210 highest $\delta^{13}\text{C}$ values of the large herbivores (−19.0 and −18.9 ‰ respectively). Similar results are
211 reported from late Pleistocene sites in Belgium (Germonpré et al., 2009) and the Czech Republic
212 (Bocherens et al., 2015) and were attributed to a high consumption of lichen, as still observed
213 nowadays for reindeer (e.g. Drucker et al., 2010).

214 In comparison with the mammoth, the Yudinovo and Eliseevichi canids had higher $\delta^{13}\text{C}$ values
215 (large canid: −19.2 and −18.8 ‰, fox: −19.9 to −18.8 ‰) but equivalent $\delta^{15}\text{N}$ values (large canid:
216 +8.1 and +9.2 ‰, fox: +4.9 to +6.3 ‰) (Fig. 3). This corresponds again to the expected “mammoth
217 steppe” configuration since mammoth has been the only herbivore species of the late Pleistocene
218 found to have $\delta^{15}\text{N}$ values as high as associated carnivores (review in Bocherens, 2015). Two
219 brown bear specimens, one from Yudinovo and the other from Eliseevichi, showed relatively high
220 $\delta^{13}\text{C}$ (−19.1 and −19.8 ‰, respectively) and $\delta^{15}\text{N}$ (+6.6 and +6.9 ‰, respectively) values that were
221 consistent with a meat-dominated diet (Bocherens, 2015). In northwest Europe, carnivorous diets
222 are a common feature before the Last Glacial Maximum, while vegetarian diets are more dominant
223 in late Pleniglacial brown bears (Bocherens et al., 2011; Münzel et al., 2011; Bocherens, 2015).

224 When considering mammoth, large canids and fox from the different sites, a huge range of $\delta^{15}\text{N}$
225 values appears for the proboscideans with an apparent correlation to the site of origin (Fig. 4). On
226 average, the highest values are found at Yudinovo, while the lowest correspond to Mezhyrich, with
227 intermediate values observed at Eliseevichi. A cluster analysis reveals two distinct groups among
228 the mammoth samples based on $\delta^{15}\text{N}$ values: one is composed of most of Yudinovo samples and
229 two specimens from Eliseevichi with values higher than 6 ‰, and another is composed of all the
230 specimens from Mezhyrich and Buzhanka 2 and those from Eliseevichi and Yudinovo with values
231 lower than 6 ‰ (Fig. 5). Since this second group is in the same range as the ungulates (horse,

232 reindeer and muskox) analysed so far for the same sites, we can conclude that it corresponds to
233 individuals that shifted from their usual ecological niche rather than a general shift in the $\delta^{15}\text{N}$
234 baseline, as was the case for the Magdalenian site of Kesslerloch in Switzerland (Bocherens et al.,
235 2011).

236 The canids exhibit among the highest $\delta^{15}\text{N}$ values, with the exception of one individual from
237 Mezhyrich whose $\delta^{15}\text{N}$ value is particularly low at +5.9 ‰, in a similar range to the foxes that tend
238 to show lower values than the large canids (Fig. 4). Interestingly, the group of large canids shows
239 $\delta^{15}\text{N}$ values consistent with those of the high $\delta^{15}\text{N}$ mammoth group, as observed previously in
240 classic mammoth steppe of the late Pleistocene in eastern Beringia (e.g. Fox-Dobbs et al., 2008).

241 We thus conclude that the low $\delta^{15}\text{N}$ mammoth group represents an unusual case.

242 If the most likely hypothesis to explain the low mammoth $\delta^{15}\text{N}$ is a drastic change in their usual diet
243 and habitat, the loss of their typical niche could be related to a geographical and/or chronological
244 change in environment. This change of diet compared to the usual one of mammoths is not a short-
245 term event before the death of the individuals but it rather reflects years of change, since bone
246 collagen remodelling takes years if not decades, especially in adult proboscideans (e.g. Merwe et
247 al., 1988; Sukumar and Ramesh, 1992; Kilgallon et al., 2008). Chronological variation is difficult to
248 assess because, although some of the studied specimens are directly dated, the precision of
249 radiocarbon measurements is not high enough to allow a fine correlation with global climatic events
250 recorded through the NGRIP curve. Except for the slightly more recent mammoth specimen of
251 Buzhanka 2 (Fig. 6a), the calibration of the few radiocarbon dates of the mammoth specimens of
252 this study does not reveal any clear diachronic pattern. As a matter of fact, after recombination of
253 the several dates on the same bone for Mezhyrich, the posterior probability distribution produced by
254 a Bayesian model using OxCal 4.2.4 (Bronk Ramsey, 2001, 2009a, b) shows a possible
255 contemporaneity amongst the dated mammoth specimens (Fig. 6b). Given that the time range of the
256 faunal accumulation is the same at the ^{14}C scale between the different sites, geographical
257 differences could explain the $\delta^{15}\text{N}$ contrast as the result of the different territories roamed by

258 mammoth and/or exploited by human through either collection or hunting. We have thus
259 investigated the $\delta^{34}\text{S}$ values of bone collagen that can be used as a tracker of mobility in the context
260 of continental terrestrial-based diets, where the $\delta^{34}\text{S}$ in plants consumed by animals should be
261 primarily controlled by the geochemical composition of the underlying bedrock (e.g. Richards et al.,
262 2001; Jay et al., 2013; Drucker et al., 2015).

263

264 **Tracking mobility using $\delta^{34}\text{S}$**

265 The $\delta^{34}\text{S}$ values of the Mezhyrich and Buzhanka 2 mammoth clustered between -4.0 and $+2.9$ ‰ and
266 encompassed the two values of the hare from Mezhyrich (-3.5 and -1.8 ‰) and those of the
267 mammoth from Yudinovo (-3.5 and -2.0 ‰) (Fig. 7). The horse from Mezhyrich and Yudinovo
268 reindeer and muskox covered a range of higher $\delta^{34}\text{S}$ values ($+0.7$ to $+1.3$ ‰). No obvious
269 correlation appeared between the $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ values of the mammoth. If the Mezhyrich and
270 Yudinovo mammoths had different mobility behaviour, it was not reflected in the $\delta^{34}\text{S}$ values
271 recorded and averaged over years in the collagen. The mammoth $\delta^{34}\text{S}$ values are different from
272 those of the associated horses at Mezhyrich, and a habitat partitioning between the two species can
273 be suggested, possibly in response to the direct forage competition suggested by their comparable
274 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. The Yudinovo mammoths also showed $\delta^{34}\text{S}$ values very different from those
275 of the reindeer and muskox. Reindeer may have migrated over areas delivering the same $\delta^{34}\text{S}$ range
276 as the more local muskox at Yudinovo and horse at Mezhyrich. As for Mezhyrich, the mammoths
277 of Yudinovo were probably feeding on territories different from those used by the other ungulates,
278 including other reputed migratory ones.

279 The range of $\delta^{34}\text{S}$ values of the large canids and foxes was -6.7 to $+1.9$ ‰ and -6.6 ‰,
280 respectively, at Mezhyrich and Buzhanka 2 and -2.4 to -0.9 ‰ and -1.1 to $+1.2$ ‰, respectively, at
281 Yudinovo and Eliseevichi (Fig. 7). Brown bears from Yudinovo and Eliseevichi plotted between $-$
282 3.0 to -1.9 ‰ very close to the large canids of the same sites. As a result, the range of sulphur
283 isotope values seen in the carnivores overlapped with that of the herbivores at the same sites. The

284 general ranges of $\delta^{34}\text{S}$ values were also comparable between the two groups of sites, except for one
285 large canid and one fox from Mezhyrich, which exhibited the lowest $\delta^{34}\text{S}$ values measured in this
286 study (-6.7 and -6.6 ‰, respectively). This large spectrum of $\delta^{34}\text{S}$ values at Mezhyrich reflects the
287 variability of the bioavailable sulphur isotopic values from the territories surrounding the site. The
288 relatively low variability in $\delta^{34}\text{S}$ values among the mammoths gives favour to the scenario of the
289 use of the same areas by all the analysed individuals and a chronological shift in the environmental
290 conditions, leading to the loss of the typical mammoth habitat. In this case, the change may be too
291 fast to be detected by significantly different radiocarbon dating. On the other hand, the low $\delta^{15}\text{N}$
292 values measured on the mammoth of Buzhanka 2, which is significantly younger by several
293 hundred years than the other dated specimens, tend to confirm a long lasting ecological
294 phenomenon.

295 Radiocarbon ages of the last mammoths of the central East European plains have been estimated to
296 be around 12.6 - 12.9 ^{14}C ka BP partly based on direct dating on molars from Eliseevichi and
297 Mezhyrich (Stuart et al., 2002). In this context, our data would indicate a significant change of the
298 mammoth habitat about two millennia before the species extinction at the onset of the Lateglacial
299 Interstadial around 12.5 ^{14}C ka BP (14.7 ka cal BP). Several elements, however, point to a possible
300 earlier disappearance in the region. Indeed, new sets of radiocarbon dates at Mezhyrich (Haesaerts
301 et al., 2015) and Yudinovo (Palkopoulou et al., 2013) have reduced the time range of mammoth
302 occurrence to around 15.1 to 14.3 ^{14}C ka BP (18.3 - 17.4 ka cal BP). A range of 15 to 14 ^{14}C ka BP
303 (ca. 18 - 17 ka cal BP) is confirmed for the central European plains when excluding dates obtained
304 on burnt bone or strong outliers, as well as results with 200 years or more as standard deviation
305 (Lister and Stuart, 2013; Iakovleva and Djindjan, 2005; Haesaerts et al., 2015). Thus, low $\delta^{15}\text{N}$
306 mammoths of this study could correspond to late if not the last survivors of the species in the
307 region. In contrast to the Lateglacial Interstadial, the range of 15.1 - 14.3 ^{14}C ka BP (18.3 to 17.4 ka
308 cal BP) covered by low $\delta^{15}\text{N}$ individuals corresponds to the beginning of the Heinrich 1 and thus a
309 cold episode, which should have been beneficial to the re-expansion of mammoth steppe vegetation

310 and presumably the associated herbivores, including the mammoth itself. The studied region is
311 close to the southern limit of the permafrost, which supports an open landscape described as a
312 periglacial steppe with open woodlands of birch, pine and larch in the river valleys, meadows in
313 wetter habitats and grasses on the flat interfluves (Velichko and Zelikson, 2005). The mean annual
314 precipitation is estimated to have been around 350 mm/year with some summer rains and a thin
315 snow cover in winter (Velichko and Zelikson, 2005). The margin of the permafrost was probably
316 sensitive to climatic shifts, even when relatively limited in amplitude. An increase in rainfall
317 amounts would lead to an increase in snow thickness that would hamper the access to forage,
318 especially in the floodplains that were easily accessible to the mammoths during winter (Velichko
319 and Zelikson, 2005). An increase in aridity would have resulted in a lower plant food supply due to
320 the development of a pure periglacial steppe (Velichko and Zelikson, 2005).

321 Humans could have taken advantage of the mammoth vulnerability, as reflected by lower $\delta^{15}\text{N}$
322 values, to access animals having died naturally and collect bones and to hunt the most fragile
323 individuals. This with the possible assistance of domesticated dogs as hunting partners could have
324 countered a possible return to more suitable conditions for mammoth (Sablin and Khlopachev,
325 2002; Shipman, 2015). Our results confirm at least that mammoth specimens from Mezhyrich,
326 Buzhanka 2 and to a lesser extent Eliseevichi were part of late mammoth populations surviving in
327 sub-optimal conditions. They were thus most likely vulnerable to any pressure from environmental
328 and/or human origin. Detecting further such cases among the late surviving mammoth populations
329 using stable isotopic tracking may be a way to test if mammoth populations still had an optimal
330 ecology or were metastable and, therefore, vulnerable to extinction. For instance, the insular
331 Holocene population of mammoth on Saint Paul Island exhibited low and variable $\delta^{15}\text{N}$ values,
332 indicating suboptimal ecological conditions preceding their final disappearance (Graham et al.,
333 2016).

334

335 **Conclusion**

336 The expanded data set of mammoth and other animal species from four sites of the Dnieper and
337 Desna Basin confirmed the anomalously low $\delta^{15}\text{N}$ values of the mammoths at Mezhyrich as well as
338 one individual from Buzhanka 2, with both sites sharing the same typology of lithic artefacts
339 (Stupak, 2014). In contrast, most of the analysed mammoths from Yudinovo exhibited the high
340 $\delta^{15}\text{N}$ values comparable to those of the associated large canids, a phenomenon typically seen in late
341 Pleistocene mammoth-steppe populations. The Eliseevichi mammoths were found to have
342 intermediate $\delta^{15}\text{N}$ values. Lower than usual $\delta^{15}\text{N}$ values in mammoth bone collagen probably reflect
343 the loss of their specialized niche due to change in the environmental conditions. The results of $\delta^{34}\text{S}$
344 analyses showed no differences among mammoth according to the site but possibly a forage range
345 partitioning between mammoth and coexisting large ungulates. Thus, variability in the mobility
346 pattern for the mammoth between the high and low $\delta^{15}\text{N}$ groups, such as migratory *versus* sedentary
347 individuals, is not supported so far. We consider that rapid environmental modifications over time,
348 probably not detectable through radiocarbon dating, can be a valid alternative explanation.
349 Combined with direct competition with other large herbivores, such as the horse, and hunting of the
350 most vulnerable individuals, the loss of their optimal habitat was likely to be the driving factor
351 behind the local extinction of the mammoth in the central East European plains.

352

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370

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543 Tables
544

Site	N°lab	Species	Anatomical piece	N° excavation	Datation ¹⁴ C yrs BP	Ref ¹⁴ C	Source	Calibrated age range (95.4% prob.)	
								from	to
Mezhyrich	MZHOS08-02	Mammoth	rib	Mzh07 Fosse 8 (C1)	14830±90	SacA-12041	Haesaerts et al., 2015	18310	17930
					14920±90	SacA-14984			
					14970±90	SacA-12259			
Mezhyrich	MZHOS07-09	Mammoth	humerus R	MzH07 Fosse 6 (C2)	14750±50	GrA-38810	Haesaerts et al., 2015	18130	17800
					14810±90	SacA-12041			
Mezhyrich	GrA-22501	Large canid	-	C1	14450±90	GrA-22501	Haesaerts et al., 2015	17900	17350
Mezhyrich	GrA-22094	Large canid	-	C2	14380±60	OxA-13044	Haesaerts et al., 2015	17830	17400
					14600±110	GrA-22094			
					14400±90	SacA-14982			
Mezhyrich	MZHOS07-06	Arctic fox	tibia L	Mzh66 56-868 (C4)	14400±90	SacA-14982	Haesaerts et al., 2015	17850	17260
Buzhanka 2	BUZHA-02	Mammoth	long bone	Buzh2-07 Fosse 1	14350±60	GrA-38555	Stupak, 2014	17690	17250
Buzhanka 2	BUZHA-01	Large canid	humerus L	Buzh2-03	13500±80	GifA-80178/SacA-12043	Stupak, 2014	16550	15990
Yudinovo	P24753	Mammoth	tooth fragment		14715±65	OxA-21004	Palkopoulou et al., 2013	18100	17690
Yudinovo	P24754	Mammoth	tooth fragment		14840±65	OxA-21005	Palkopoulou et al., 2013	18260	17860
Yudinovo	P24755	Mammoth	tooth fragment		14910±65	OxA-21006	Palkopoulou et al., 2013	18330	17920
Yudinovo	P24756	Mammoth	tooth fragment		14,955±65	OxA-21007	Palkopoulou et al., 2013	18370	17960
Yudinovo	P24757	Mammoth	tooth fragment		14,820±60	OxA-21033	Palkopoulou et al., 2013	18230	17840
Elisseevichi 1	LU-126	Mammoth	Tooth	LU-126	14470±100	LU-126	Velichko et al., 2005	17930	17360
Elisseevichi 1	GIN-4186	Mammoth	Tooth	GIN-4186	14590±140	GIN-4186	Velichko et al., 2005	18120	17410
Elisseevichi 1	KIA-18760	Dog	Skull	KIA-18760	13905±55	KIA-18760	Sablin and Khlopachev 2003	17080	16580

545

546 Table 1: Selected direct radiocarbon ages of mammoth, wolf and arctic fox specimens from Mezhyrich, Buzhanka 2, Yudinovo and Eliseevichi.

547 Calibrations were performed using OxCal 4.2.4 (Bronk Ramsey, 2001, 2009a, b). The radiocarbon ages are calibrated using the interim INTCAL09

548 dataset (Reimer et al., 2009). For Eliseevichi, radiocarbon dates with strong outlying values or performed on burnt material or with a standard

549 deviation of 200 years or more have been excluded (see discussion).

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Site	N° lab	Species	Anatomical piece	N° excavation	C (%)	N (%)	C:N	δ ¹³ C (‰)	δ ¹⁵ N (‰)	S (%)	δ ³⁴ S (‰)	C:S (%)	N:S (%)	Source ¹³ C ¹⁵ N
Mezhyrich	5/1	Mammoth	tusk	n.g.	44.1	15.6	3.3	-19.7	5.3					lacumin et al. 2000
Mezhyrich	5/2	Mammoth	bone	n.g.	41.9	14.4	3.4	-20.1	4.6					lacumin et al. 2000
Mezhyrich	5/3	Mammoth	bone	n.g.	43.7	15.0	3.4	-20.1	4.7					lacumin et al. 2000
Mezhyrich	MZHOS06-01	Mammoth	femur R	C4 N111	41.5	14.8	3.3	-20.3	4.9	0.13	-2.0	838	257	Drucker et al, 2014
Mezhyrich	MZHOS06-05	Mammoth	femur L	C4 N370	23.6	8.8	3.1	-20.3	4.4					Drucker et al, 2014
Mezhyrich	MZHOS06-06	Mammoth	femur L	Mzh99 Fosse 5 (C4)	44.9	15.6	3.3	-20.5	4.8	0.14	-2.6	863	258	Drucker et al, 2014
Mezhyrich	MZHOS06-04	Mammoth	humerus R	Mzh98 Fosse 7 (C1) N102	41.2	14.7	3.3	-20.5	3.9	0.13	-4.0	846	258	Drucker et al, 2014
Mezhyrich	MZHOS07-07	Mammoth	femur L	Mzh06 Fosse 7 (C1) N77	38.3	14.0	3.2	-20.6	4.0	0.12	-3.5	832	261	Drucker et al, 2014
Mezhyrich	MZHOS06-02	Mammoth	femur L	Mzh98 Fosse 8 (C1)	44.8	15.5	3.4	-20.1	4.9	0.14	-3.5	869	257	Drucker et al, 2014
Mezhyrich	MZHOS08-02	Mammoth	rib	Mzh07 Fosse 8 (C1)	41.4	13.9	3.5	-20.3	3.1	0.12	(-3.7)	<u>906</u>	261	Drucker et al, 2014
Mezhyrich	MZHOS06-03	Mammoth	femur L	Mzh98 Fosse 6 (C2)	40.3	14.7	3.2	-20.4	3.6	0.13	-3.3	821	256	Drucker et al, 2014
Mezhyrich	MZHOS07-09	Mammoth	humerus R	Mzh07 Fosse 6 (C2)	41.1	14.4	3.3	-20.5	2.9	0.15	-1.9	740	223	Drucker et al, 2014
Mezhyrich	MZHOS07-04	Horse	mandible	Mzh02 Fosse 5 (C4)	40.3	13.8	3.4	-19.9	4.6	0.12		886	260	Drucker et al, 2014
Mezhyrich	MZHOS07-05	Horse	premola/molar inf	Mzh02 Fosse 5 (C4) N6	41.7	14.9	3.3	-19.9	4.9	0.14	1.9	780	238	Drucker et al, 2014
Mezhyrich	MZHOS07-01	Hare	femur R	Mzh87 56-5007	42.8	15.3	3.3	-19.7	2.0	0.17	-3.5	688	210	Drucker et al, 2014
Mezhyrich	MZHOS07-02	Hare	femur	Mzh87	42.8	15.1	3.3	-21.0	1.6	0.16	-1.8	703	212	Drucker et al, 2014
Mezhyrich	MZHOS07-08	Large canid	tibia R	Mzh06 Fosse 7 (C1) N49	34.5	12.6	3.2	-18.7	8.4	0.14	-1.7	674	211	Drucker et al, 2014
Mezhyrich	MZHOS08-01	Large canid	metacarpal	Mzh07 Fosse 6 (C2)	43.7	15.6	3.3	-18.9	5.9	0.22	1.9	534	163	Drucker et al, 2014
Mezhyrich	GrA-22501	Large canid	-	C1	48.1	16.5	3.4	-19.3	8.0	0.18	-6.7	720	211	Drucker et al, 2014
Mezhyrich	GrA-22094	Large canid	-	C2	49.3	16.7	3.4	-19.3	8.1	0.17	-3.7	782	227	Drucker et al, 2014
Mezhyrich	MZHOS07-06	Arctic fox	tibia L	Mzh66 56-868 (C4)	47.2	15.4	3.6	-19.4	3.9	0.18	-6.6	716	200	Drucker et al, 2014
Buzhanka 2	BUZHA-02	Mammoth	long bone	Buzh2-07 Fosse 1	40.0	15.4	3.0	-20.6	5.2	0.15	-2.2	713	236	this study
Buzhanka 2	BUZHA-01	Large canid	humerus L	Buzh2-03	41.6	15.2	3.2	-18.7	7.8	0.18	0.6	612	192	this study
Yudinovo	4/1	Mammoth	bone	n.g.	44.8	15.4	3.4	-19.7	7.4					lacumin et al. 2000
Yudinovo	4/2	Mammoth	bone	n.g.	43.1	15.2	3.3	-19.5	7.4					lacumin et al. 2000
Yudinovo	4/3	Mammoth	bone	n.g.	44.0	14.9	3.4	-19.6	7.7					lacumin et al. 2000
Yudinovo	P24753	Mammoth	tooth fragment	n.g.	45.8	15.8	3.4	-20.7	8.9	0.14	-3.5	862	254	this study
Yudinovo	P24754	Mammoth	tooth fragment	n.g.	44.6	15.2	3.4	-20.4	5.0	0.13	(-3.8)	<u>931</u>	273	this study
Yudinovo	P24755	Mammoth	tooth fragment	n.g.	44.7	16.0	3.3	-20.4	6.8	0.11	(-4.2)	<u>1044</u>	<u>320</u>	this study
Yudinovo	P24756	Mammoth	tooth fragment	n.g.	44.9	15.9	3.3	-20.7	7.7	0.11	(-1.7)	<u>1107</u>	<u>335</u>	this study
Yudinovo	P24757	Mammoth	tooth fragment	n.g.	45.6	16.0	3.3	-20.4	7.5	0.13	(-2.0)	<u>947</u>	285	this study
Yudinovo	A/JUD/B/6	Mammoth	tusk	n.g.	36.2	13.4	3.2	-20.8	7.1	0.12	-2.0	804	255	this study
Yudinovo	A/JUD/B/3	Reindeer	bone	n.g.	41.6	15.3	3.2	-19.0	3.3	0.18	0.7	621	196	this study
Yudinovo	A/JUD/B/8	Muskox	bone	n.g.	42.9	15.7	3.2	-18.9	2.9	0.15	1.3	757	238	this study
Yudinovo	A/JUD/B/5	Brown bear	bone	n.g.	43.3	16.0	3.2	-19.1	6.6	0.16	-3.0	729	231	this study

Yudinovo	A/JUD/B/9	Large canid	bone	n.g.	43.8	16.1	3.2	-19.2	8.1	0.16	-2.4	715	226	this study
Yudinovo	A/JUD/B/1	Arctic fox	bone	n.g.	43.3	15.7	3.2	-18.8	6.3	0.17	0.5	660	205	this study
Yudinovo	A/JUD/B/4	Arctic fox	bone	n.g.	42.1	15.5	3.2	-19.0	6.0	0.17	1.2	664	210	this study
Yudinovo	A/JUD/B/7	Arctic fox	bone	n.g.	43.3	15.9	3.2	-19.9	5.1	0.17	-0.8	690	217	this study
Eliseevichi	1/1	Mammoth	tooth	n.g.	44.2	15.2	3.4	-20.2	5.2					lacumin et al. 2000
Eliseevichi	1/2	Mammoth	bone	n.g.	43.8	14.6	3.5	-20.1	6.1					lacumin et al. 2000
Eliseevichi	1/3	Mammoth	bone	n.g.	39.7	13.7	3.4	-20.6	6.7					lacumin et al. 2000
Eliseevichi	1/4	Mammoth	bone	n.g.	42.1	14.3	3.4	-20.6	4.8					lacumin et al. 2000
Eliseevichi	1/5	Mammoth	bone	n.g.	42.7	14.4	3.5	-20.6	5.3					lacumin et al. 2000
Eliseevichi	A/EVC/B/1	Brown bear	bone	n.g.	43.4	14.9	3.4	-19.8	6.9	0.17	-1.9	664	196	this study
Eliseevichi	A/EVC/B/3	Large canid	tooth	n.g.	36.0	13.3	3.2	-18.8	9.2	0.19	-0.9	515	163	this study
Eliseevichi	A/EVC/B/2	Arctic fox	bone	n.g.	41.7	15.2	3.2	-19.5	4.9	0.17	-1.1	651	203	this study

552

553 Table 2: Results of stable isotope analyses of collagen ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{34}\text{S}$) from the mammoth and associated animal species. The carbon, nitrogen and

554 sulphur composition of the collagen is given through elemental composition (C, N, S) and atomic ratio (C:N, C:S, N:S).

555

556 **Figure captions**

557 Figure 1: Location of the sites considered in this study.

558

559 Figure 2: Measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values on bone collagen of mammoth, horse, hare, large canid
560 and fox from Mezhyrich (M) and Buzhanka 2 (B).

561

562 Figure 3: Measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values on bone collagen of mammoth, horse, reindeer, muskox,
563 bear, large canid and fox from Yudinovo (Y) and Eliseevichi (E).

564

565 Figure 4: Measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values on bone collagen of mammoth, large canid and fox from
566 Mezhyrich (M), Buzhanka 2 (B), Yudinovo (Y) and Eliseevichi (E).

567

568 Figure 5: Cluster analysis using the Ward's minimum variance method performed on $\delta^{15}\text{N}$ values of
569 mammoth bone collagen, with the software SAS JMP version 12.2.0.

570

571 Figure 6: a) Calibrated radiocarbon for the dated mammoth specimens of Mezhyrich, Buzhanka 2
572 and Yudinovo ; b) Bayesian age model for the dated mammoth specimens of Mezhyrich and
573 Mezhyrich produced using OxCal 4.2.4 (Bronk Ramsey, 2001, 2009a, b). The radiocarbon ages are
574 calibrated using the interim INTCAL09 dataset (Reimer et al., 2009). See Table 1 for details.

575

576 Figure 7: Measured $\delta^{34}\text{S}$ and $\delta^{15}\text{N}$ values on bone collagen of mammoth, large canid and fox from
577 Mezhyrich (M), Buzhanka 2 (B), Yudinovo (Y) and Eliseevichi (E).

FIGURE 1



FIGURE 2

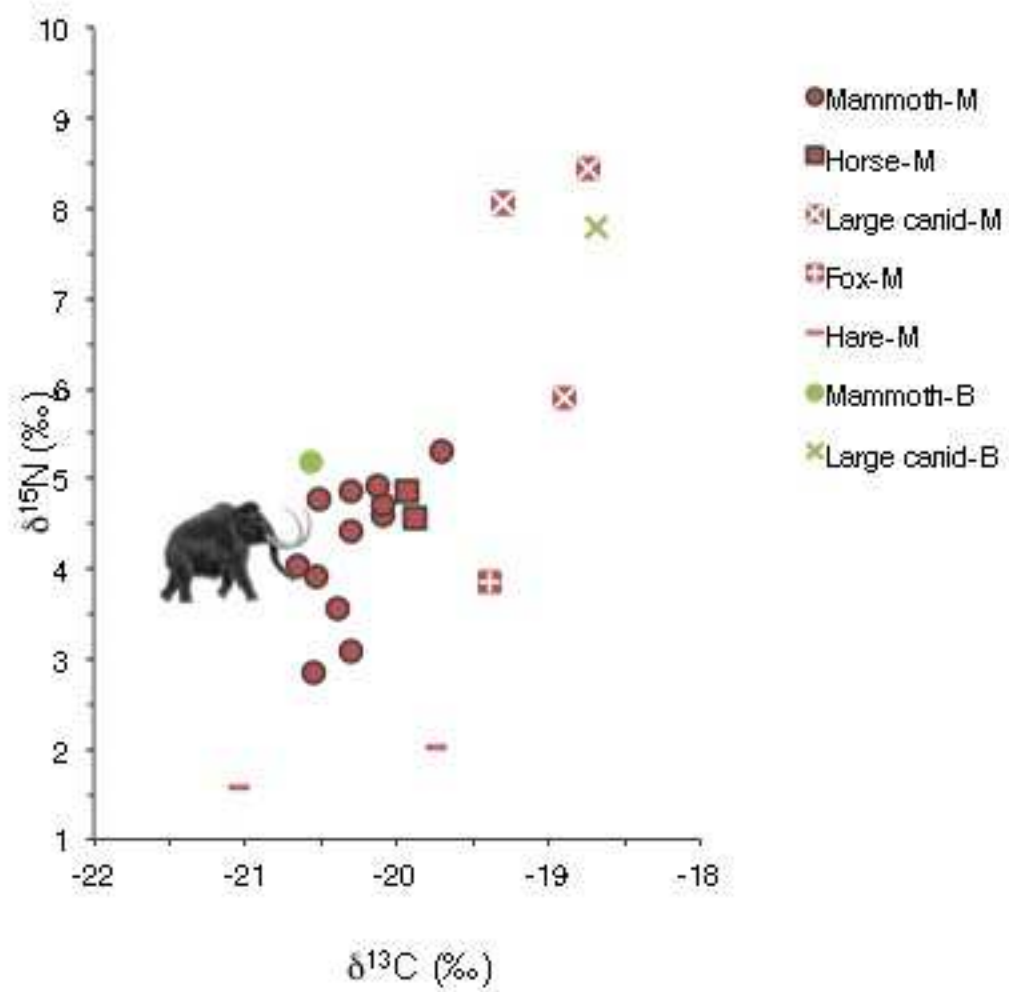


FIGURE 3

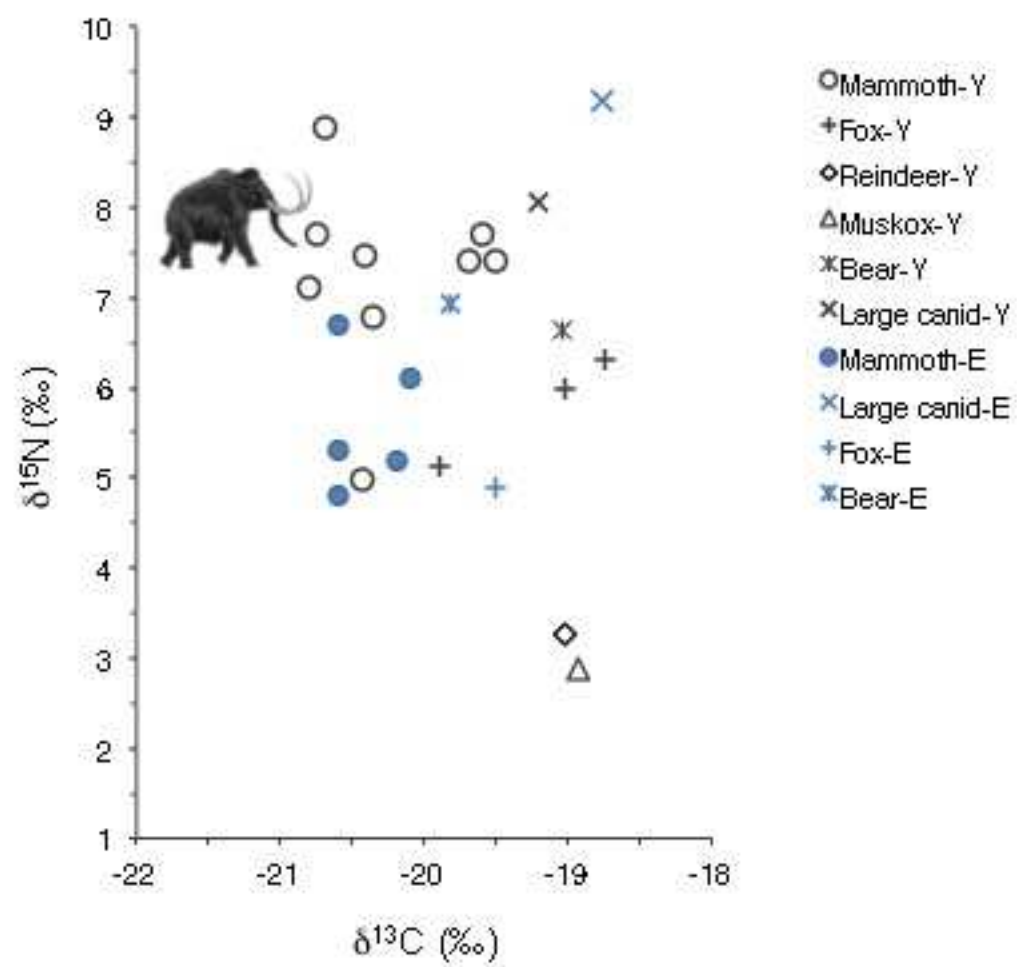


FIGURE 4

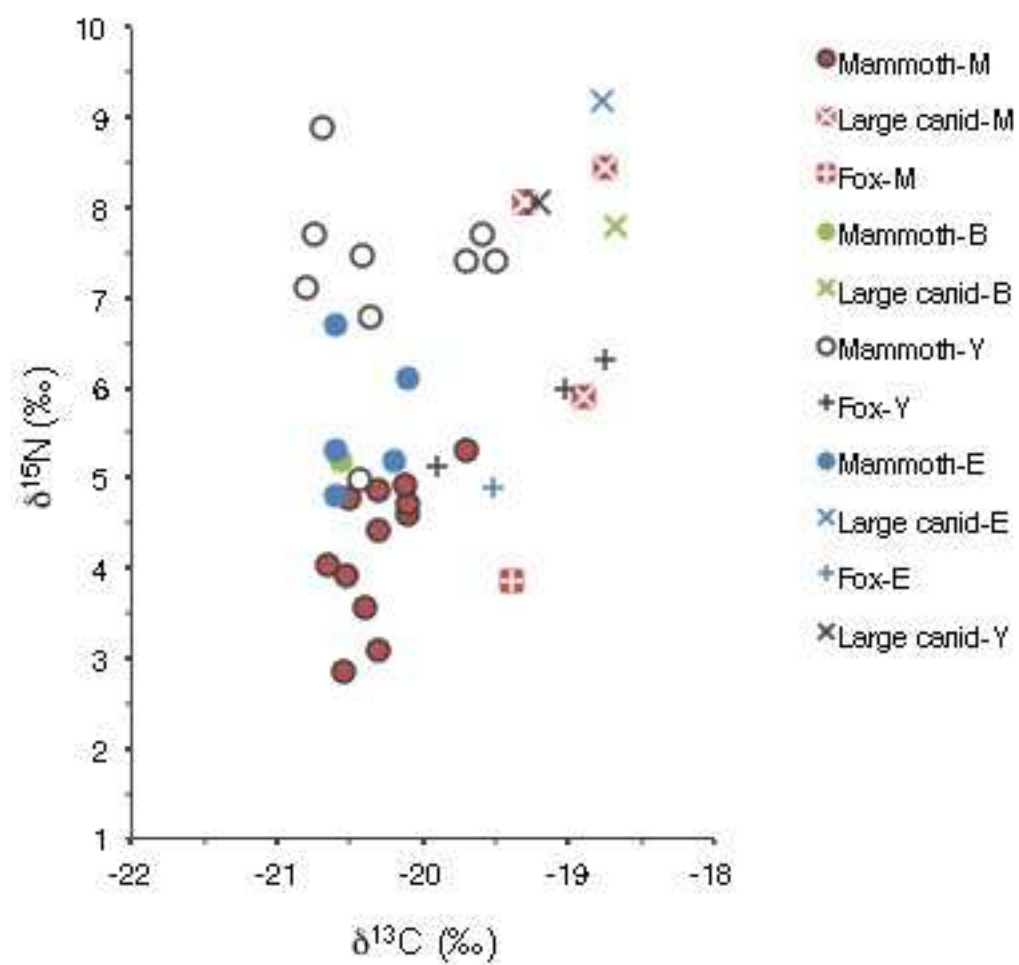


FIGURE 5

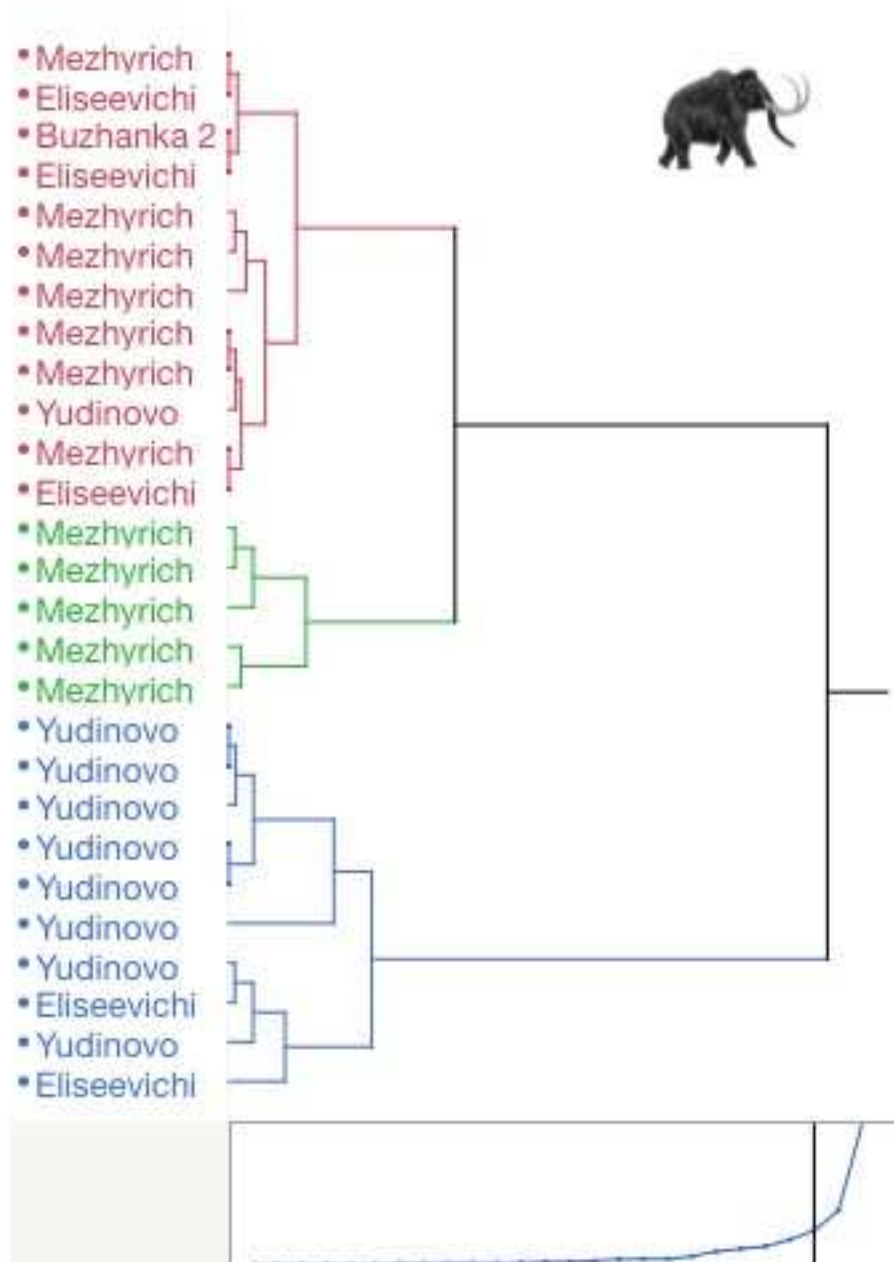
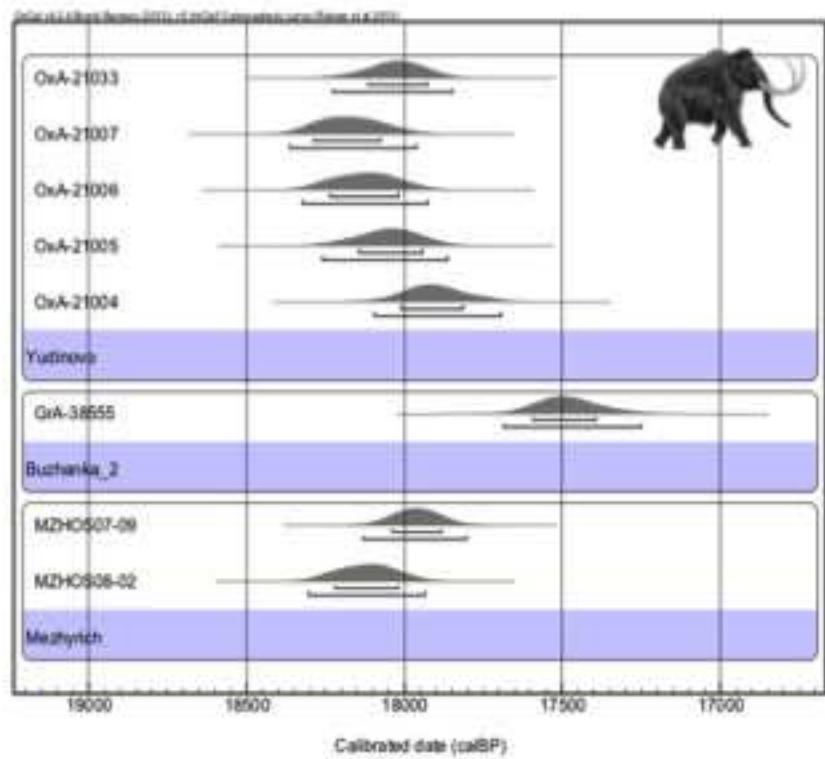


Figure 6

a)



b)

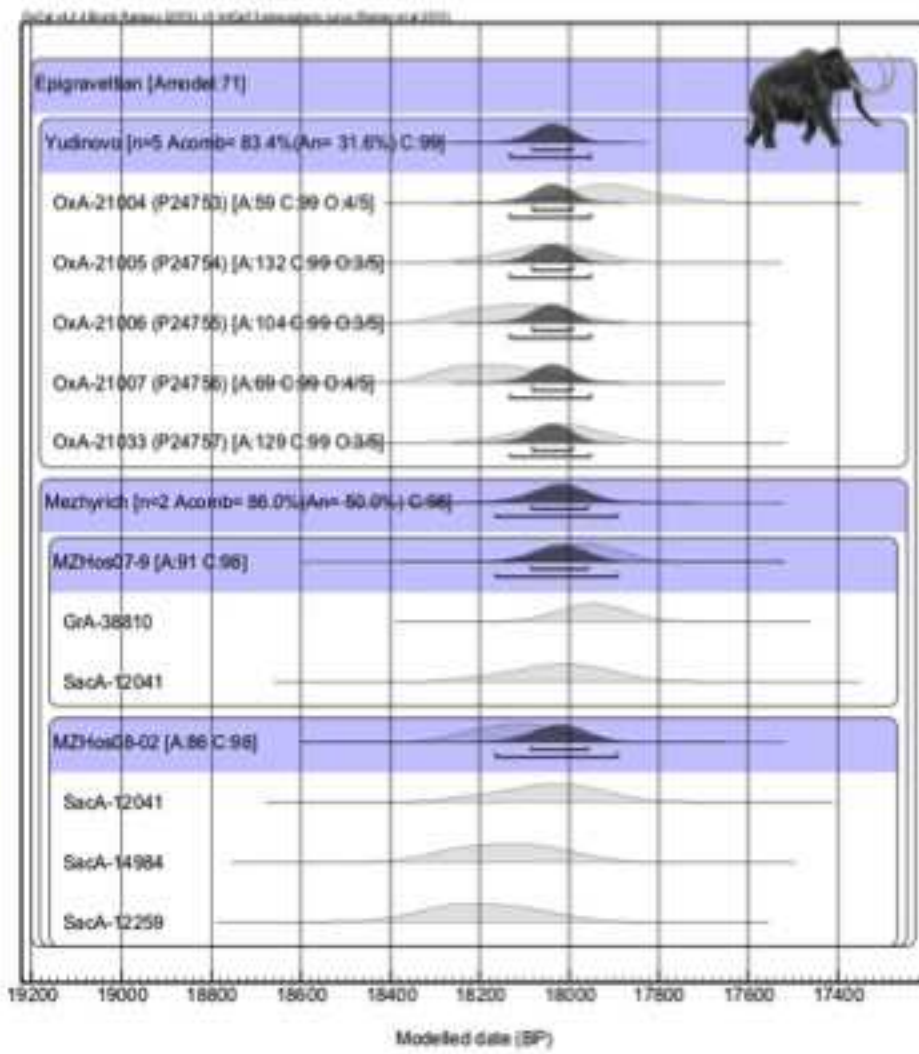


FIGURE 7

