

1 **Proboscideans on Parade: A Review of the Migratory Behaviour of Elephants, Mammoths,**
2 **and Mastodons.**

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8 **Abstract**

9 The ecology and behaviour of woolly and Columbian mammoths and mastodons have been
10 extensively studied. Despite this their patterns of mobility, and particularly the question of whether
11 or not they migrated habitually, remains unclear. This paper summarises the current state of
12 knowledge regarding mobility in these species, reviewing comparative datasets from extant elephant
13 populations as well as isotopic data measured directly on the ancient animals themselves.

14 Seasonal migration is not common in modern elephants and varies between years.
15 Nonetheless, non-migratory elephants can still have considerable home ranges, whose size is affected
16 mainly by habitat, seasonal availability of water and food, and biological sex. Strontium isotope
17 analyses of woolly mammoths, Columbian mammoths, and mastodons demonstrate plasticity in their
18 migratory behaviour as well, probably in response to spatio-temporal variations in ecological
19 conditions. However, biological sex is difficult to establish for most proboscidean fossils and its
20 influence on the results of Sr analyses can therefore not be assessed. Advances in intra-tooth sampling
21 and analytical methods for strontium isotope analysis have enabled research on intra-annual
22 movement, revealing nomadic behaviour in all three species. Sulfur isotopes have been analysed from
23 woolly mammoth remains numerous times, but its methodology is not yet developed well enough to
24 inform on past proboscidean mobility in as much detail as strontium studies.

25 The inter- and intra-individual variation in migratory behaviour in mammoths and mastodons
26 implies that their role in the subsistence strategies of Palaeolithic people may have fluctuated as well.
27 Further assessment of hominin-proboscidean predator-prey interactions will require a more detailed
28 understanding of proboscidean habitual mobility in specific contexts and places. Strontium isotope
29 studies based on multi-year enamel sequences from multiple individuals have the potential to provide
30 this insight.

31 **Highlights**

- 32 • Proboscidean mobility has been widely studied but a broader synthesis is lacking.
- 33 • Proboscidean-focussed $^{87}\text{Sr}/^{86}\text{Sr}$ and $\delta^{34}\text{S}$ studies are collated and reviewed here.
- 34 • Plasticity in migratory behaviour is found in both extinct and extant proboscideans.
- 35 • Prey-predator relations with Palaeolithic people may have fluctuated as a result.
- 36 • Future studies should beware of inter- and intra-individual variation in migration.

37 **Keywords**

38 Proboscideans; Migration; Mobility; Strontium isotopes; Sulfur isotopes; Pleistocene;
39 Palaeontology; Archaeology

40 **1. Introduction**

41 The woolly mammoth (*Mammuthus primigenius*) is among the most iconic and best studied
42 of Pleistocene fauna with particular focus given to its palaeoecology and issues around human-
43 mammoth interactions. Its large bones and teeth occur frequently and preserve well at archaeological
44 and palaeontological sites across northern latitudes, while soft tissues regularly preserve in regions
45 with permafrost. The ontogeny (Haynes, 1991; Maschenko, 2002; Metcalfe et al., 2010; Rountrey et
46 al., 2012), physiology (Campbell et al., 2010; Grigoriev et al., 2017; Lynch et al., 2015) and diet (Drucker
47 et al., 2018b; van Geel et al., 2011; Kirillova et al., 2016; Kuitems et al., 2019; Szpak et al., 2010) of
48 woolly mammoths are therefore well understood. Before advanced, detailed studies revealed
49 information about these tangible traits, however, most of what was inferred about woolly mammoths
50 and other extinct proboscideans – such as the Columbian mammoth (*Mammuthus columbi*), and the
51 American mastodon (*Mammuthus americanum*) – was derived from environmental reconstructions and
52 analogies with extant relatives, the elephants. The same is true for the presumed behavioural traits of
53 extinct proboscideans, such as inferences regarding congregation in matriarchal herds, intraspecific
54 conflict during musth, and seasonal migration. While the congregation in all-female herds and inter-
55 male conflict have more or less been confirmed by the fossil record (Haynes, 1991; Hoppe, 2004; Lister
56 & Bahn, 2007; Maschenko, 2002), the issue of seasonal migration is still unresolved.

57 The migration of mammoths has been subject of speculation for decades. Various Soviet
58 palaeontologists assumed them to be migratory without justification for this assumption (see Soffer
59 1985). Churcher (1980) was the first to look into the matter in more detail. Citing reports of African
60 elephants making seasonal migrations of up to 550 km one way, Churcher reasoned that Columbian
61 mammoths may have made biannual, seasonal migrations as well. Each one-way, cross-continental
62 trip between the Laurentian icesheet at Saskatoon in the north and the Gulf Coast in the south could
63 have lasted about 3 months according to Churcher's assumptions that the mammoths spent four
64 months in the south during winter and two in the north during summer, separated by migrations of
65 up to 2,400 km. Olivier (1982) was more conservative and reasoned from analogies with modern

66 elephants that woolly mammoths could have endured winters by digging for food through the snow
67 with their tusks and toenails. If mammoths migrated seasonally after all, those trips would not have
68 covered more than 650 km, a distance reported for modern African elephants (Sikes 1971 in Olivier
69 1982). Guthrie (1982), on the other hand, speculated that woolly mammoths were either seasonal
70 migrants or had larger home ranges than elephants, because Guthrie thought the quantity of available
71 grass in a single region would have been insufficient for mammoths. Guthrie also postulated that
72 mammoths would not have been able to penetrate snow cover, as striations on the tusks do not
73 indicate snow shovelling and mammoths would therefore have been limited to wind-blown winter
74 ranges. It has since been suggested, however, that the mammoth steppe was rather arid with thin
75 snow cover in winter (Guthrie, 2001; Kienast et al., 2005; Pitulko et al., 2007; Schirmermeister et al.,
76 2002). Soffer (1985) also believed that the movement of woolly mammoths in Eastern Europe would
77 have been regulated by vegetation availability. Grasses would have been present in sufficient quantity
78 only during the summers and mammoths would have had to resort to perennial and woody vegetation
79 during winter. These types of vegetation would have been more prevalent in the south and would
80 therefore constitute the winter habitat of mammoths. Rising temperatures at the start of summer
81 would have triggered a quick re-growth of grasses in northern regions and thereby a seasonal
82 northward migration of mammoths. Haynes (1991) argued, however, that late Pleistocene climates at
83 northern latitudes would have been characterised by equability, meaning that seasonal variation in
84 temperatures and precipitation was reduced compared to modern conditions. This, in turn, would
85 have given the vegetation longer and more productive growing seasons and mammoths would
86 consequently have had little reason to make annual long-distance seasonal migrations (also referred
87 to by Haynes as “special-purpose treks” (Haynes, 1991 p.95)). Haynes’ interpretation referred to the
88 late Pleistocene only, however, and conditions would have varied much during the long time
89 mammoths roamed over Eurasia and North America. Furthermore, in Arctic regions, where
90 mammoths were found as well (Kahlke, 2015), the polar twilight and night are limiting factors on the
91 length of the growing season of plants (Arnold et al., 2018), regardless of environmental conditions.

92 With the information and techniques available at that time, Haynes (1991) summarised the
93 situation thus: “It does not seem possible to convincingly falsify the migration hypothesis [i.e. the
94 hypothesis that mammoths migrated seasonally] using the evidence obtainable from the fossil record,
95 nor can it be falsified by calling up ecological models of the behaviours of modern large mammals”
96 (Haynes, 1991 p.99).

97 In the decades following these debates, methodological developments have enabled
98 researchers to study past animal mobility directly through isotope analysis ($^{87}\text{Sr}/^{86}\text{Sr}$ and $\delta^{34}\text{S}$) of
99 fossils, culminating in the recent development and refinement of laser ablation and micromilling
100 methods, which produce high-resolution, intra-tooth data (Hoppe et al., 1999; Lazzarini et al., 2021;
101 Lewis et al., 2014; Metcalfe et al., 2011; Willmes et al., 2016). Numerous studies have applied these
102 methods to proboscidean remains and thereby produced direct evidence of mammoth mobility. A
103 critical mass of data has now been reached, providing scope for assessing how the direct data align
104 with or contradict the earlier models. Understanding the migratory behaviour of extinct
105 proboscideans not only contributes to our general knowledge of proboscidean ecology but can also
106 reveal the effect past climate change had on their lives and provides further information regarding the
107 nature of human-proboscidean interactions in the past.

108 This paper summarises the latest data on mobility and migration in modern elephants and
109 critically reviews and assesses all papers which have used either $^{87}\text{Sr}/^{86}\text{Sr}$ or $\delta^{34}\text{S}$ to study mobility in
110 extinct proboscideans during the Pleistocene. Through this, we try to establish whether there is
111 evidence of habitual migratory behaviour in woolly mammoths, Columbian mammoths, and
112 mastodons. With this information, in turn, we can begin to get a better understanding of their seasonal
113 availability as prey to Palaeolithic hominins and establish a new baseline for understanding hominin-
114 proboscidean interactions.

115 **2. Defining migration**

116 The concept of *migration* is rarely defined in articles concerned with proboscidean mobility.
117 Migration is seen by many as an annually repeated movement of a species over an enormous distance,
118 but the term can be used in various ways (but see Dingle & Drake 2007 for a complete review). The
119 definitions given below were chosen because they are used in ecological mobility studies, including
120 studies focused on modern elephant migration.

121 Henceforth in this paper, *migration* is used to describe regular and irregular movement of an
122 individual animal between two non-overlapping home ranges (following Dingle & Drake 2007 and
123 Purdon et al. 2018) and *ranging* is the movement within a single home range or between and within
124 two overlapping home ranges. Migrating animals can be either *obligate* or *facultative migrators*. The
125 former always migrate, while the latter only do so in reaction to local deterioration of conditions.
126 When not all individuals within a species migrate, the migration is classified as either *partial* or
127 *differential*. *Partial* migration means that a fraction of the population stays in the same area while the
128 remainder travels to another region and *differential* migration implies that age or sex influences
129 whether an animal migrates or not. *Nomadism* here refers to irregular movement patterns on both
130 an inter- and intra-annual scale and can thus be synonymous with facultative migration and
131 differential migration. While Dingle and Drake (2007, p.115) defined *annual* and *seasonal* migrations
132 as “round trips synchronised with the annual cycle” and “particular stages of these annual journeys”,
133 respectively, *seasonal migration* is here defined as obligate and regular migrations between two
134 distinct regions in relation to particular seasons.

135 The terms *territory* and *home range* may appear synonymous but are rather different. Burt
136 (1943, p.351) defined *home range* as “that area traversed by the individual in its normal activities of
137 food gathering, mating, and caring for young”. This home range is not, however, the total area covered
138 by an animal its entire life, as animals can abandon home ranges and set up new ones. Migrating
139 animals can have distinct home ranges between which they move, which are referred to as, for

140 example, wet- and dry season ranges. Together, but excluding the migration route, these form the
141 total home range. Every terrestrial mammal has a home range, but only when all or part of this is
142 defended from conspecifics by fighting or aggressive gestures can one speak of a *territory*.

143 Animals do not necessarily have to migrate to be characterised as mobile, and movement
144 within home ranges can consist of treks of tens of kilometres. Ecologists use a variety of methods to
145 estimate home range sizes, of which one is the minimum convex polygon (MCP)(Gregory, 2017). This
146 method uses all gathered location points for an animal or group to create an all-encompassing convex
147 polygon (a polygon of which all internal angles are smaller than 180 degrees). MCP is the most
148 commonly used method in studies on elephant home range sizes, allowing for comparisons between
149 many studies, but it is not a perfect method. A downside of the method is that it overestimates the
150 land actually used by elephants as it records movement related to both normal and non-normal
151 activities (e.g. brief explorative trips), and assumes equal use of all visited parts. A kernel density map,
152 on the other hand, visualises which areas are used more often and therefore more reliably predicts
153 presence of elephants. The advantage of MCP, however, is that it gives an impression of the extensive
154 distances elephants can travel, even if the most distant regions are only rarely visited.

155 **3. The evolution and ecology of proboscideans**

156 The Elephantidae family includes two extant genera (*Loxodonta* and *Elephas*) and at least two
157 extinct genera (*Mammuthus* and *Primelephas*). Phylogenetic DNA research has shown that
158 *Mammuthus* spp. are more closely related to Asian elephants (*Elephas maximus*), than to either of the
159 African elephants (African savannah elephant, *Loxodonta africana*, and African forest elephant,
160 *Loxodonta cyclotis*)(Figure 1)(Brandt et al., 2012; Palkopoulou et al., 2018; Roca et al., 2001; Rohland
161 et al., 2007, 2010). While some have suggested that woolly mammoths and Columbian mammoths
162 last shared an ancestor between ~1.7 and 0.7 Mya (Palkopoulou et al., 2018), there is evidence for
163 later interbreeding between the two (Enk et al., 2011, 2016; Lister & Sher, 2015; Widga et al., 2017b).
164 More recent data has shown that Columbian mammoths are the product of hybridisation between

165 ancient woolly mammoths and a previously unidentified mammoth lineage, with later unidirectional
166 gene-flow from woolly mammoths into Columbian mammoths (van der Valk et al., 2021). The
167 Mammutidae family, which American mastodons (*Mammut americanum*) are part of, separated from
168 the Elephantidae between ~28 and 10 Mya (Palkopoulou et al., 2018; Rohland et al., 2007).

169 The habitats of the three extant elephant species are rather diverse. African savannah
170 elephants range over various habitats, such as tropical forests, grasslands and even deserts (Haynes,
171 1991), while the current dispersal of African forest elephants (Blake, 2002) and Asian elephants
172 (Sukumar, 2006) is more limited to forests.

173 Both woolly and Columbian mammoths are thought to have lived mainly in open
174 environments (e.g. steppe and tundra) (Agenbroad & Mead, 1996; Guthrie, 1982; Haynes, 1991;
175 Kirillova et al., 2016). Contrarily, mastodon remains are predominantly found in forested areas
176 containing wet regions, such as bogs and ponds (Dreimanis, 1967; Hoppe & Koch, 2006; Saunders,
177 1996; Saunders et al., 2010).

178 All three extant elephant species are generalist feeders and their diets change in response to
179 food availability. Grasses predominate in the diets of African savannah and Asian elephants during the
180 wet season, when grasses grow rapidly, while leaves and woody material are consumed in large
181 quantities during the rest of the year (Codron et al., 2006; Haynes, 1991; Sukumar, 2006). African
182 forest elephants also consume grasses and tree material, such as leaves and bark, with fruits forming
183 an important part of their diet as well (Blake, 2002; Tchamba & Seme, 1993).

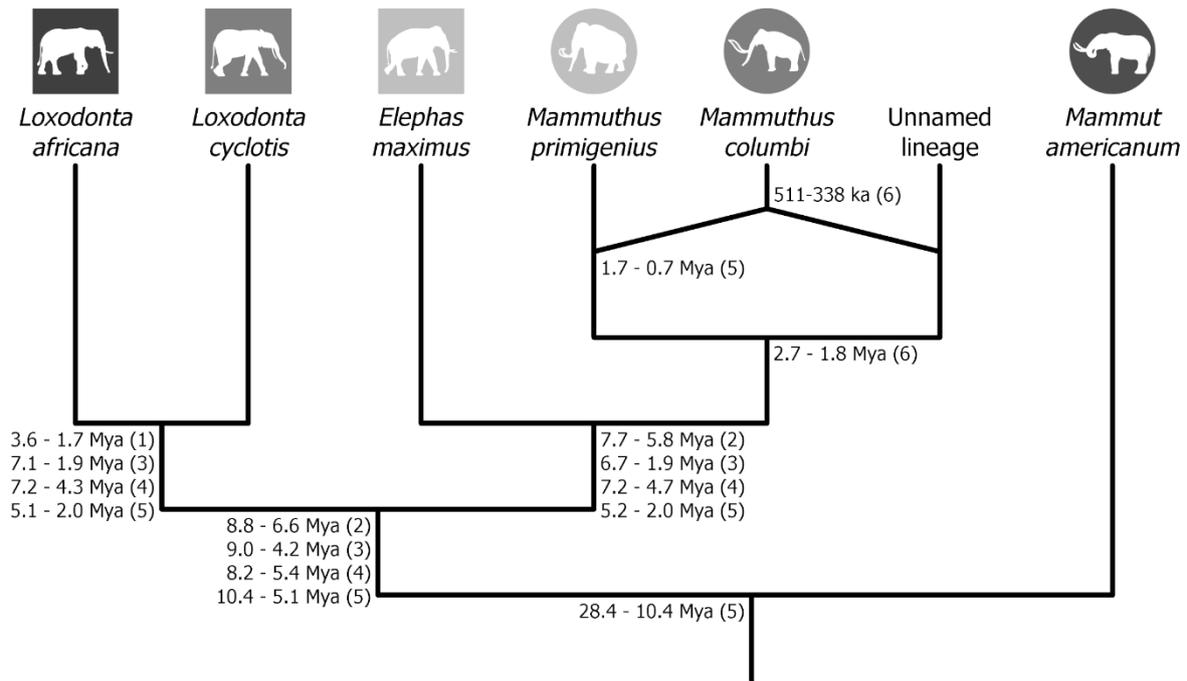


Figure 1 Simplified phylogenetic tree of the proboscidean species discussed in this text with conservative estimates of dates of last common ancestor. Branch lengths, splits and distance between species is not to scale. Sources: 1 (Roca et al., 2001); 2, (Rohland et al., 2007); 3, (Rohland et al., 2010); 4, (Brandt et al., 2012); 5, (Palkopoulou et al., 2018); 6, (van der Valk et al., 2021).

184 Mammoths are often characterised as grazers, though grasses, sedges, shrubs, and mosses
 185 have all been found physically or detected via DNA analysis in mammoth dentition, stomach contents,
 186 and dung (van Geel et al., 2011; Kirillova et al., 2016; Kosintsev et al., 2012; Polling et al., 2021; Smith
 187 & DeSantis, 2018). Mastodons are thought to have been predominantly browsers (Cocker et al., 2021;
 188 Haynes, 1991; Newsom & Muhlbachler, 2006; Saunders, 1996), though various studies have revealed
 189 that mastodon occasionally grazed as well (Gobetz & Bozarth, 2001; Green et al., 2017; Saunders,
 190 1996; Smith & DeSantis, 2018). Mammoths and mastodons were thus likely generalist feeders as well,
 191 able to adjust their diets according to food availability and personal needs.

192 Sexual segregation is present in all three extant elephant species. This means that females
 193 spend most of their lives in matriarchal herds, usually consisting of five to 20 individuals, but larger
 194 herds have been observed as well (Haynes, 1991; Sukumar, 2006). Herd sizes are generally smaller in
 195 African forest elephants, possibly due to higher resource competition (Blake, 2002; Goldenberg et al.,
 196 2021). In all three extant elephant species, male elephants (bulls) leave their maternal herd when they
 197 reach maturity between the ages of 12 to 14 years old. After leaving the herd they either travel alone

198 or join up in bachelor groups (Allen et al., 2020; Haynes, 1991; Poole, 1987; Sukumar, 2006). When
199 bulls reach the age of ca. 24 years, they first start to experience musth, a hormonal period in which
200 the bulls become restless and aggressive (Poole, 1987; Poole & Moss, 1981). Intraspecific violence
201 during musth is not uncommon and can have lethal consequences (Poole, 1989; Prusty & Singh, 1995).
202 The winner of non-lethal conflict can chase losers for several kilometres. When in musth, bulls actively
203 search for females to mate with and can cover extensive distances.

204 Because mammoths are genetically and morphologically similar to both extant elephant
205 species (though built slightly stockier), their ontogeny and behaviour are thought to have been roughly
206 similar (Haynes, 1991; Maschenko, 2002; Roth, 1984; Rountrey et al., 2012). Males were likely solitary
207 or joined in bachelor groups after reaching maturity, while females likely spent their entire life in
208 matriarchal herds. The ontogeny and behaviour of mastodons is less clear, as they are genetically
209 much further removed from elephants and inhabited substantially different environments. However,
210 sites with multiple mastodons have been found and it is likely that these animals thus also lived in
211 herds, with adult males living a more solitary life (Haynes, 1991; Haynes & Klimowicz, 2003; Saunders,
212 1977; Widga et al., 2017a). It is possible that, in line with their commonly forested habitats, mastodon
213 herds were on average smaller than mammoth herds (Haynes, 1991). Evidence for musth in
214 mammoths and mastodons has been demonstrated via decreased tusk growth rate during summer
215 months, when tusk growth rate is usually highest (El Adli et al., 2015; Fisher, 2018). The increased
216 expenditure of energy during musth is thought to have impeded the tusk growth rate.

217 **4. Migration in extant elephants**

218 The earliest papers discussing past proboscidean migration relied on analogies with modern
219 elephants rather than direct evidence (strontium and sulfur isotope data, discussed in Section 5).
220 Sources for these analogies are often minimal and limited to anecdotal evidence gathered prior to the
221 establishment of national parks and other human cultural barriers that constrain elephant movement,
222 and before objective methods such as radiotracking and GPS collars were used to study spatial

223 movement of elephants. While some of these sources state that elephants used to travel longer
224 distances before encroachment of human settlements and the formation of national parks (e.g.
225 Roberts 1951 in Churcher 1980, and Sikes 1971 in Olivier 1982), the credibility of these anecdotes has
226 been questioned (Haynes, 1991; Leuthold, 1977). An overview is given here of recent studies on
227 elephant movement, and we discuss the factors that influence proboscidean movement, which might
228 also have affected mammoths and mastodons in the past.

229 *4.1 Modern elephant migration*

230 There is limited data on seasonal migration in modern elephants. African savannah elephants
231 are partial, facultative migrators, meaning that not all individuals migrate and that those that do
232 migrate, do not necessarily do so every year. Analysis of savannah elephants across southern Africa
233 revealed that only 25 (17 females, eight males) out of 139 elephants (79 females – each from a
234 different herd (R. van Aarde, personal communication, 10 November 2021), 42 males) with full-year
235 or multi-year tracking data migrated (Purdon et al., 2018). Only 15 of these had multi-year data, of
236 which four migrated annually, nine switched between being migratory and non-migratory, and two
237 migrated but in non-consecutive years. One way migration distances varied between 20 and 249 km.
238 Examination of female elephants in Hwange NP (Zimbabwe) revealed that nine out of 31 collared
239 elephants (each from a different herd) moved >50 km between dry and wet season ranges, with trips
240 of up to 172 km (maximum distance between measured location points was 260 km)(Tshipa et al.,
241 2017). Reasons for inter-individual and inter-annual differences are not well understood, but it has
242 been hypothesised that food availability and competition for food and water are key factors. However,
243 individual needs and personalities, as well as complex social interactions and prior knowledge and
244 experience can also have played a part. Though moving in quasi-circular routes (maximum distance
245 between two points ca. 225 km) rather than moving directly between two separate home ranges, the
246 north-south movement of four female (each from a different herd) and five male desert dwelling
247 African savannah elephants from Mali coincides with increased rainfall and the thereto related
248 increase in plant productivity (Wall et al., 2013).

249 *4.2 Elephant ranging behaviour*

250 Elephants that do not migrate following the definition used here display mobility within a
251 home range that may still include treks of tens of kilometres. To quantify this mobility and evaluate
252 how it is affected by species, biological sex and habitat, data was collected on total (i.e. year-round)
253 minimum convex polygon (MCP) home range sizes from the published record.

254 *4.2.1 Data collection and analysis*

255 Reported MCP values for modern elephant total home range sizes were collected from
256 available literature. Data were deemed reliable if they were collected via long-distance tracking
257 methods (i.e. GPS, VHF radiotracking, and satellite tracking) and if the observation time was
258 continuous (i.e. during all seasons) for at least 95% of a full year. Data on elephant home range sizes
259 retrieved from field observations alone was not considered reliable, as this method relies on chance
260 encounters, while long-distance tracking methods allow the location of elephants to be determined
261 at regular intervals. Data obtained from elephants that were not observed continuously and/ or for
262 less than 95% of a full year were excluded, as these might underestimate total home range sizes. When
263 an animal was tracked for multiple years and an MCP value calculated from all observation points
264 combined was available, this value was included in our analyses. If multi-year data was available, but
265 no total MCP value was calculated, the largest full-year MCP value was included in our analysis as we
266 wanted to examine the maximum mobility of elephants. For each tracked individual, information was
267 collected on sex, home range size, observation time, habitat, and tracking method (Supplementary
268 Table 1). Habitats were simplified to three categories *canopy*, *mixed*, and *open*. Forests and woodland
269 were considered canopy, while grasslands and savannah qualified as open. Animals that inhabited
270 both approximately equally were considered to occupy a mixed habitat. No differentiation was made
271 between home range sizes reported for bulls that did and did not experience musth while they were
272 studied, because this information was rarely available. In total, home range size data was collected for
273 123 African savannah elephants, 28 African forest elephants, and 33 Asian elephants (Tables 1 and 2;
274 Figures 2 and 3). Each female included in the analyses belonged to a separate herd or family unit.

275 *Table 1 Summarised data on the number of individual elephants for which MCP has been reported by species, sex, and habitat.*

	Canopy	Mixed	Open	Total
African savannah elephant – <i>Loxodonta africana</i>				
Male	1	25	19	45
Female	29	40	9	78
Total	30	65	28	123
African forest elephant – <i>Loxodonta cyclotis</i>				
Male	3	7		10
Female	13	5		18
Total	16	12		28
Asian elephant – <i>Elephas maximus</i>				
Male	5	3		8
Female	16	9		25
Total	21	12		33

276 All statistical analyses were performed in IBM SPSS Statistics for Windows 10, version 26.0
 277 (IBM Corp., Armonk, N.Y., USA). Data were always split by species, and subsequently by sex and/ or
 278 habitat. Because histograms and Q-Q plots revealed a logarithmic distribution for nearly all data-
 279 subsets, the data was log-normalised. A log of data-subsets was considered normally distributed at p
 280 $> .050$ in either the Kolmogorov-Smirnov or the Shapiro-Wilks test. The log data-subsets were tested
 281 for homogeneity with Levene’s test, because of the large variation in sample sizes. If log data-subsets
 282 were determined to have equal variance ($p > .050$), the log data-subsets were compared with
 283 Student’s t -test and otherwise with Welch’s unequal variance t -test. Data were considered
 284 significantly different at $p < .050$.

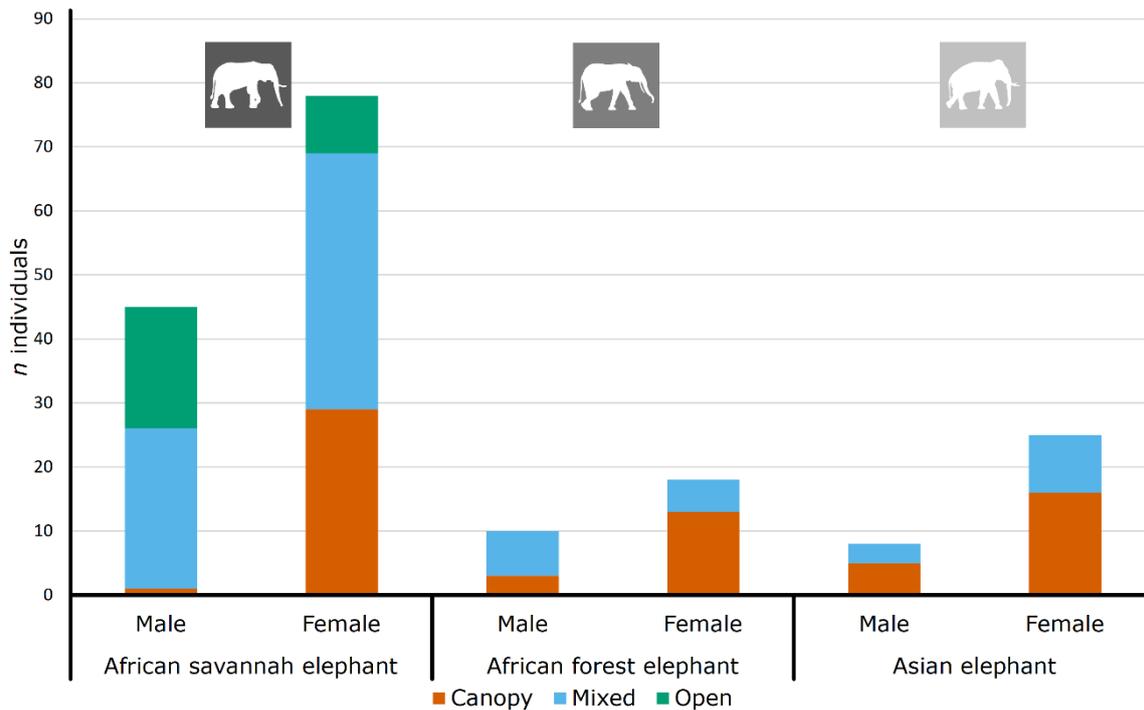


Figure 2 Stacked bar-chart visualising number of individuals for which home range size has been estimated by species, sex, and predominant habitat.

285 4.2.2 Home range size results

286 Home range sizes were largest and most varied in African savannah elephants (37 – 32,062
 287 km²; Table 2), followed by African forest elephants (36.9 – 2,253 km²) and finally Asian elephants (41
 288 – 997.1 km²)(Figure 3). A comparison of log home range size between all three species revealed
 289 significant differences between African savannah elephants and African forest elephants (Welch's
 290 $t(53.095) = 10.248, p = .002$; Supplementary Table 2) and between African savannah elephants and
 291 Asian elephants (Welch's $t(96.731) = 32.092, p < .001$), but not between African forest elephants and
 292 Asian elephants (Student's $t(49) = 1.301, p = .198$). Comparison between males and females within
 293 species revealed significantly larger log home range sizes in males of African savannah elephants
 294 (Student's $t(121) = 2.090, p = .039$) and African forest elephants (Student's $t(26) = 1.742, p = .005$), but
 295 not in Asian elephants (Student's $t(31) = -.134, p = .895$). However, when data was also split by habitat,
 296 there was only a significant difference in the log home range size between males and females in
 297 African forest elephants in mixed habitats (Welch's $t(8.323) = 20.693, p = .002$). Comparison of log
 298 home range size between habitats revealed that African savannah elephants in open habitats had
 299 larger home ranges than animals in canopy or mixed habitats (Student's $t(56) = -6.921, p < .001$ and

300 Student's $t(91) = -6.881, p < .001$, respectively), but no difference between log home range sizes from
 301 canopy and mixed habitats (Student's $t(93) = -1.958, p = .053$). The latter result was also found in
 302 African forest elephants (Student's $t(26) = -2.024, p = .053$), while log home range sizes from canopy
 303 habitats were significantly larger in Asian elephants (Welch's $t(14.334) = 15.417, p = .001$).
 304 Interestingly log home range size increased from canopy to mixed to open in African savannah
 305 elephants and from canopy to mixed in African forest elephants, while it decreased from canopy to
 306 mixed in Asian elephants. Possibly, this is due to the fact that open parts of the mixed habitats in
 307 African elephants consisted of natural open environments, such as grasslands, while in Asian
 308 elephants these open parts were often anthropogenic, such as palm oil plantations.

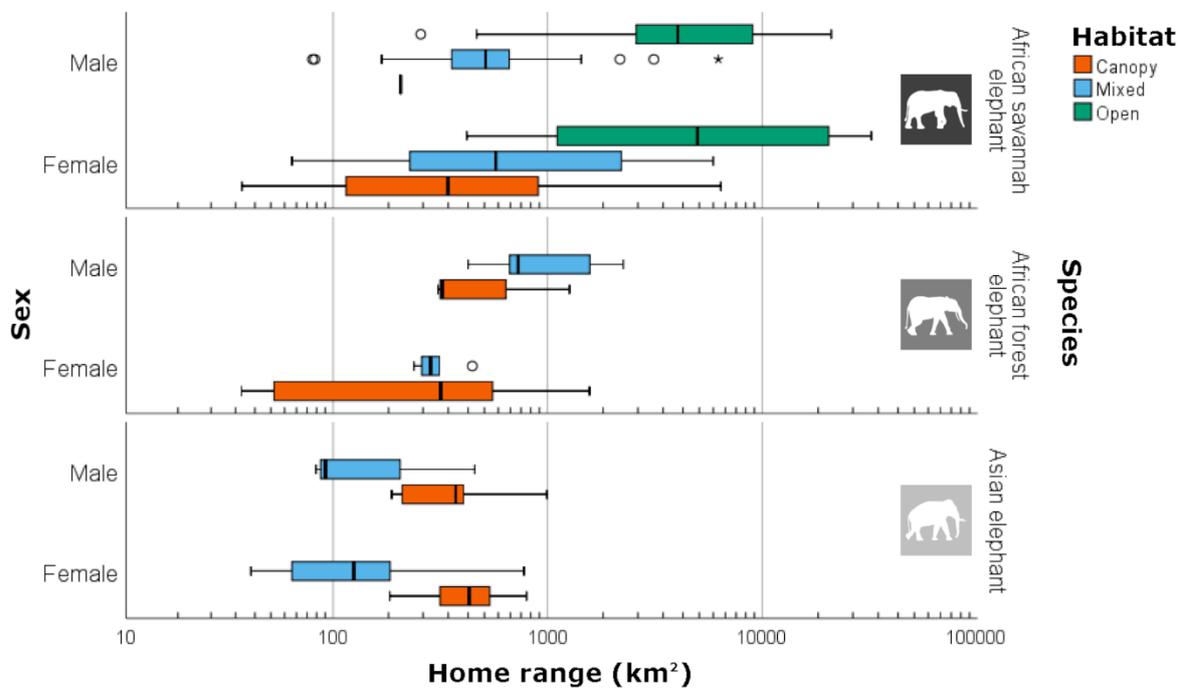


Figure 3 Box-and-whisker plots for home range sizes of modern elephants by species, sex, and habitat. Open circles denote outliers, while asterisks denote extremes. Note that the horizontal axis is on a logarithmic scale.

Table 2 Overview of MCP home ranges reported for African and Asian elephants. All data collates at least one full year of movement and was gathered using radio-telemetry methods.

Tracking method	Location	Habitat	Rainfall (mm/yr)	No. /sex	Min.	Max.	\bar{x}	1 σ	Ref.
African savannah elephant – <i>Loxodonta africana</i>									
VHF tracking	Middle Zambezi Valley, Zimbabwe	Canopy	782-802	7 female	37	348	161.3	±110.8	1
Satellite and VHF tracking	Kalamaloué National Park, Cameroon	Mixed	700	1 female			3066.0		2
VHF tracking	Laikipia-Samburu, Kenya	Mixed	400-750	17 females	102	5527	2291.5	±1757.7	3
Satellite tracking	Chobe, Nxai Pan National Park, and Moremi Wildlife Reserve, Botswana	Canopy	450-650	9 female	239	3309	1204.7	±941.0	4
VHF tracking				9 female	52	6412	1698.8	±2151.8	
Satellite tracking	Maputo Elephant Reserve, Mozambique	Canopy	690-1000	4 female	95.4	156.3	119.0	±23.6	5
				1 male			206.8		
GPS	Kunene Region, Namibia	Open	50-350	1 female			5900		6
				4 male	1564	12800	6177.2	±4048.7	
GPS	Sabi Sand Reserve and Kruger National Park, South Africa	Mixed	300-750	1 female			2244		7
Satellite	Waza region, Cameroon	Mixed	700	1 female			5895.75		8
GPS	Laikipia District, Kenya	Mixed	300-750	5 female	64	1190	661.2	±367.1	9
				7 male	665	6235	2233	±1811.8	
GPS	Gourma, Mali	Open	110-600	3 female	20347	32062	25355.7	±4931.0	10
				3 male	12023	20906	16847.0	±3666.6	
GPS	Kenya/Tanzania borderland	Open	250-600	2 female	3444	4995	4219.5	±775.5	11
				9 male	2005	100016	4334.3	±2277.1	
VHF tracking	Queen Elizabeth Protected Area, Murchison Falls Protected Area, and Kidepo Valley Conservation Area, Uganda & Virunga National Park, Democratic Republic of Congo	Mixed	/	15 females	144	447	270.1	±93.2	12
				17 male	80	637	396.5	±170.6	
		Open		3 females	421	1111	839	±300	
				3 males	257	1080	601.7	±349	

Table 2 (continued)

African forest elephant – <i>Loxodonta cyclotis</i>									
GPS	Congo Basin, Congo, Central African Republic and Gabon	Canopy	/	13 females	36.9	1570.3	429.3	439.8	13
				3 males	309.6	1265.5	633.2	447.2	
GPS	Wonga Wongué Presidential Reserve, Gabon	Mixed	/	5 female	239	447	309.2	±73.3	14
				7 male	427	2253	1131	±633.7	
Asian elephants – <i>Elephas maximus</i>									
VHF tracking and sightings	Nilgiri Biosphere Reserve, India.	Canopy	600-2000	3 female	530.5	799.5	651.1	±111.6	15
				2 male	210.6	374.5	292.6	±82	
VHF tracking	Yale protected area complex, Sri Lanka	Mixed	750-1000	7 female	41	185	103.6	±54.4	16
				3 male	83	459	211.3	±175.2	
VHF tracking	Rajaji National Park, India	Canopy	1300-1900	3 females	184	326.6	272.3	±93	17
				2 males	188	407.4	297.7	±91.8	
GPS	Sabah, Malaysia	Mixed	/	2 female	291.5	778.62	535.1	±243.54	18
GPS	Northern Johor, Malaysia	Canopy	/	1 female			411		19
GPS	Bukit Tigapuluh, Sumatra	Canopy	2577	5 female	373.7	624.26	504.3	±85.2	20
				1 male			997.1		21
GPS	Aceh, Sumatra	Canopy	3000-5000	3 females	259.3	500.7	375.4	98.8	

References: 1, (Dunham, 1986); 2, (Tchamba et al., 1995); 3, (Thouless, 1996); 4, (Verlinden & Gavor, 1998); 5, (Ntumi et al., 2005); 6, (Leggett, 2006); 7, (Thomas et al., 2008); 8, (Foguekem et al., 2009); 9, (Graham et al., 2009); 10, (Wall et al., 2013); 11, (Ngene et al., 2017); 12, (Grogan et al., 2020); 13, (Blake et al., 2008); 14, (Mills et al., 2018); 15, (Baskaran et al., 1993); 16, (Fernando et al., 2008); 17, (Williams et al., 2008); 18, (Alfred et al., 2012); 19, (Aini et al., 2015); 20, (Moßbrucker et al., 2016); 21, (Wilson et al., 2020).

309 **5. Migration in extinct Proboscideans**

310 *5.1 Strontium isotopes*

311 Strontium isotope analysis is a well-established method for studying mobility and migration
312 of humans and animals in the past (Bentley, 2006; Ericson, 1985). The stable but radiogenic isotope
313 ^{87}Sr accumulates in lithological units as the product of radioactive decay of ^{87}Rb , which has a half-life
314 of $\sim 4.96 \times 10^{10}$ years (Rotenberg et al., 2012), while ^{86}Sr is a stable isotope. The $^{87}\text{Sr}/^{86}\text{Sr}$ ratio in bedrock
315 is therefore influenced by geological age and initial ^{87}Rb content, leading to differences between
316 lithological units. In most regions, a majority of bioavailable (water-soluble) strontium comes from
317 weathering of underlying bedrock and to a lesser extent from river-water (Britton et al., 2020; Sillen
318 et al., 1998), sea-spray (Chadwick et al., 2009; Hoogewerff et al., 2019; Whipkey et al., 2000), and
319 atmospheric input, such as rain and dust (Drouet et al., 2007; Erel & Torrent, 2010; Frumkin & Stein,
320 2004; Goede et al., 1998). It has been shown, however, that in regions where only limited amounts of
321 bioavailable Sr are released from weathered bedrock, Sr brought in by aeolian and fluvial processes
322 can be the main factor influencing bioavailable Sr values (Chadwick et al., 2009; Whipkey et al., 2000).
323 There is little to no detectable fractionation of strontium isotopes between trophic levels (Flockhart
324 et al., 2015), and the local Sr signal can be determined in various ways, including analysis of soil and
325 water samples, plants and small, non-migratory animal remains. The $^{87}\text{Sr}/^{86}\text{Sr}$ ratios found in
326 herbivores are predominantly an average of the plants they have consumed, with some Sr coming
327 from drinking water (Glorennec et al., 2016; Lewis et al., 2017; Weber et al., 2020) and consumed
328 mineral particles, such as dust and soil (Weber et al., 2020), as well. As these are representative of the
329 bioavailable Sr in their direct surroundings, the values found in herbivores are a reflection of the Sr-
330 distinct regions they foraged on.

331 Archaeological and paleontological investigations often focus on the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio of dental
332 enamel. Bone and dentine are less mineralised than enamel and therefore susceptible to diagenetic
333 alterations (Becker et al., 2008; Budd et al., 2000; Hoppe et al., 2003; Nelson et al., 1986), meaning
334 that the original Sr values in fossil bone and dentine may be largely over-written with the Sr isotope

335 ratios of surrounding sediments. Additionally, bone is remodelled continuously throughout an
336 animal's life meaning the associated Sr isotope ratios are a product of very long-term averaging during
337 bone formation and remodelling (van der Merwe et al., 1988; Widga et al., 2021). Dentine and enamel,
338 on the other hand, form gradually from the occlusal end of the tooth towards the cervical margin and
339 do not remodel after mineralisation (Hillson, 2005). Although some averaging of Sr occurs during the
340 enamel secretion and mineralisation phases, dentine and enamel strontium archives demonstrably
341 preserve information about mobility with a resolution of months to weeks in some species (Lazzerini
342 et al., 2021). In mammoths and elephants, enamel forms on average 1.5 cm per year along the crown-
343 root axis, although growth rates can vary considerably across approximately 5 to 23 mm per year
344 between and within individuals (Dirks et al., 2012; Metcalfe & Longstaffe, 2012; Uno et al., 2013,
345 2020). By taking bulk samples that cover approximately full years' worth of tooth enamel growth and
346 comparing the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio to local environmentally available values, inferences can be made about
347 proboscidean movement. Individuals that have resided in the same region year-round will display
348 $^{87}\text{Sr}/^{86}\text{Sr}$ ratios that match local values, while individuals that visited areas with different Sr values may
349 yield $^{87}\text{Sr}/^{86}\text{Sr}$ ratios deviating from the local signal. Bulk samples may thus indicate whether
350 mammoths ranged only locally or foraged in regions with distinct $^{87}\text{Sr}/^{86}\text{Sr}$ ratios as well, but they lack
351 the resolution necessary to differentiate between seasonal migrants and nomads. Contrarily, studying
352 intra-tooth values measured sequentially along the tooth cusp can reveal movement between
353 isotopically distinct regions at a sub-monthly scale (Metcalfe, 2017).

354 Sequential analysis of enamel $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ can be important complements to the $^{87}\text{Sr}/^{86}\text{Sr}$
355 data. Intra-annual variations in $\delta^{13}\text{C}$ can reveal shifts in diet, while intra-annual variations in $\delta^{18}\text{O}$ are
356 influenced by temperature and precipitation. This means that $\delta^{18}\text{O}$ is affected by the seasons and its
357 intra-annual values generally show a sinusoidal pattern (Dansgaard, 1964; Fricke et al., 1998; Fricke &
358 O'Neil, 1996; Pederzani & Britton, 2019) and $\delta^{18}\text{O}$ values can therefore reveal during which season an
359 animal was foraging in a certain $^{87}\text{Sr}/^{86}\text{Sr}$ region. These seasonal fluctuations in $\delta^{18}\text{O}$ values, however,
360 are strongest in middle to high latitudes and inland regions due to the higher seasonal fluctuations in

361 temperature compared to lower latitudes or coastal regions. Furthermore, in regions that regularly
 362 experience heavy rainfall (e.g. monsoons), precipitation can have a bigger impact on $\delta^{18}\text{O}$ values than
 363 temperature (Liu et al., 2014; Posmentier et al., 2004). Additionally, the $\delta^{18}\text{O}$ pattern in animal teeth
 364 can be severely affected by the consumption of non-meteoric water (e.g. groundwater or glacial melt-
 365 water).

366 5.2 $^{87}\text{Sr}/^{86}\text{Sr}$ analysis of fossil proboscideans

367 In the existing, published record, we found that Sr isotope analysis has been carried out on
 368 fossil material belonging to 75 Columbian mammoths, 69 woolly mammoths, 11 *Mammuthus* sp., and
 369 32 mastodons (Tables 3 and 4). Most studies focussed on the conterminous United States, though
 370 material from Mexico, Alaska and Northeast Russia has been analysed and published as well. Sr
 371 analysis has also been carried out on woolly mammoth material from Central and Eastern Europe, but
 372 results have so far only been presented at conferences and are not yet published. Of the published
 373 data, non-local (as judged by the respective authors) Sr values have been detected in 44 Columbian
 374 mammoths (59%), 16 woolly mammoths (23%), 2 *Mammuthus* sp. (18%), and 20 mastodons (63%).
 375 However, this is calculated from all data combined ignoring context-specific variables, which
 376 undoubtedly affected the percentages. For example, twenty-eight woolly mammoths analysed from
 377 Wrangel Island were dated to the period after Wrangel Island was separated from the mainland, which
 378 condemned them to a non-migratory lifestyle.

379 *Table 3 Overview of number of studied individuals by species and geological age. Numbers in brackets indicate number of*
 380 *individuals with non-local Sr values (as judged by the respective authors). Approximate starting date for each stage: MIS 6 -*
 381 *191 ka BP; MIS 5e - 130 ka BP; MIS 4 - 71 ka BP; MIS 3 - 57 ka BP; MIS 2 - 29 ka BP; MIS1 - 11.7 ka BP.*

	Total	MIS 6	MIS 5e	MIS4	MIS 3	MIS 2	MIS 1
Columbian mammoth	75 (44; 59%)	1 (0; 0%)			3 (2; 67%)	16 (10; 63%)	27 (14; 52%)
Woolly mammoth	67 (14; 21%)				5 (5; 100%)	8 (8; 100%)	28 (0; 0%)
<i>Mammuthus</i> sp.	11 (2; 18%)		1 (1; 100%)	1 (0; 0%)	1 (1; 100%)		
Mastodon	32 (20; 63%)				3 (0; 0%)	12 (9; 75%)	5 (4; 80%)

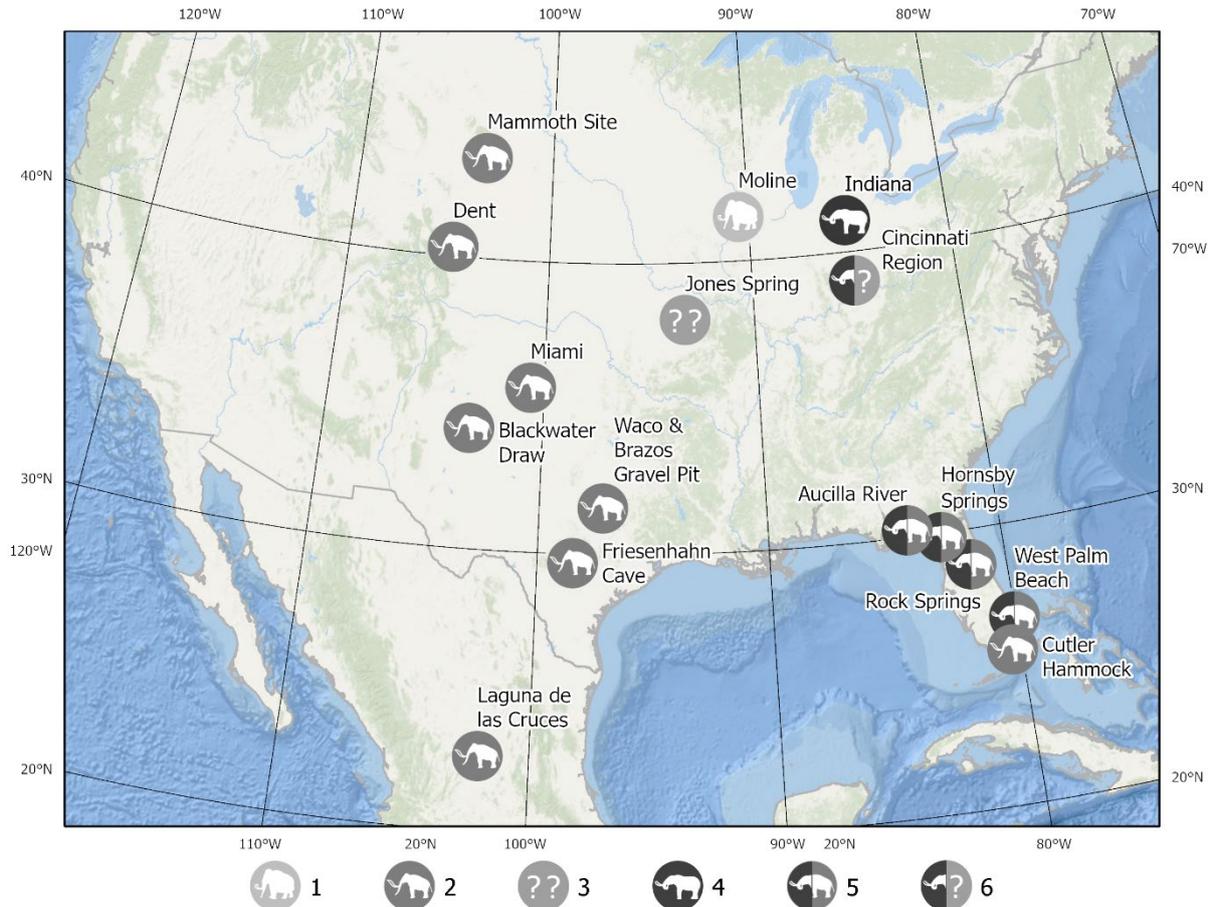


Figure 4 Overview of sites in the conterminous United States and Mexico where proboscidean remains have been analysed for $^{87}\text{Sr}/^{86}\text{Sr}$. See Table 4 for references. The Aucilla River includes the sites: Page-Ladson, Ohmes collection, Sloth Hole, Little River Rapids, and Latvis-Simpson. Symbols indicate which species was examined: 1, *Mammuthus primigenius*; 2, *Mammuthus columbi*; 3, *Mammuthus sp.*; 4, *Mammuthus americanus*; 5, *Mammuthus americanus* and *Mammuthus columbi*; 6, *Mammuthus americanus* and *Mammuthus sp.*

382 The first application of $^{87}\text{Sr}/^{86}\text{Sr}$ analysis on an extinct proboscidean species was performed on
 383 Columbian mammoth and mastodon molars from several sites in Florida, USA (Figure 4; Table
 384 4)(Hoppe et al., 1999; Hoppe & Koch, 2006, 2007). Bulk samples of dental enamel suggested that Late
 385 Glacial mammoths (~12 – 15 ^{14}C ka BP; Page-Ladson, Little River Rapids, Hornsby Springs, and Cutler
 386 Hammock) and Full Glacial mammoths (~25 – 32 ^{14}C ka BP; West Palm Beach) did not move outside
 387 Florida (Sr values 0.7080 - 0.7097)(Figure 5). Some mammoths with unclear dating (either Late or Full
 388 Glacial; Rock Springs, Sloth Hole, and material from the ‘Ohmes collection’), on the other hand, were
 389 interpreted as having occasionally resided in the Appalachian Mountains in Georgia (≥ 0.7110) – ~250
 390 km north of the sites where they were found. The strontium value of mastodons from the Late Glacial
 391 or with unsure dating indicated that most of these animals (17 out of 19) moved between Florida and
 392 the Appalachian Mountains, while none of the mastodons from the Full Glacial (West Palm Beach and

393 Latvis Simpson) appeared to have moved outside Florida. Possibly, changes in vegetation triggered a
 394 more mobile lifestyle in mastodons after the Full Glacial (Hoppe & Koch, 2007). It has been postulated,
 395 however, that the higher Sr values could also have come from rivers in Florida but with an origin in
 396 the Appalachian Mountains, the nearest of which is ~120 km (Hoppe et al., 1999). Moreover, it was
 397 noted by Hoppe et al. (1999) that Florida mammoths and mastodons may have made migrations of
 398 nearly 700 km within Florida without encountering higher $^{87}\text{Sr}/^{86}\text{Sr}$ ratios.

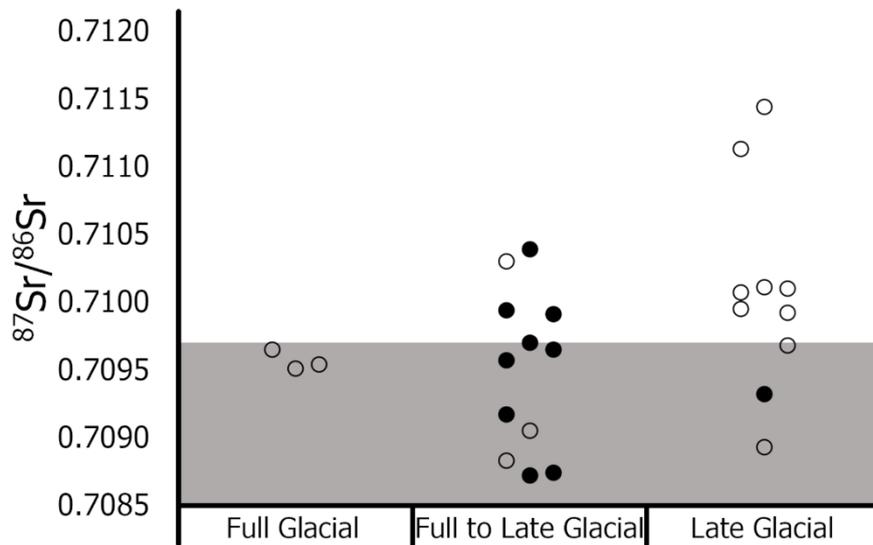


Figure 5. Dental enamel $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of mammoth and mastodon from Aucilla River fauna (Little River Rapids, Page Ladson, Sloth Hole, Ohmes Collection, and Latvis-Simpson). Open circles: Mastodon; Closed circles: Columbian mammoth. Shaded grey area indicates modern bioavailable $^{87}\text{Sr}/^{86}\text{Sr}$ ratio in Florida as determined by Hoppe and Koch 2007 (adapted from Hoppe and Koch 2007, Figure 2).

399 Comparing these results to an improved Sr isoscape (Reich et al., 2021), it becomes clear that
 400 $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of 0.711-0.713 can indeed be found near rivers with an origin in the Appalachian
 401 Mountains, but also in large parts of central Florida. Additionally, $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of 0.713-0.715 can
 402 be found in north-eastern and central-eastern parts of Florida. Mastodon mobility in Florida may thus
 403 have been more restricted than previously assumed.

404 As part of the same research, one mammoth tooth with an unknown provenance dated to
 405 $15,910 \pm 160$ ^{14}C BP and one mastodon molar from Page-Ladson (Florida, USA) dated to between 14.4
 406 and 14.8 ^{14}C ka BP were micro-sampled for analysis of intra-tooth variation in $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and $^{87}\text{Sr}/^{86}\text{Sr}$
 407 (Hoppe et al., 1999; Hoppe & Koch, 2006). Samples were taken from petrographic thin sections over
 408 approximately 4.5 mm of enamel at ca. 0.25 mm intervals parallel to enamel growth increments for

409 the mastodon, while sample interval and length of enamel sampled is unreported for the mammoth
410 molar. For the mammoth, seven samples were analysed for $^{87}\text{Sr}/^{86}\text{Sr}$, plotted next to five samples
411 analysed for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$. The $\delta^{18}\text{O}$ values showed two “peaks” and one valley, and the samples were
412 therefore interpreted as reflecting one full year of enamel growth. Assuming a sample interval of ~ 0.25
413 mm for the mammoth (similar to the sample interval from the mastodon molar), these five samples
414 covered 1.25 cm, which is slightly lower than the average enamel growth rate of 1.5 cm per year
415 reported by Dirks et al. (2012), Metcalfe and Longstaffe (2012), and Uno et al. (2013, 2020). The
416 $^{87}\text{Sr}/^{86}\text{Sr}$ ratios throughout this part of the molar were very stable (~ 0.7095) and show less variation
417 than the various environmental reference samples from all over Florida. The mammoth was therefore
418 thought to have been non-migratory within a small home range. For the mastodon, 18 enamel samples
419 were analysed for $^{87}\text{Sr}/^{86}\text{Sr}$ and 14 were analysed for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$. There was a very slight repeated
420 pattern in the $\delta^{18}\text{O}$, which was seen as evidence for approximately two years of enamel growth (Hoppe
421 et al., 1999 p.441). Sr isotope values in the mastodon molar fluctuated between ~ 0.708 and ~ 0.712 .
422 Low Sr values were found in correlation with high $\delta^{18}\text{O}$, and vice versa. Hoppe and colleagues (1999;
423 2006) postulated that the mastodon may have spent its summers at high altitudes in the Appalachian
424 and moved to the coast in Florida in winter. It should be noted, however, that we now know that the
425 higher Sr values can also be found in various parts of Florida, particularly in central Florida (Reich et
426 al., 2021).

427 Three Columbian mammoths from Laguna de los Cruces, Mexico, were analysed for $^{87}\text{Sr}/^{86}\text{Sr}$
428 by Pérez-Crespo et al. (2016) as an addition to previous analysis of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}_{\text{carbonate}}$ from the same
429 individuals (Pérez-Crespo et al., 2012). The animals were dated to the Late Pleistocene and have
430 ontogenetic, African elephant equivalent years (AEY) ages of 47 ± 2 , 43 ± 2 , and 20 ± 1 . One bulk sample
431 was taken from pre-cleaned enamel per individual. Each sample was leached with acetic acid three
432 times to remove diagenetic strontium. The size of the samples is not reported.

433 The Sr values of the residual samples showed that only one of the three mammoths (0.705947;
434 DP-1978) was foraging mainly locally (0.705870 – 0.706109), while the other two (0.705506, DP-1975,

435 and 0.705667, DP-1976) had different, unidentified foraging areas. It was noted, however, that these
436 samples likely represented only a short period of enamel formation, and that foraging areas may have
437 changed throughout the lives of the mammoths. The $\delta^{13}\text{C}$ (VPDB) values did not differ much between
438 the three individuals (-3.2‰ for the local animal versus -3.5‰ and -3.7‰ for the other animals), while
439 the $\delta^{18}\text{O}_{\text{carbonate}}$ (VPDB) of the local animal (-3.5‰) was more enriched than the values retrieved from
440 the other two mammoths (-6.1‰ and -5.6‰). This further indicated different foraging areas between
441 the mammoths.

442 Hoppe (2004) published $^{87}\text{Sr}/^{86}\text{Sr}$, $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ data of Columbian mammoths from the sites
443 of Friesenhahn Cave, Waco, Miami (all located in Texas, USA), Blackwater Draw A and B (New Mexico,
444 USA), and Dent (Colorado, USA). The dataset consisted of 39 bulk samples of enamel from 38
445 individual mammoths and are all thought to cover approximately one year of growth.

446 The $^{87}\text{Sr}/^{86}\text{Sr}$ ratio of the Blackwater Draw B mammoths (0.7096 ± 0.0004) was also significantly
447 different from the Blackwater Draw A mammoths (0.7083 ± 0.0004), but not from the Miami
448 mammoths (0.7089 ± 0.0004). Hoppe (2004) suggested that the Blackwater Draw B mammoths ranged
449 into the Rocky Mountains (ca. 200 km away from the site) rather than deriving high $^{87}\text{Sr}/^{86}\text{Sr}$ ratios
450 from nearby river water, because low $\delta^{13}\text{C}$ values retrieved from these mammoths suggested they
451 lived in cool climatic conditions with primarily C_3 grasses, which would have been found in the high-
452 elevation regions of the Rocky Mountains. Contrarily, the mammoths from Blackwater Draw A and
453 Miami would have inhabited the local region only or ranged over areas with a homogenous Sr signal.
454 Comparing these data against a more recent Sr isoscape (Bataille & Bowen, 2012), however, reveals
455 that the Blackwater Draw B mammoths would have been able to obtain similar $^{87}\text{Sr}/^{86}\text{Sr}$ ratios on the
456 Great Plains surrounding the site, while the Blackwater Draw A mammoths would have had to travel
457 >50 km westwards before encountering similar Sr isotope values. The Miami mammoths, on the other
458 hand could have incorporated Sr values similar to what has been found in their teeth at a relatively
459 short distance east of the site.

460 The Dent mammoths displayed the highest $^{87}\text{Sr}/^{86}\text{Sr}$ ratios (0.7114 ± 0.0003). Because this site
461 is located near a tri-junction of igneous and metamorphic bedrock, continental sedimentary bedrock,
462 and marine sedimentary bedrock, however, it was difficult to make clear assumptions about the
463 movement of these animals from bulk samples alone. Each lithological unit has a distinct $^{87}\text{Sr}/^{86}\text{Sr}$ ratio
464 (Bataille & Bowen, 2012) and the mammoths could therefore have consumed material with a wide
465 variety of Sr values without travelling significant distances. Intra-tooth variation would have great
466 potential to examine seasonal movement of mammoths from this site.

467 Analysis of the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios showed larger variability in the Waco mammoths (0.7096
468 ± 0.0007) than in both the expected local signal and the Friesenhahn mammoths (0.7093 ± 0.0003).
469 Hoppe (2004) suggested that the greater range of Sr values in the soil near Waco was due to an influx
470 of higher $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in waters of the nearby Bosque River. While the Sr values near the Bosque
471 River indeed appear to deviate from the Sr values generally found in the region (between 0.7080 and
472 0.7093 as seen in Figure 4 in Esker et al. 2019), this difference is not big enough to explain the
473 discrepancy in Sr isotope values between the soil near Waco and the mammoth molars from Waco
474 entirely. Instead, we would like to propose that the mammoths analysed by Hoppe (2004) behaved in
475 a similar manner to three mammoths from Waco analysed by Esker et al. (2019)(see below). Esker et
476 al. (2019) suggested that mammoths with intra-tooth Sr values varying between 0.7082 and 0.7103
477 may have ranged over both the Smithson Paleosol (~ 0.7082) surrounding the site and Upper Cenozoic
478 Clastic sediments (0.7093 – 0.7110) found southeast of Waco. Hoppe (2004) suggested that the
479 environment near Friesenhahn Cave too was subject to external Sr as well, possibly brought in by
480 nearby river, and that this affected the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in the mammoths from the site. This hypothesis
481 appears to be confirmed by the improved Sr isoscape for the region made by Esker et al. (2019). The
482 highest $^{87}\text{Sr}/^{86}\text{Sr}$ ratio was found in a bull from Waco (0.7107), which was interpreted as evidence that
483 males ranged farther than females. This is difficult to confirm however, due to the equifinality of Sr
484 isotope values in bulk samples; higher Sr isotope values could indeed be the result of further treks to
485 regions with higher biogenic $^{87}\text{Sr}/^{86}\text{Sr}$ values, but the bull may also have ranged in the same region(s)

486 as the other mammoths and stayed in a region with high $^{87}\text{Sr}/^{86}\text{Sr}$ ratios for a longer period than the
487 other individuals. Again, intra-tooth isotope data might help resolve this conundrum.

488 During a re-investigation of the Columbian mammoths from Waco (Texas, USA) by Esker et al.
489 (2019), intra-tooth Sr isotope data was indeed produced. A molar from a mammoth from the nearby
490 Brazos Gravel Pit (BGP) was added as a control to four molars from Waco. The Waco mammoths have
491 been dated to 66.8 ± 5.0 ka BP (Nordt et al., 2015), while the BGP mammoth had no clear dating but
492 was thought to be older than the Waco fossils. The age and sex of the latter was left undetermined,
493 while the molars from Waco were thought to belong to a juvenile (8 – 10 AEY) and three females (~33
494 AEY, 15 – 29 AEY, and ~25 AEY).

495 Sequential samples of enamel were collected from as close to the enamel-dentine junction as
496 possible through computerised micromilling, after the outer enamel was removed with micromilling
497 as well. Samples were taken from the innermost enamel, because the innermost enamel mineralises
498 significantly faster than enamel further towards the outer enamel surface (Zazzo et al. 2005; Tafforeau
499 et al. 2007; Blumenthal et al. 2014; Trayler & Kohn 2017; Müller et al. 2019). The innermost enamel
500 should therefore yield an Sr signal that is least affected by time lag and dampening, which occurs
501 during the slow mineralisation phase of tooth formation.

502 Samples from the juvenile mammoth came from 1.55 mm wide micromilling grooves and each
503 sample should thus cover enamel growth of ≥ 44 days, while the other mammoths were micromilled
504 with a 0.5 mm wide drill bit and each of their samples should cover ~14 days of enamel growth (Esker
505 et al., 2019). The distance between each sample was approximately 1 mm and ten to twenty samples
506 were taken per tooth. The length of molar covered by sampling was 84.7 mm (~2380 days; 6.5 years)
507 for the juvenile mammoth versus 15 mm (~420 days; 1.2 years), 20.9 mm (~590 days; 1.6 years), and
508 22 mm (~620 days; 1.7 years) for the other Waco mammoths and 17.8 mm (~500 days; 1.4 years) for
509 the BGP mammoth.

510 Only five samples were analysed for the juvenile mammoth. All yielded higher $^{87}\text{Sr}/^{86}\text{Sr}$ ratios
511 (0.71147 – 0.715547) than can be found on the Smithson Paleosol directly surrounding Waco
512 (~0.7082), but lower than the values found on the pre-Cambrian granite of the Llano Uplift (0.7283
513 \pm 0.0055; approximately 180 km southwest of Waco). The Sr in the enamel of this individual was thus
514 interpreted as a mix of the Smithson Paleosol and the pre-Cambrian Granite.

515 The three other Waco mammoths had $^{87}\text{Sr}/^{86}\text{Sr}$ ratios (0.708902 – 0.710345; 0.708732 –
516 0.709953; 0.709192 – 0.710285) that are remarkably similar to the bulk sample data collected by
517 Hoppe (2004) (0.7096 \pm 0.0007). These values are slightly higher than that of the Smithson Paleosol,
518 but substantially lower than those of the juvenile mammoth and the pre-Cambrian granite. The values
519 of the mature mammoths instead appeared to be a mix of the Smithson Paleosol and Upper Cenozoic
520 Clastic sediments (0.7093 – 0.7110) found ~70 km southeast of Waco. The seven, eleven, and ten
521 samples per mature mammoth, respectively, did show intra-individual variation, but a clear repetitive
522 pattern or inter-individual similarity in the intra-tooth variations was absent. The lack of data on the
523 exact distances between the samples and/ or related sequential $\delta^{18}\text{O}$ samples precluded
524 interpretations about seasonal movement.

525 The $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of the nine samples taken from the BGP mammoth samples were relatively
526 stable (0.708236 – 0.708566) and generally in agreement with the local signal. This individual would
527 thus have had either more limited movement in comparison to the Waco mammoths or only moved
528 in regions with a similar, homogenous Sr signal.

529 Four mastodon and six mammoth molars found in the Cincinnati area (Ohio, USA) were
530 analysed for $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and $^{87}\text{Sr}/^{86}\text{Sr}$ by Baumann and Crowley (2015). The ages of the specimens were
531 unknown, but they were thought to be from the Late Pleistocene. Mammoths from this region (the
532 Midwestern United States) are morphologically (Widga et al., 2017b) intermediate between woolly
533 and Columbian mammoths, possibly because of gene flow between these in the Midwestern United
534 States (Enk et al., 2011, 2016). The mammoths studied by Baumann and Crowley were therefore

535 identified to the genus level only (*Mammuthus* sp.). Bulk samples of the enamel covered 2 to 3 cm in
536 length, so that at least one year of growth was sampled. There were no significant differences between
537 the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of mammoths (0.70912–0.71008), mastodons (0.70998–0.71029), and local water
538 samples (0.70870–0.71153*), except for one mastodon (0.71476). This individual may have drunk
539 water originating from the Appalachian Mountains, which were expected to have much higher Sr
540 values. Not all local rivers springing from the Appalachian Mountains, however, have high enough
541 values to explain the high Sr values found in the mastodon (Licking River 0.71153, Red River 0.71206,
542 and Cumberland River 0.7145). Strontium ratios similar to the anomalous mastodon can presently be
543 found at the Scioto Brush Creek (~150 km from the study area), central or eastern Tennessee (~320
544 km), and north-western Georgia (~500 km), which could all have been the origin of anomalous Sr
545 values found in this individual. Comparison with the new isoscape by Reich et al. (2021), however,
546 reveals that $^{87}\text{Sr}/^{86}\text{Sr}$ ratios between 0.713 and 0.715 can also be found in parts of western Kentucky,
547 in western West Virginia, and sparsely in eastern Kentucky, which are located at a shorter, though still
548 substantial distance from the site of the anomalous mastodon (~200–250 km). Whether the animal
549 moved because of dietary reasons or social ones (e.g. a young male that has recently left his maternal
550 herd) is unknown.

551 Widga et al. (2021) analysed three mammoth molars from Jones Spring (Hickory County,
552 Missouri, USA) dated to MIS 3, MIS 4, and MIS 5e, respectively. The mammoths were identified to
553 genus level only (*Mammuthus* sp.), since mammoths from the Midwestern United States form a
554 separate population, intermediate in morphology between woolly and Columbian mammoths (Widga
555 et al., 2017b). Two molars (MIS 3 and 4) were sampled with a micromill (Figure 6) and one molar (MIS
556 5e) was sampled manually. For the micromilling, a 0.5 mm drill bit was used to take a sample of the
557 innermost enamel every millimetre (cf. Esker et al. 2019), while the MIS 5e molar was sampled serially

* The $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of the water samples from Red River (0.71206) and Cumberland River (0.71405) are excluded both here and in the original study, as they were marked as outliers in the box-and-whisker plots (Baumann & Crowley 2015, Figure 5).

558 (semi-bulk) with a 5 – 10 mg sample approximately every centimetre. The micromilled samples from
 559 the MIS 3 and MIS 4 molars were too small to analyse both the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}_{\text{carbonate}}$, and the $^{87}\text{Sr}/^{86}\text{Sr}$,
 560 and these were therefore analysed alternately (i.e. one sample per 2 mm for either $\delta^{13}\text{C}$ and
 561 $\delta^{18}\text{O}_{\text{carbonate}}$ or $^{87}\text{Sr}/^{86}\text{Sr}$). The samples of the MIS 5e mammoth were large enough to analyse both $\delta^{13}\text{C}$
 562 and $\delta^{18}\text{O}_{\text{carbonate}}$, and $^{87}\text{Sr}/^{86}\text{Sr}$ from the same sample.

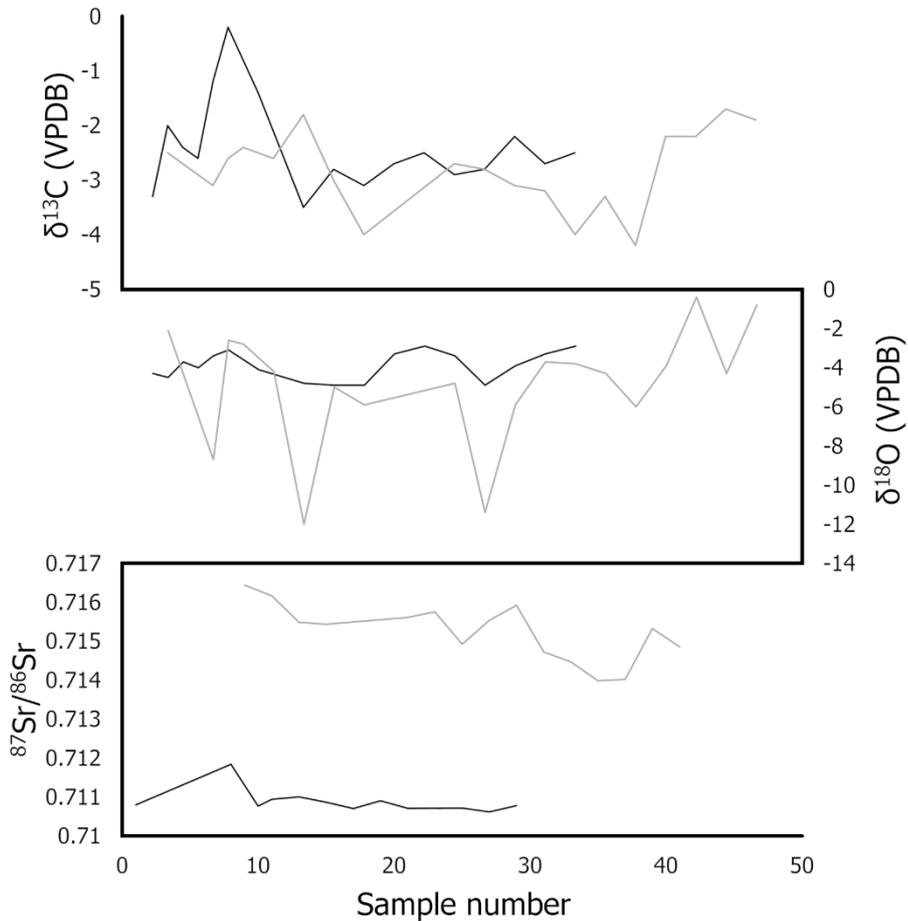


Figure 6 Intra-tooth isotope values from two micromilled mammoth molars from Jones' Spring. Light grey lines: MIS 3 mammoth; dark grey lines: MIS 4 mammoth (adapted from Widga et al. 2021, Figure 5).

563 The MIS 5e mammoth displayed the highest average $^{87}\text{Sr}/^{86}\text{Sr}$ ratios (0.71465 – 0.717712) of
 564 the three analysed mammoths. The region of Jones Spring has $^{87}\text{Sr}/^{86}\text{Sr}$ ratios between ~ 0.709 and
 565 ~ 0.711 and the MIS 5e mammoth did thus forage in a non-local environment(s). The nearest location
 566 with such radiogenic values is the central Ozark uplift (>0.71400), which is approximately 250 km
 567 removed from Jones Spring. The MIS 3 mammoth also yielded high $^{87}\text{Sr}/^{86}\text{Sr}$ ratios (0.71399 – 0.71644)
 568 and travelled a long distance between the formation of its molar and its death. The MIS 4 mammoth,

569 on the other hand, displayed a local signal (0.71062 – 0.71184) and could have been non-migratory in
570 the western Ozarks or only travelled over a homogenous $^{87}\text{Sr}/^{86}\text{Sr}$ region.

571 A molar of a male Columbian mammoth from the Mammoth Site (Hot Springs, South Dakota,
572 USA) was analysed via micromilled samples by Harrington (2021). Based on tooth wear, the individual
573 was thought to have been between 28 (± 2) and 30 (± 2) AEY. The site has been dated to the Illinoian
574 Glaciation (MIS 6) and its environment probably was an arid shrub steppe. Sr values of 20 samples
575 taken at 1 mm intervals ranged between 0.71049 and 0.71193. Comparing these results with newly
576 produced Sr isoscapes, Harrington revealed that this range of values could have been obtained within
577 a relatively small area in the southern Black Hills, which surround the site. Harrington furthermore
578 proposed that the hot springs at the mammoth site made it an excellent refugium year-round, which
579 made it possible for the mammoth to remain in the area for at least two years.

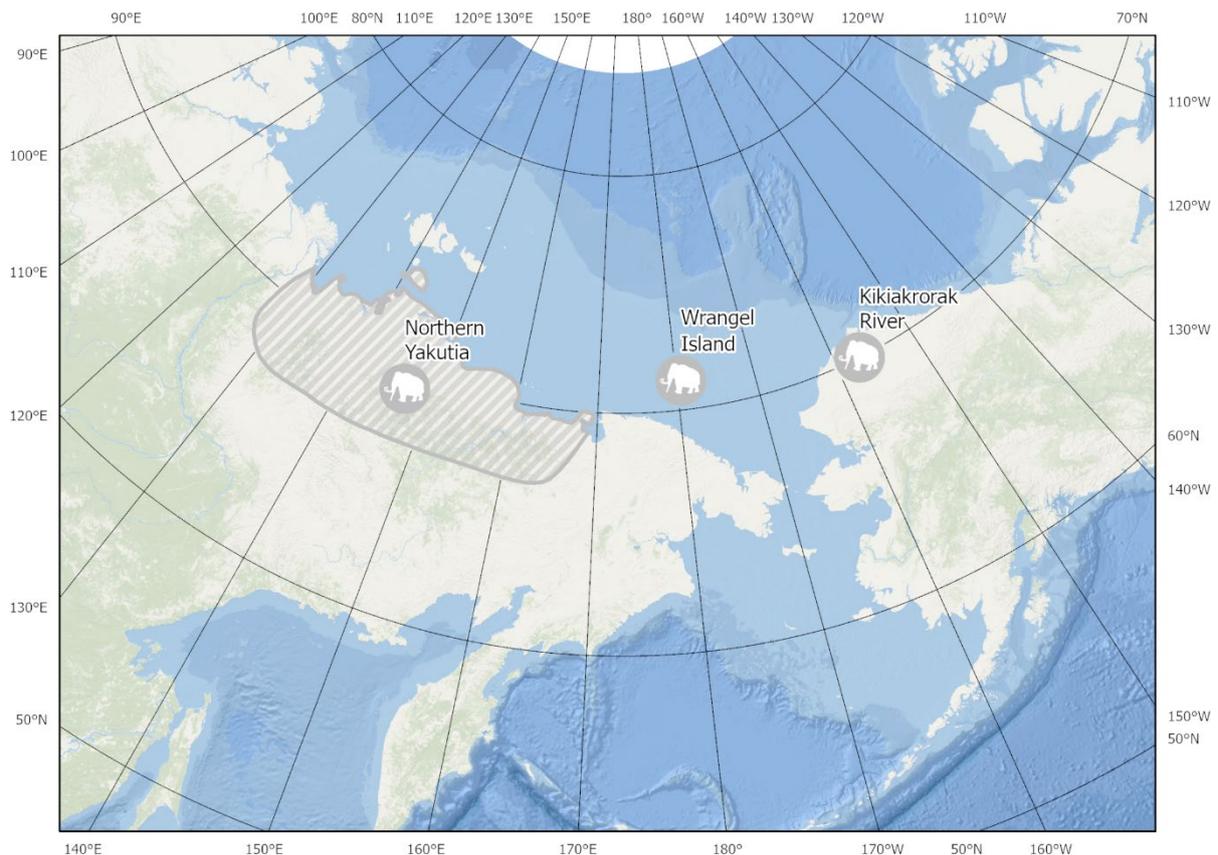


Figure 7 Overview of sites in Beringia where woolly mammoth remains have been analysed for $^{87}\text{Sr}/^{86}\text{Sr}$. See Table 2 for references; shaded area indicates region from which samples have been collected in Northern Yakutia.

580 A complete tusk of a woolly mammoth found by the Kikiakrorak River (Iñupiat name:
581 Qikitaḡruraq) in Alaska (USA) was studied in incredible detail by Wooller et al. (2021)(Figure 6).

582 Radiocarbon dating and DNA analysis revealed that the 1.7-meter-long tusk belonged to a male
583 mammoth that died approximately 17,100 years ago while growth structures in the ivory indicated
584 that the tusk grew over approximately 28-years. The tusk was cut in half and samples were taken along
585 the core of the tusk for $^{87}\text{Sr}/^{86}\text{Sr}$, $\delta^{18}\text{O}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ analyses. Samples for Sr analysis were analysed
586 with laser ablation multi-collector inductively coupled plasma mass spectrometry (LA-MC-ICPMS),
587 while the other samples ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$) were taken by hand at ~ 7 mm intervals.

588 Based on the $^{87}\text{Sr}/^{86}\text{Sr}$ and $\delta^{18}\text{O}$ isotope data Wooller et al. (2021) identified four life stages:
589 neonate (0 – ~ 1 year old), juvenile (2 – 16 years old), adult (16 – ~ 26 years old), and end of life (last
590 ~ 1.5 years). According to their interpretation, the mammoth remained mainly in the lower Yukon River
591 basin during the neonate stage. As a juvenile, the mammoth regularly made north-south movements
592 in a large core area, comprising the lowlands of interior Alaska. Several long-distance trips were made
593 as well during its juvenile stage. The regular movements as a juvenile were interpreted as a reflection
594 of herd movement. At approximately 16 years old, the range of the mammoth apparently increased
595 as $^{87}\text{Sr}/^{86}\text{Sr}$ values became more variable. Its range now included the interior lowlands of Alaska, as
596 well as the North Slope of the Brooks Range. The change was possibly caused by an expulsion from its
597 maternal herd as the male mammoth matured. The increased variance in $^{87}\text{Sr}/^{86}\text{Sr}$ was also thought
598 to be related to the seasons and the related variation in resources, as indicated by changed in $\delta^{13}\text{C}$
599 and $\delta^{15}\text{N}$ values.

600 Changes in $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in mammoth enamel from Wrangel Island, Russia, throughout the
601 transition from the terminal Pleistocene to the Holocene (calibrated radiocarbon dates range from
602 $>43,000$ to 4,024 calendar BP) were studied by Arppe et al. (2009). Four bones dating prior to the
603 separation of Wrangel Island from the mainland were added to a dataset of 36 bulk enamel samples
604 to make the time covered by the study more comprehensive. Bone samples were not pre-treated, but
605 their $^{87}\text{Sr}/^{86}\text{Sr}$ ratios (0.71098, 0.71199, 0.71271, and 0.71423)(Figure 7) were generally lower than the
606 local Sr signal (0.71245 – 0.71584). This was interpreted by Arppe et al. as evidence for little to no
607 effect from diagenetic strontium in the bones.

625 that diagenetic strontium was removed from the osseous samples via pre-treatment with 1.0N acetic
626 acid.

627 Of the 26 studied tusks, only one had an $^{87}\text{Sr}/^{86}\text{Sr}$ ratio that deviated from nearby reference
628 samples. This tusk from the Ozhogina River valley (a tributary of the Kolyma River) yielded a Sr value
629 of 0.71241, which is substantially higher than those retrieved from nearby silts (0.70998-0.71000).
630 Barbieri et al. (2008) saw this as evidence that Yakutian mammoths only undertook migrations over
631 limited distances, though they do not rule out that the individual from the Ozhogina River valley was
632 a non-resident.

633 Finally, studies focussed on intra-tooth variations in $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in woolly mammoths from
634 Kraków Spadzista, Poland (Kowalik et al., 2014, 2018), and Moline, Illinois, USA (Harrington et al.,
635 2019), and a mastodon from Indiana, USA (Miller et al., 2019) have been presented at various
636 conferences (Figures 4 and 9). Moreover, datasets including strontium, oxygen, and carbon isotope
637 results of mammoths from Pavlov I, Czech Republic, and Kostenki, Russia, are currently being written
638 up for publication by AJEP. Preliminary data from each of these currently unpublished studies imply
639 migration in one form or another in all studied specimens, though details are currently unavailable.

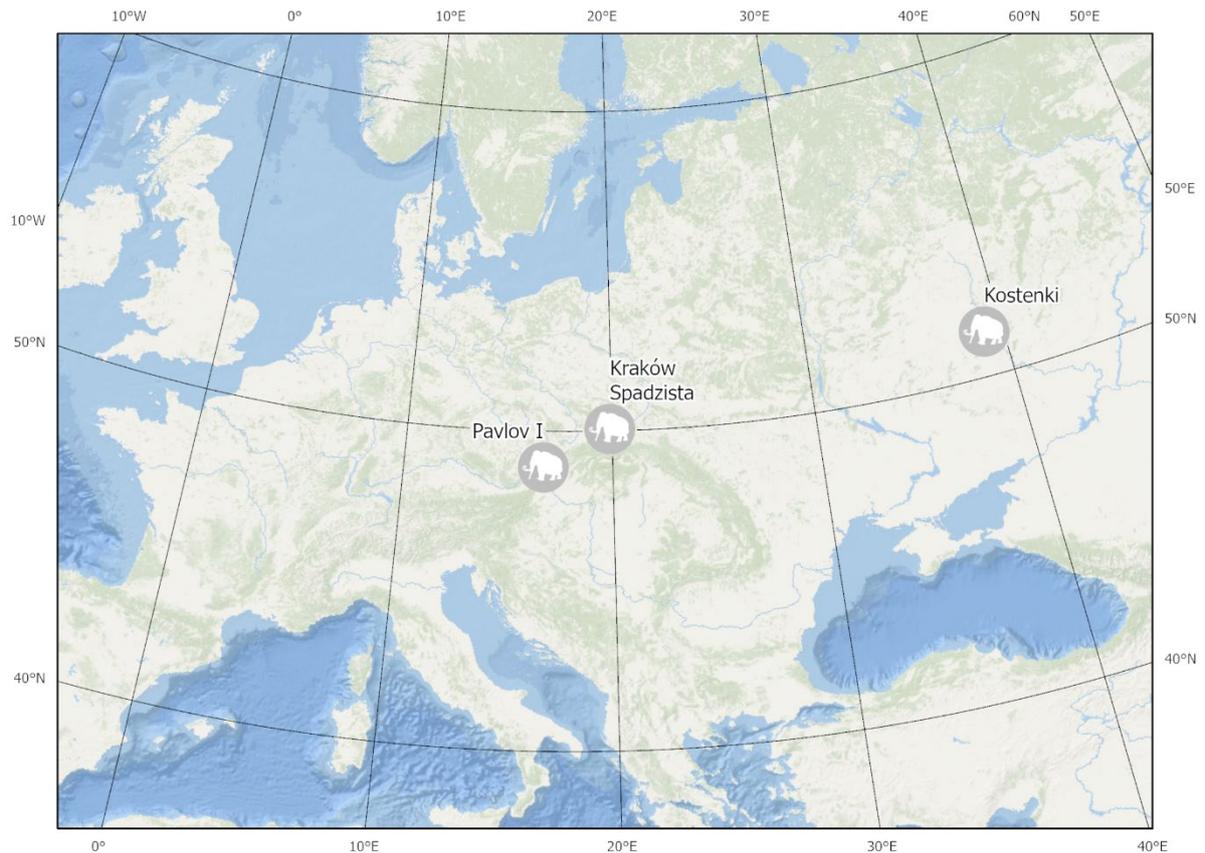


Figure 9 Overview of sites in Europe where woolly mammoth remains have been analysed for $^{87}\text{Sr}/^{86}\text{Sr}$. See Table 2 for references.

640 **5.4 Sulfur isotopes**

641 Another isotope system used to investigate past mobility is sulfur ($\delta^{34}\text{S}$). Sulfur isotope values
 642 are controlled largely by underlying bedrock, though bioavailable $\delta^{34}\text{S}$ does not always reflect the
 643 bedrock due to processes such as differential weathering and admixture (Nehlich, 2015). Furthermore,
 644 there is significant input of $\delta^{34}\text{S}$ from oceans through the so-called ‘sea-spray effect’, rivers, and rain
 645 coming from either the continent or the ocean, as well as modern contamination such as fossil fuels.

646 Trophic fractionation varies between both plant and animal species, though it is thought to
 647 be limited to only a few per mille (Nehlich, 2015). There appears to be a weak correlation between
 648 $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$, which might reflect the maturity of the soils on which herbivores have foraged (Drucker
 649 et al., 2011, 2012).

650 Sulfur is only present in small proportions in keratin and collagen, while completely absent in
 651 bioapatite (Nehlich, 2015). It can therefore be analysed in hair, bone, and tooth dentine, but not from
 652 dental enamel. Since it is only present in small quantities, large samples are necessary and results from

653 tooth dentine will show an average of a period of months to years, while samples from bone will
654 always be an average of over a decade or more of bone growth and remodelling.

655 There is no standard yet on how to establish the past local $\delta^{34}\text{S}$ value, which makes
656 interpretations problematic. The current trend involves analysing large datasets including a variety of
657 herbivorous species to establish the general value for a large region and focus on clear outliers, which
658 should indicate long-distance mobility, or inter-regional differences.

659 *5.5 $\delta^{34}\text{S}$ analysis of fossil proboscideans*

660 Several studies have analysed woolly mammoth remains from Europe (Bocherens et al., 2015;
661 Drucker et al., 2015, 2016, 2018b, 2018a; Wißing et al., 2019) and northern Siberia (Arppe et al., 2019),
662 but the implications for mobility of mammoths are not always discussed. Instead, the results from
663 large mammals are used to establish the past local $\delta^{34}\text{S}$ range and deviating $\delta^{34}\text{S}$ values are interpreted
664 in light of human and Neanderthal mobility, as the analysed material often comes from archaeological
665 sites. Exceptions are the publications by Drucker et al. (2018b) and Arppe et al. (2019).

666 Drucker et al. (2018b) analysed mammoths and other medium- and large mammals from the
667 Gravettian sites of Buzhanka 2, Mezhyrich (Ukraine), and Yudinovo (Russia). The $\delta^{34}\text{S}$ values of
668 mammoths from the three sites overlapped (-4.0 to -1.9‰ for Buzhanka 2 and Mezhyrich vs -3.5 and
669 +2.0‰ for Yudinovo), which might imply that their home ranges were similar or that if they had
670 different mobility behaviours, this is not visible in the $\delta^{34}\text{S}$ data. This was supported by $\delta^{34}\text{S}$ data from
671 carnivores from Mezhyrich, which varied across a bigger range (-6.7 to +1.9‰), suggesting that the
672 relatively low variability in mammoth $\delta^{34}\text{S}$ values could indicate that these all foraged in the same
673 area.

674 Data from mammoths from Wrangel Island, collected by Arppe et al. (2019), showed a trend
675 similar to what was previously found in strontium isotopes (Arppe et al., 2009); mammoths dated
676 ~10 ka BP, at which time Wrangel was separated from the mainland, and younger showed higher
677 $\delta^{34}\text{S}$ values than earlier, pre-isolation mammoths. This elevation in $\delta^{34}\text{S}$ values could be the result of

678 an increased input of oceanic aerosols (i.e. sea-spray effect) as the island got smaller, because ocean
679 water generally has much higher $\delta^{34}\text{S}$ values than terrestrial ecosystems. If increased sea-spray
680 caused the elevated $\delta^{34}\text{S}$ values, it would be expected that Sr values would have decreased
681 accordingly, as oceanic waters have lower $^{87}\text{Sr}/^{86}\text{Sr}$ ratios (~ 0.71000) than the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios found in
682 both pre- and post-isolation mammoths (> 0.71000). This, however, does not seem to be the case.
683 Instead, Arppe et al. (2019) suggested that increased ranging over, or weathering of Neoproterozoic
684 bedrock found in the central geology of Wrangel Island led the elevation of $\delta^{34}\text{S}$ and $^{87}\text{Sr}/^{86}\text{Sr}$ values
685 found in post-isolation mammoths.

Table 4 Overview of extinct proboscidean remains analysed for $^{87}\text{Sr}/^{86}\text{Sr}$ ratios. The column 'Nature' refers to the site's origin; 'P' stands for Paleontological, 'A' for Archaeological. 'NR' in the column 'Sample interval' means 'Not reported'. The numbers in brackets in the column 'Non-local $^{87}\text{Sr}/^{86}\text{Sr}$ signal' denote the number of studied remains that either do or do not have a $^{87}\text{Sr}/^{86}\text{Sr}$ ratio that does not correspond with the signal of the modern local environment they were found in. 'A' 'Yes' or 'a' 'No' only in this column means that all studied remains conform to this result. 'Micromill GI' in the column 'Sample strategy' means that micromilled samples were taken from a petrographic thin section parallel to enamel growth increments; 'micromill IE' means that micromilled samples were taken from the innermost enamel.

Site	Age	Nature	No. of	Sex	Sample material	Sample strategy	Sample	Additional	Non-local	Ref.
Columbian Mammoth – <i>Mammuthus columbi</i>										
West Palm Beach, Florida, USA	~25 ka BP	P	2	-	Enamel	Bulk	-	-	No	1
Rock Springs, Florida, USA	Rancholabrean	P	4	-	Enamel	Bulk	-	-	Yes (2) No (2)	1
Page-Ladson, Florida, USA	14,410 – 14,750 BP	P	2	-	Enamel	Bulk	-	$\delta^{13}\text{C}$, $\delta^{18}\text{O}$	No	1
Hornsby Springs, Florida, USA	10,750 – 12,000 BP	P	2	-	Enamel	Bulk	-	-	No	1
Cutler Hammock, Florida, USA	9.5 – 11 BP	P	6	-	Enamel	Bulk	-	-	No	1
Waco, Texas, USA	~67 ka BP*	A	11	1 male	Enamel	Bulk	-	$\delta^{13}\text{C}$, $\delta^{18}\text{O}$	Yes	2
Friesenhahn Cave, Texas, USA	17 – 20 ka BP	P	10	-	Enamel	Bulk	-	$\delta^{13}\text{C}$, $\delta^{18}\text{O}$	Yes	2
Blackwater Draw A, New Mexico, USA	11,380 – 12,790 ^{14}C BP A	A	2	-	Enamel	Bulk	-	$\delta^{13}\text{C}$, $\delta^{18}\text{O}$	No	2
Blackwater Draw B, New Mexico, USA	11,290 \pm 240 ^{14}C BP A	A	3	-	Enamel	Bulk	-	$\delta^{13}\text{C}$, $\delta^{18}\text{O}$	Yes	2
Dent, Colorado, USA	10,980 – 11,200 ^{14}C BP A	A	11	-	Enamel	Bulk	-	$\delta^{13}\text{C}$, $\delta^{18}\text{O}$	Yes	2
Miami, Texas, USA	10 – 11.4 ka BP	A	2	-	Enamel	Bulk	-	$\delta^{13}\text{C}$, $\delta^{18}\text{O}$	No	2
Unknown, Florida, USA	15,910 \pm 160 ^{14}C BP	P	1	-	Enamel	Serial (micromill GI)	NR	$\delta^{13}\text{C}$, $\delta^{18}\text{O}$	No	3
Ohmes collection (Aucilla River) Florida, USA	11 – 40 ka ^{14}C BP	P	6	-	Enamel	Bulk	-	$\delta^{13}\text{C}$, $\delta^{18}\text{O}$	Yes (2) No (4)	3, 4
Sloth Hole, Florida, USA	12 – >42 ka ^{14}C BP	P	3	-	Enamel	Bulk	-	-	Yes (2) No (1)	4
Little River Rapids, Florida, USA	11.5 – 12.1 ka ^{14}C BP	P	1	-	Enamel	Bulk	-	-	No	4
Laguna de los Cruces, México	Late Pleistocene	P	3	-	Enamel	Bulk	-	$\delta^{13}\text{C}$, $\delta^{18}\text{O}$	Yes (2) No (1)	5
Waco, Texas, USA	~67 ka BP	P	4	3 females; 1 unknown	Enamel	Serial (micromill IE)	1 – 1.5 mm	-	Yes (1) No (3)	6
Brazos Gravel Pit, Texas, USA	Late Pleistocene	P	1	-	Enamel	Serial (micromill IE)	1 mm	-	No	6
Mammoth Site, South Dakota, USA	MIS 6	P	1	1 male	Enamel	Serial (micromill IE)	1 mm	^{13}C , $\delta^{18}\text{O}$	Yes	7
Mammoth – <i>Mammuthus</i> sp.										
Cincinnati Region, Ohio, USA	Late Pleistocene	P	8	-	Enamel	Bulk	-	$\delta^{13}\text{C}$, $\delta^{18}\text{O}$	No	8
Jones Spring, Missouri, USA	MIS 3	P	1	-	Enamel	Serial (micromill IE)	2 mm	$\delta^{13}\text{C}$, $\delta^{18}\text{O}$	Yes	9
	MIS 4	P	1	-	Enamel	Serial (micromill IE)	2 mm	$\delta^{13}\text{C}$, $\delta^{18}\text{O}$	No	
	MIS 5e	P	1	-	Enamel	Serial (semi-bulk)	10 mm	$\delta^{13}\text{C}$, $\delta^{18}\text{O}$	Yes	

Table 4 (continued)

Woolly Mammoth – <i>Mammuthus primigenius</i>									
	Late Pleistocene	P	26	Tusk	Bulk	-	Yes (1)	No (25)	10
Northern Yakutia, Russia									
Wrangel Island, Russia	Mid-Holocene	P	28	Enamel	Bulk	-	No		11
	Terminal Pleistocene	P	8	Enamel	Bulk	-	Yes		
	Terminal Pleistocene	P	4	Bone	Bulk	-	Yes		
Kikiakrorak River, Arctic Alaska, USA	17 ka BP	P	1	Tusk	LA-MC-ICPMS	0.0030 mm	$\delta^{13}\text{C}$, $\delta^{18}\text{O}$, $\delta^{15}\text{N}$	Yes	12
Kraków Spadzista, Poland	22 – 24 ka BP	A	1	Enamel	LA-MC-ICPMS	NR	$\delta^{18}\text{O}$	Yes	13, 14
Moline, Illinois, USA	20,085 – 19,530 BP	P	1	-	Serial (semi-bulk)	6 – 7 mm	$\delta^{13}\text{C}$, $\delta^{18}\text{O}$	Yes	15
					Serial (micromill IE)	1 – 3 mm	$\delta^{13}\text{C}$, $\delta^{18}\text{O}$	Yes	
Pavlov I, Czech Republic	29 – 33 ka BP	A	NR	Enamel	LA-MC-ICPMS	NR	$\delta^{13}\text{C}$, $\delta^{18}\text{O}$	Yes	16
Kostenki, Russia	22 – 25 ka BP	A	NR	Enamel	LA-MC-ICPMS	NR	$\delta^{13}\text{C}$, $\delta^{18}\text{O}$	Yes	16
Mastodon – <i>Mammuthus americanus</i>									
Rock Springs, Florida, USA	Rancholabrean	P	4	Enamel	Bulk	-	Yes		1
West Palm Beach, Florida, USA	~25 ka BP	P	3	Enamel	Bulk	-	No		1
Hornsby Springs, Florida, USA	10,750-12,000 BP	P	5	Enamel	Bulk	-	Yes (4)		1
							No (1)		
Page-Ladson, Florida, USA	14,4 – 14,8 ka BP	P	1	Enamel	Serial (micromill GI)	0.25 mm	$\delta^{13}\text{C}$, $\delta^{18}\text{O}$	Yes	1, 3
Page-Ladson, Florida, USA	12,350 \pm 50 ^{14}C BP	P	7	Enamel	Bulk	-	$\delta^{13}\text{C}$, $\delta^{18}\text{O}$	Yes	1, 3, 4
Latvis-Simpson, Florida, USA	31,6 – 32,7 ka ^{14}C BP	P	3	Enamel	Bulk	-	-	No	4
Sloth Hole, Florida, USA	12 – >42 ka ^{14}C BP	P	3	Enamel	Bulk	-	-	Yes (1)	4
							-	No (2)	
Little River Rapids, Florida, USA	11,5 – 12,1 ka ^{14}C BP	P	1	Enamel	Bulk	-	-	Yes	4
Cincinnati Region, Ohio, USA	Late Pleistocene	P	4	Enamel	Bulk	-	$\delta^{13}\text{C}$, $\delta^{18}\text{O}$	Yes (1)	8
							-	No (3)	
Indiana, USA	Terminal Pleistocene	P	1	-	-	-	$\delta^{18}\text{O}$	Yes	17

*In the original paper (Hoppe, 2004), the site is said to be dated to ~28 ka BP. Recent analysis of seven OSL samples determined that the age of the site should instead be 66.8 \pm 5.0 ka BP (Nordt et al., 2015).

References: 1, (Hoppe et al., 1999); 2, (Hoppe, 2004); 3, (Hoppe & Koch, 2006); 4, (Hoppe & Koch, 2007); 5, (Pérez-Crespo et al., 2016); 6, (Esler et al., 2019); 7, (Harrington, 2021); 8, (Baumann & Crowley, 2015); 9, (Widga et al., 2021); 10, (Barbieri et al., 2008); 11, (Arppe et al., 2009); 12, (Wooler et al., 2021); 13, (Kowalik et al., 2014); 14, (Kowalik et al., 2018); 15, (Harrington et al., 2019); 16, (Pryor et al., unpublished data); 17, (Miller et al., 2019).

687 **6. Discussion**

688 *6.1 Implications of modern elephant ranging data*

689 The home range data summarized in this paper has demonstrated a wide variety of mobility
690 in modern elephants. Modern elephants generally have small home range sizes and the maximum
691 distance between any two points in a single home range is 250 km. This is nowhere near one-way
692 migration distances reported in anecdotal studies (650 km biannually by Sikes 1971 in Olivier 1982;
693 550 km biannually by Roberts 1951 in Churcher 1980). The anecdotal long trips could reflect behaviour
694 when there were fewer restrictions on elephant movement by, for example, villages, fenced parks,
695 and agricultural fields, which have been demonstrated to influence current home range sizes in African
696 elephants (Wall et al., 2021). The complexity of migratory behaviour in elephants is demonstrated by
697 recently documented migration of 15 Asian elephants who left their nature reserve and travelled 500
698 km across China, capturing global media attention (e.g. Yuan 2021 in National Geographic). It has been
699 suggested that these animals left their usual home range in response to a steadily increasing food
700 shortage and habitat degradation due to population growth, which were worsened by recent droughts
701 (Wang et al., 2021). Despite finding abundant food outside the reserve, the elephants continued for
702 hundreds of kilometres, possibly because they encountered unfamiliar plants, a high human density,
703 and increasing attention from people following them (Campos-Arceiz et al., 2021).

704 From the elephant ranging data it becomes clear that habitat and the thereto related water
705 and food availability are key factors in the size of home ranges of proboscideans. Habitats with (semi-
706)closed canopies, such as woodlands and forests, may experience less seasonal change in temperature
707 and preserve water better than open habitats, such as grasslands and savannahs, thereby offering
708 more reliable water- and food-sources year-round (Ellison et al., 2017; Morecroft et al., 1998).
709 Elephants in canopy environments therefore generally have smaller home ranges than elephants living
710 in open environments. An exception to this are occasional long-distance treks (>50 km) made by
711 African forest elephants in forested habitats in response to ripening of specific fruits during different
712 seasons (Blake, 2002). These findings agree with those of Wall et al. (2021), who also found larger

713 home ranges in modern African elephants in open habitats (especially deserts), compared to forest
714 inhabitants. Additionally, they found that home ranges became smaller with increasing tree density,
715 protected area intersection, human footprint index, and topographic slope. Home range sizes became
716 larger in their study with higher values of permanent water intersection (especially in open habitats),
717 increased normalized difference vegetation index (NDVI), land surface temperature, and tropical
718 rainfall estimates.

719 Similar to modern elephants, mammoths would have required large amounts of food and
720 water and their mobility would thus have been affected by the seasonal availability of these as well.
721 Both woolly and Columbian mammoths lived mainly in arid, open landscapes, such as steppe and
722 grasslands and high mobility within large home ranges may be expected for most of these animals.
723 This is especially true for mammoths living in Arctic regions where polar night severely limits plant
724 growth for weeks or months (Arnold et al., 2018), and these animals are therefore expected to have
725 lived a mobile life (similar to reindeer in Arctic Alaska)(Fancy et al., 1989). Similar to elephants,
726 however, there is likely to have been variability in the migratory and ranging behaviour of mammoths
727 depending on differences in, among others, climate, environment, and personal needs and
728 preferences. Mastodons are commonly found in association with indicators of forested ecosystems
729 with rather wet conditions and small home range sizes would be expected for this species. However,
730 a specialised diet could also incite occasional long distance movement, similar to the long treks for
731 fruit undertaken by African forest elephant (Blake, 2002),.

732 The ecological and geographical environments in which the mammoths lived varied
733 significantly throughout time and space. Research into migration habits of past proboscideans should
734 therefore be aware of spatio-temporal variability in environmental conditions and the potential of
735 varying responses of proboscideans to these.

736 While biological sex did not have a significant effect on home range size in the overall data, it
737 did in some studies of recent elephant populations (Leggett, 2006; Mills et al., 2018; Ngene et al.,

738 2017; Ntumi et al., 2005; Wall et al., 2021). This is because male elephants are more mobile when they
739 experience musth than when they don't (Fernando et al., 2008; Taylor et al., 2020), but also because
740 matriarchal herds with young are more conservative in their movement (Mills et al., 2018; Ngene et
741 al., 2017). Adult male mammoths and mastodons may therefore be expected to have a higher chance
742 of yielding deviating Sr values than females and juveniles.

743 Besides water, food, and sex, the movement of elephants within their home range is also
744 affected by their environment and behaviour. Examples are human presence and human-made
745 obstacles (Alfred et al., 2012; Fernando et al., 2008; Shannon et al., 2006; Wall et al., 2021), predation
746 by carnivores, and topography (e.g. fast flowing rivers (Douglas-Hamilton et al., 2006) and steep slopes
747 (>30°)(Wall et al., 2006)). Behaviour such as geophagy can also affect an animal's movement.
748 Geophagy is the consumption of essential minerals from mineral licks (Bowell et al., 1996; Holdø et
749 al., 2002; Ruggiero & Fayz, 1994; Weir, 1969), and is thought to also have been practiced by
750 mammoths (Haynes, 2006, 2012; Leshchinskiy, 2012, 2017; Soffer, 1993; Zenin et al., 2006). These
751 factors, however, rarely prompt elephants to travel tens of kilometres.

752 The effect of the complex social behaviour of elephants on their migration and ranging
753 behaviour has unfortunately not been investigated widely. Elephants have complex social lives and
754 distinct personalities, which can affect their mobility substantially (Beirne et al., 2021). It has been
755 shown, for example, that during the dry season in northern Kenya dominant matriarchs moved less,
756 had smaller home ranges, concentrated more around permanent water, and spent more time in
757 protected areas with a smaller human threat than subordinate matriarchs (Wittemyer et al., 2007).
758 Interestingly, these differences were not observed during the wet season, probably because there is
759 less competition for resources as primary productivity is higher during the wet season.

760 *6.2 Pitfalls and possibilities of $^{87}\text{Sr}/^{86}\text{Sr}$ studies*

761 While Sr isotope analysis is a well-established and often-used method, it is not without
762 shortcomings. There are, for example, many large regions in which the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio is rather

763 homogenous. Animals that migrated within or between such regions will yield a homogenous $^{87}\text{Sr}/^{86}\text{Sr}$
764 ratio throughout their teeth and these might therefore wrongly be assumed to have been non-
765 migratory. Moreover, brief foraging trips outside an animal's usual home range could be invisible in
766 the tooth Sr archive due to time averaging effects caused by the slow growth and maturation of
767 enamel and dentine.

768 Connected to these issues are the Sr isoscapes which underpin all strontium isotope mobility
769 studies. Several of the discussed studies had to make use of, for today's standards, rather simplistic Sr
770 isoscapes that were based on limited data available at the time. In the past decades, many more
771 environmental samples have been collected around the world and new methods have been developed
772 for interpolating isotopic variability across landscapes (Bataille et al., 2020; Holt et al., 2021). This has
773 led to improved isoscapes for nearly all regions from which proboscideans have been analysed for Sr
774 isotopes, such as Europe (Bataille et al., 2018; Willmes et al., 2018), Eastern Beringia (Funck et al.,
775 2021; Wooller et al., 2021), and the conterminous United States (Bataille & Bowen, 2012; Harrington,
776 2021; Reich et al., 2021; Widga et al., 2017c). In this paper we have shown that comparing original Sr
777 data to recent isoscapes can reveal alternative explanations for inter- and intra-individual
778 discrepancies in Sr values. As Sr isoscapes are developed further, reconstructions of past mobility will
779 become more accurate and further revisions may have to be made to previously published data.

780 Most of the studies reviewed here made use of bulk samples of dental enamel. While practical
781 and straightforward, this is not the ideal practise for multiple reasons. Bulk samples of 1.5 cm should
782 generally cover one full year of enamel growth in proboscideans (Dirks et al., 2012; Metcalfe &
783 Longstaffe, 2012; Uno et al., 2013, 2020), but the growth rate changes throughout the formation of
784 the molars and is substantially lower for mastodons (Metcalfe & Longstaffe, 2014). In mammoths, the
785 enamel can grow as fast as 2.28 cm per year at the occlusal end of the molar, while the enamel near
786 the cervical margin of the tooth may grow as slow as 0.52 cm per year (Dirks et al., 2012; Metcalfe &
787 Longstaffe, 2012). In mastodons, the vertical growth of tooth enamel is substantially lower, ranging
788 from 0.8 cm per year near the occlusal end of the molar, to 0.2 cm per year near the cervical margin

789 of the tooth (Metcalf & Longstaffe, 2014). Bulk samples of 1.5 cm could therefore cover a season too
790 few or too many in mammoths, while 1.5 cm of bulk enamel could cover nearly eight years in
791 mastodons if it was sampled near the cervix. Additionally, the length of enamel covered by a sample
792 is not always consistent (e.g. Baumann & Crowley 2015) or reported (e.g. Pérez-Crespo et al. 2016).
793 Results therefore do not always reliably reflect an $^{87}\text{Sr}/^{86}\text{Sr}$ ratio averaged over a full years' worth of
794 enamel growth. This will lead to uncontrolled variability between individual mammoths and
795 mastodons and between samples taken by different researchers. Furthermore, the origin of
796 anomalous values in bulk samples cannot be ascertained. Higher or lower Sr values than found locally
797 could be explained both by a long time spent in a region with only slightly deviating values or by a
798 short period in a region with highly deviating values. Also, bulk samples do not allow one to distinguish
799 between animals with a large home range and animals that migrated. Finally, bulk samples only focus
800 on a small part of the animal's life and do not necessarily reflect typical behaviour. This is especially
801 relevant for male individuals, who travel with their matriarchal herd until they are 12 to 14 years old
802 before they start wandering more extensively.

803 Bone and dentine are seldomly used as direct mobility indicators in Sr isotope analysis, as it
804 has been shown that these tissues are significantly more susceptible to diagenetic Sr than enamel
805 (Becker et al., 2008; Budd et al., 2000; Hoppe et al., 2003; Nelson et al., 1986). Even bones of less than
806 a thousand years old from west Greenland were significantly affected by exogenous Sr (Hoppe et al.,
807 2003). The effect of permafrost on this process, however, has not been explicitly studied yet. The
808 continuous low temperatures of the permafrost allow bone and dentine to keep their compact
809 structures, which should in theory inhibit diagenetic Sr from entering the internal structures of bone
810 and dentine and consequently altering the Sr signal. The discrepancy between modern biogenic Sr
811 values and fossil bone Sr values on Wrangel Island (Arppe et al., 2009), as well as the variation in
812 $^{87}\text{Sr}/^{86}\text{Sr}$ ratios throughout a tusk from Alaska, rather than a homogenous Sr signal (Wooller et al.,
813 2021) can be seen as indications that bone and dentine preserved in permafrost may indeed retain
814 their original signal. Contrarily, 25 out of 26 tusks from northern Yakutia yielded Sr values similar to

815 their respective locally presumed biogenic Sr values (Barbieri et al., 2008) and may thus demonstrate
816 that permafrost does not always prevent diagenetic alteration of Sr values. However, for the latter
817 study the exact sampling procedure is unknown. Samples may have been taken from the outer layer
818 of the tusks rather than from the more diagenesis-resistant inner core (cf. Wooller et al. 2021), or
819 mammoths in this region indeed only roamed locally. Further research is thus required to assess the
820 effect of permafrost on the preservation of the original Sr signal in bone and dentine.

821 The most detailed and informative analyses focus on intra-tooth variations in $^{87}\text{Sr}/^{86}\text{Sr}$ ratios.
822 These data can come from sequential samples collected either by hand or with a micromill and
823 analysed with thermal ionisation mass spectrometry (TIMS), or from strips of enamel analysed via
824 laser ablation multi-collector inductively coupled plasma mass spectrometry (LA-MC-ICPMS), all of
825 which can produce data at an intra-annual scale. This can help establish whether extinct
826 proboscideans yielding non-local $^{87}\text{Sr}/^{86}\text{Sr}$ ratios were seasonal migrants or wandering nomads,
827 especially when multiple years of dental enamel growth are covered. An advantage of analysing
828 sequential samples with TIMS is that pure strontium is isolated chemically from the sampled enamel,
829 which removes the possibility of isobaric interferences from ions of the same mass during analysis
830 (Horstwood et al., 2008; Simonetti et al., 2008). Additionally, if samples are large enough, multiple
831 isotopes (e.g. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) can be analysed alongside $^{87}\text{Sr}/^{86}\text{Sr}$ from the same enamel sample,
832 thereby ensuring that these isotopes come from the same period of enamel formation. Meanwhile,
833 analysis by LA-MC-ICPMS requires careful monitoring to assess and subtract the effects of various
834 isobaric interferences (Copeland et al., 2008; Lewis et al., 2014; Müller & Anczkiewicz, 2016; Willmes
835 et al., 2016), and the precision of analysis is also lower (typically to 5 significant figures compared to
836 7 with TIMS). On the other hand, the high spatial resolution of LA-MC-ICPMS generates essentially
837 continuous data along the enamel growth axis, which substantially reduces the chances that short-
838 term fluctuations in $^{87}\text{Sr}/^{86}\text{Sr}$ ratios are missed. Additionally, LA-MC-ICPMS is less time-consuming and
839 less costly when analysing large numbers of teeth than the collection and analysis of sequential
840 samples (Resano et al., 2010).

841 6.3 Results and implications of $^{87}\text{Sr}/^{86}\text{Sr}$ studies

842 Results and inferred implications of $^{87}\text{Sr}/^{86}\text{Sr}$ analyses on extinct proboscideans have been
843 shown to vary between species, regions, and time periods as well as between individuals with the
844 same provenance and chronology. Mammoths and mastodons from the same time period and regions
845 in Florida, for example, yielded disparate Sr values suggesting that some individuals migrated and
846 others did not.

847 Most data come from bulk samples, which do not allow one to distinguish a migrant animal
848 from one with a large home range and this might skew results. Looking only at intra-tooth data, we
849 found that two Columbians and four *Mammuthus* sp. appeared to have been non-migratory animals,
850 while one mastodon, three *Mammuthus* sp. and one woolly mammoth yielded variable and/ or non-
851 local $^{87}\text{Sr}/^{86}\text{Sr}$ ratios throughout their molars or tusks. We interpret this as evidence for variability in
852 migratory behaviour in mammoths and mastodons. However, we acknowledge that this dataset is
853 limited and includes samples from various regions and time periods.

854 The variation present in the Sr results from both mammoths and mastodons can be explained
855 in a number of ways. It is possible that these species were partial or facultative migrators rather than
856 seasonal migrators and only migrated at certain ages or in response to changes in environmental
857 conditions, similar to modern elephants. Mammoths and mastodons could also have had large home
858 ranges, of which some covered $^{87}\text{Sr}/^{86}\text{Sr}$ -homogenous regions and others not. Intra-tooth data from
859 more individuals and sites is required to investigate these possibilities, though comparing old data to
860 improved Sr isoscapes could provide valuable insights as well.

861 Another factor possibly causing the variation in Sr values could be local $^{87}\text{Sr}/^{86}\text{Sr}$ ratio
862 deviations near rivers. Rivers transport strontium (both in solution and as suspended particles) from
863 upstream regions and the deposition of strontium-bearing deposits along the river's flow influence
864 the bioavailable $^{87}\text{Sr}/^{86}\text{Sr}$ ratio in their near vicinity (Britton et al., 2020; Sillen et al., 1998; Widga et
865 al., 2017c). The impact of a river on local bioavailable Sr is affected by several factors, such as the

866 relative difference in $^{87}\text{Sr}/^{86}\text{Sr}$ between the regions of erosion and deposition, and the Sr concentration
867 in the river-water. Animals foraging mainly near rivers are thus more likely to be affected than those
868 foraging mainly further away from rivers. Sr transported by rivers could therefore have had a
869 significant impact on female mammoths, as female elephants usually stay closer to rivers due to the
870 presence of vulnerable calves than males who wander more freely. Particularly in earlier studies,
871 reference sample densities were low and local variations in bioavailable $^{87}\text{Sr}/^{86}\text{Sr}$ near rivers could
872 have been overlooked. Here again, comparing old data against updated Sr isoscapes could provide
873 valuable insights.

874 Sexual segregation could also be an explanation for some of the intra-specific variation in Sr
875 results, as this demonstrably impacts home range sizes in modern elephants, which are largest in
876 males experiencing musth. Unfortunately, testosterone and dihydrotestosterone (the hormones
877 found in elevated levels in bulls experiencing musth)(Hall-Martin, 1987; Jainudeen & Katongole, 1971;
878 Poole et al., 1984), cannot be detected in enamel or dentine. Extensive movement in extinct
879 proboscideans, can therefore not be checked directly against a relation with musth. However,
880 determining the sex of studied proboscidean remains through post-cranial morphology (Averianov,
881 1996; Lister, 1996), low-coverage genome analysis (de Flamingh et al., 2020; Pečnerová et al., 2017;
882 Wooller et al., 2021) or sex-related proteins (Stewart et al., 2016, 2017) could help examine the effect
883 sex had on the mobility of past proboscideans. Particularly the recent developed low-coverage
884 genome analysis, in which the presence of the X chromosome relative to other chromosomes is
885 analysed (de Flamingh et al., 2020; Pečnerová et al., 2017; Wooller et al., 2021), could make the
886 determination of sex of molars and tusks more accessible. The analysis of sex-related proteins in tooth
887 enamel (Stewart et al., 2016, 2017) could have a similar effect and could be a solution for samples
888 with poor DNA preservation, though this method has to be developed further before it can be applied
889 to proboscidean material.

890 *6.4 Results and implications of $\delta^{34}\text{S}$ studies*

891 Sulfur isotope studies could theoretically provide useful information about the migration of
892 mammoths and other animals in the past. However, more studies are required to understand its
893 variation between and within ecosystems as well as its spatial variation. The results of several sulfur
894 isotope studies on mammoths currently do not have substantial implications for our understanding of
895 mobility in extinct proboscideans as most $\delta^{34}\text{S}$ studies that include mammoth material do not discuss
896 this aspect. Drucker et al. (2018b) found no differences in $\delta^{34}\text{S}$ values between mammoths from three
897 East European sites and suggested they all ranged over the same area of an undetermined size, while
898 Arppe et al. (2019) demonstrated that mammoths from Wrangel Island experienced a change in
899 ingested $\delta^{34}\text{S}$ values during the isolation of Wrangel from the mainland, which is in agreement with
900 prior results of Sr analysis (Arppe et al., 2009). Future studies analysing $\delta^{34}\text{S}$ from mammoth material
901 could focus on developing $\delta^{34}\text{S}$ isoscapes (as suggested in, for example, Nehlich 2015 and Drucker et
902 al. 2016, 2018b) or compare their results against the recently published $\delta^{34}\text{S}$ isoscape for western
903 Europe (Bataille et al., 2021). Other future endeavours could focus on comparing $\delta^{34}\text{S}$ and $^{87}\text{Sr}/^{86}\text{Sr}$
904 values from the same individuals and analysing intra-tooth variations in $\delta^{34}\text{S}$; especially the large tusks
905 of proboscideans are suitable for the latter. The possibility that dentine can preserve reliable Sr values
906 when preserved in permafrost makes this an even more exciting prospective line of research.

907 *6.5 Implications for Palaeolithic archaeology*

908 Proboscideans first appeared in the archaeological record nearly 2 million years ago (Backwell
909 & D’Errico, 2004; Berthelet & Chavaillon, 2001; Domínguez-Rodrigo et al., 2007; Shipman, 1989), but
910 direct, unambiguous evidence for hunting – in the form of proboscidean bones with hunting lesions –
911 remains sparse until the Upper Palaeolithic (Mothé et al. 2020; Nikolskiy & Pitulko 2013; Pitulko et al.
912 2016; Sinitsyn et al. 2019; Wojtal et al. 2019; Zenin et al. 2006; but see Adam 1951 and Thieme & Veil
913 1985). Mass accumulations of mammoths at archaeological sites in Eurasia like Kraków Spadzista
914 (Wilczyński et al., 2012; Wojtal et al., 2019), and Yana RHS (Basilyan et al., 2011; Nikolskiy & Pitulko,
915 2013) may have been produced entirely by human hunting practices, although some natural input

916 cannot be excluded. In North America, no direct evidence has yet been found for mammoth or
917 mastodon hunting by humans, at least not in the form as defined here and elsewhere (e.g. Wojtal et
918 al. 2019). Mammoth and mastodon remains have, however, been found numerous times in
919 association with lithic projectile points and other lithic tools, and/ or with cutmarks and other forms
920 of anthropogenic modifications. Many of these sites have convincingly been interpreted as the
921 product of hunting as well (e.g. Brunswig & Pitblado 2007 and Haynes & Krasinski 2021 and references
922 therein).

923 The results presented in this paper suggest a degree of variability in proboscidean mobility
924 patterns. Migratory behaviour of reindeer has been demonstrated to have affected subsistence
925 strategies of Neanderthals and anatomically modern humans (Britton et al., 2011; Price et al., 2017).
926 Given the frequency with which proboscidean remains are found in Eurasian and North American
927 Upper Palaeolithic sites, it is not unreasonable to suggest that a degree of migration in mammoths
928 and mastodons may have affected human hunting and subsistence strategies as well.

929 The uniquely large size of proboscidean prey presents specific challenges for contemporary
930 hunters attempting to locate, track, and kill these animals, as does it have an effect on their ways of
931 processing and transporting the food remains and other by-products used within their subsistence
932 economies (e.g. Ichikawa 2021). Assessing how past communities interacted with proboscidean prey
933 and addressed these challenges thus provides a route into reconstructing a range of important aspects
934 of their societies. For example, modern hunter-gatherers adapt their subsistence strategies in
935 accordance with environmental factors, such as (seasonal) abundance and accessibility of flora and
936 fauna (Kelly, 1983; Olsthoorn, 2017). Options to store food for extended periods of time (e.g. Fisher
937 2021) may also factor into their decisions, as well as cultural factors such as diet breadth, hunting
938 specialisation, and a community's customs and beliefs. Given the potential for year-to-year variation
939 in proboscidean mobility, it is likely that hunters were required to respond flexibly to whatever natural
940 variations in mammoth distribution they experienced and it is important that 'messy' data lacking

941 clear patterning is not forgotten, disregarded, or averaged away when making interpretations of these
942 past practices.

943 Only one study has been published to date in which mammoths from archaeological sites were
944 analysed for their $^{87}\text{Sr}/^{86}\text{Sr}$ ratios though their implications for Palaeolithic humans were not discussed
945 (Hoppe, 2004), while more are currently underway (e.g. Kowalik et al. 2018). The effect that different
946 migratory behaviours (seasonal migration, nomadism, or non-migration) had on Palaeolithic
947 subsistence strategies can therefore not yet be properly determined, though it is likely to have varied
948 through time, and between regions and cultures. The temporal variation in mobility of the mastodons
949 in Florida (Hoppe et al., 1999; Hoppe & Koch, 2006, 2007) and the mammoths from Wrangel Island
950 (Arppe et al., 2009) and Jones Spring (Widga et al., 2021) demonstrate the need for detailed
951 investigations for each palaeoenvironmental, chronological and archaeological context. Ideally,
952 multiple individuals would be analysed for intra-tooth $^{87}\text{Sr}/^{86}\text{Sr}$ ratio variations over several years'
953 worth of enamel formation per site. Only then can confident inferences be made about the
954 predictability and perils of mammoths and mastodons as prey to Palaeolithic hominins.

955 **7. Conclusion**

956 This review of modern ecological and archaeological/paleontological $^{87}\text{Sr}/^{86}\text{Sr}$ studies has
957 demonstrated that the complexity of extinct proboscidean mobility cannot be captured by a simple
958 yes-no question (sensu Churcher 1980 *'Did the North American Mammoth Migrate?'*). Instead,
959 evidence points to both inter- and intra-species variation in mobility, which can vary between
960 individuals and between years. Data on African savannah elephants show some individuals are
961 seasonal migrants, others adjust their behaviour to the annually changing ecological conditions, and
962 others still stay true to a single home range. Habitat appears to be a key factor influencing mobility in
963 all modern elephant species, with the largest home ranges found in open environments. The
964 difference in water-preservation abilities between open and canopy habitats is probably the most
965 important characteristic, as this influences the year-round availability of water, as well as food

966 quantity and quality. Water and food availability will also have played an important part in the mobility
967 of extinct proboscideans, both within and between species, and it is expected that mammoths had
968 high mobility because they are often found in association with open, arid environments in northern
969 latitudes. While mastodons were most common in forested environments, they too could have been
970 very mobile at times due to a specialised diet or food-resource competition. Biological sex is an
971 important factor affecting mobility in modern elephants as well, with bulls in musth ranging farther
972 than non-musth bulls and females, and sex is expected to have had a substantial effect on the mobility
973 of extinct proboscideans as well. Unfortunately, sex can rarely be determined for proboscidean fossils
974 and its effect on $^{87}\text{Sr}/^{86}\text{Sr}$ and $\delta^{34}\text{S}$ results is therefore unknown. With the recent development of
975 genome-based sexing (de Flamingh et al., 2020; Pečnerová et al., 2017; Wooller et al., 2021),
976 determining the sex of morphologically indiscriminate molars and tusks will hopefully become more
977 accessible.

978 Recent advances in isotope studies have enabled researchers to examine past proboscidean
979 mobility through analysis of $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in bones and teeth. Analyses of woolly and Columbian
980 mammoth and mastodon fossils from Europe, northern Asia, and North America have produced
981 evidence for variability in the migratory behaviour both between and within species. The mobility of
982 woolly mammoths has also been studied through the analysis of $\delta^{34}\text{S}$. The behaviour of $\delta^{34}\text{S}$ in nature
983 and osseous material is not yet understood well-enough to add insights as detailed as those from
984 $^{87}\text{Sr}/^{86}\text{Sr}$ studies, but it holds great potential for future studies.

985 Because of the demonstrated variation in mobility in both modern and extinct proboscideans,
986 it is important for future studies – both archaeological and paleontological – to analyse intra-tooth
987 data covering multiple years of dental enamel formation from multiple individuals. Ideally, molars are
988 analysed via closely spaced sequential samples or LA-MC-ICPMS, as bulk samples of 1.5 cm are too
989 vulnerable to the variability in proboscidean mobility and results will inevitably be affected by this
990 variability. The recent increase in quantity and resolution of analyses of intra-tooth $^{87}\text{Sr}/^{86}\text{Sr}$ data

991 offers the opportunity to examine inter-individual variation in mobility in more detail and therefore is
992 an exciting prospect for the improvement of our understanding of past proboscidean mobility.

993 **CRedit author statement**

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