

1 **Title:** Late Pleistocene prey mobility in southwestern France and its implications for
2 reconstructing Neandertal ranging behaviors

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34 **Highlights**

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36 • **We use strontium isotope data from two Late Pleistocene (Middle Palaeolithic) sites**
37 **in southwestern France to explore the movement behaviors of large ungulates**
38 • **Our results suggest that the main prey species (reindeer and bison) did not**
39 **undertake movements across the Massif Central and that their range use did not**
40 **extend beyond the basins of France.**

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43 **Key Words**

44 $^{87}\text{Sr}/^{86}\text{Sr}$ analysis, Neandertal prey mobility, reindeer migration, Aquitaine, Dordogne, Pech de

45 l'Azé IV, Roc de Marsal, paleoecology

46

47 **ABSTRACT**

48
49 As hunter-gatherers, Neandertal mobility and corresponding adaptations were influenced
50 by the mobility of their prey; thus, it is critical to track how the movement patterns of each
51 species varied over time at specific sites. Here, prey paleomobility is reconstructed by
52 measuring radiogenic strontium isotope ratios ($^{87}\text{Sr}/^{86}\text{Sr}$) in herbivore teeth recovered from two
53 archaeological sites (Pech de l'Azé IV and Roc de Marsal) in the Dordogne Valley (Aquitaine
54 Basin) of southwestern France that span marine isotope stages (MIS) 5-3. These ratios are
55 compared to a published isoscape as well as new environmental samples (soil, *Helix* shells,
56 rodent teeth, water, and wine). Our results show that reindeer (*Rangifer*) likely moved within the
57 sedimentary basins of France and did not venture into mountainous regions. Instead, reindeer,
58 bison (*Bison*) and other prey species were available year-round in the Aquitaine and Paris basins.
59 Red deer (*Cervus*) and horse (*Equus*) may have ventured into the mountains. These results
60 suggest that Neandertals could find year-round faunal resources in these basins, at least during
61 MIS 4 and 3.

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64 **1. Introduction**

65 In interpreting Neandertal hunting behaviors, it is often thought that European Pleistocene
66 ungulates, particularly reindeer (*Rangifer tarandus*), undertook long distance round-trip
67 migrations (Bahn, 1977; Burch, 1972; Gordon, 1988; Morin, 2004; Straus, 1997; Sturdy, 1975).
68 For example, zooarchaeological studies in France proposed *Rangifer* spent their winters in
69 southwestern France and northern Spain, but during the summer they would move to areas with
70 tundra (e.g., Scandinavia or Switzerland), or up into the mountains close to glaciers (e.g., the
71 Massif Central or Pyrénées), or that they would make seasonal movements between the Massif

72 Central and the Bay of Biscay (Arbos, 1932; Bahn, 1977; Dibble and Rolland, 1992; Gordon,
73 1988; Mellars, 1985; Straus, 1997). Archaeological evidence supporting the hypothesis that
74 *Rangifer* in southern France were migratory came from seasonality studies based on the eruption,
75 wear, and cementum growth of herbivore teeth and on antler growth patterns (Bahn, 1977; Burke
76 and Pike-Tay, 1997; Delpech, 1983; Enloe and David, 1997; Gordon, 1988). Limited isotope
77 studies undertaken in the region to date also provided some evidence of seasonal migration, but –
78 given the lack of diversity in local bioavailable strontium – distances of such migrations have been
79 difficult to infer. Britton et al. (2011) conducted a radiogenic strontium (Sr) isotopic study of three
80 *Rangifer* and a single *Bison* individual from the Quina Mousterian unit W-22 of Jonzac (also
81 known as Chez-Pinaud), located in the Charente-Maritime region of southwestern France, and
82 concluded that *Rangifer* from that site were likely migratory (i.e., demonstrated intra-tooth
83 variation in strontium consistent with seasonal movements). However, given that all $^{87}\text{Sr}/^{86}\text{Sr}$
84 ranges fell within variability found within the broader Aquitaine and Paris basins, distances could
85 not be estimated and indeed seasonal movements may have been restricted to those regions with
86 no evidence of traversing mountainous areas. The single *Bison* specimen from Jonzac fell within
87 local variability immediate to the site and, in contrast to the reindeer, showed no seasonal
88 variability. A radiogenic Sr study of the Middle Paleolithic fauna from the nearby Les Pradelles
89 also did not find evidence of basin-mountain migration (Kelly, 2007). Furthermore, some analyses
90 of antler growth patterns, tooth wear and other palaeoecological studies based on fauna have
91 argued that *Rangifer* in this region were not migrating long distances (see Bouchud, 1966; Mellars,
92 1985), with some authors suggesting that at least some groups of *Rangifer* were present year-round
93 (Bouchud, 1966; Delpech, 1983; Lartet and Christy, 1875; Pike-Tay, 1991; White, 1985).
94 Evidence suggesting that *Rangifer* did not move into the mountains within and surrounding France

95 and that *Bison* ranged locally is intriguing, and of course mobility patterns of prey species can be
96 variable by location and time, so it is important to track these movements site by site and through
97 different climatic phases.

98 In a broad analysis including stone tool reduction, faunal remains and paleoclimatic
99 reconstructions, Dibble and Rolland (1992) suggested that during cold glacial cycles when
100 *Rangifer* dominated faunal assemblages Neandertals may have had long winter occupations in
101 southwestern France, moving little during the winter months. During interglacial cycles when
102 *Bison*, *Cervus*, and *Equus* dominated archaeological sites Neandertals may have been more mobile,
103 occupying sites for short periods of time. Other researchers have pointed out that the abundance
104 of animal species present during the Middle and Upper Paleolithic of southwestern France may
105 have created a stable and predictable supply of food year-round, possibly leading to less mobile
106 hunter-gatherer groups (Mellars, 1985; Spiess, 1979). Burke and Pike-Tay (1997) have suggested
107 that if seasonality data on *Cervus*, *Rangifer* and *Equus* remains from Late Upper Paleolithic sites
108 in southwestern France are compared to each other, the data point to an annual hunting range of
109 only 40-50 km within the northeastern portion of the Aquitaine basin. If hunter-gatherers living in
110 the Aquitaine basin had access to reliable resources year-round, they may have sustained higher
111 population concentrations (Mellars, 1985; Spiess, 1979), although ethnographic studies of groups
112 whose hunting economy is concentrated on many different terrestrial herbivores have been
113 reported to live in small family groupings (Speck and Eiseley, 1942).

114 With the goal of exploring the paleoecology of the prey-species Neandertals depended on
115 in southwestern France, thus contextualizing Neandertal behavior, here we use radiogenic
116 strontium isotope analysis of *Rangifer*, *Bison*, *Equus*, *Cervus* and *Capreolus* (roe deer) teeth
117 excavated from two French Neandertal sites: Pech de l'Azé IV (Bordes' 1970-1977 excavation)

118 and Roc de Marsal (the most recent excavations; hereafter Pech IV and RDM, respectively) in the
119 Dordogne Valley (Aquitaine Basin, SW France) to explore whether or not these species' ranging
120 habits were extending beyond the sedimentary basins of France at that time. We predict that if
121 herbivores were spending time in the mountains, the $^{87}\text{Sr}/^{86}\text{Sr}$ in their teeth should range from
122 relatively low values consistent with foraging in the sedimentary basins of France, to relatively
123 high values consistent with foraging in areas with older geological substrates.

124

125 **2. Background**

126 Understanding Neandertal behavior and local ecology requires knowledge of the behaviors
127 of their prey, including whether animals were long distance migrants or stayed within smaller
128 ranges. Relying on supposedly species-typical behaviors to infer prey mobility can be problematic
129 when there is environmentally-mediated variation in how animals move. For example, populations
130 of ungulates that live in more wooded environments migrate less than ungulates that live in tundra
131 and grassland environments because food resources are distributed in patches that are
132 geographically closer together in woodland environments than in open tundra and grassland
133 ecosystems (Johnson et al., 2002a, 2002b, 2001; Senft et al., 1987; Skogland, 1984; Tyler and
134 Øritsland, 1989). Thus, robust paleobiological reconstruction of Neandertal prey mobility should
135 draw on multiple lines of evidence including environmental proxies and direct or indirect evidence
136 for animal movement (e.g., strontium stable isotopes).

137 Ecologists have emphasized that the word 'migration' is used to describe many types of
138 movement patterns including (but not restricted to): round trip 'seasonal' travel, one-way
139 movements, (often seasonal) altitudinal shifts, and even nomadism, in which an animal does not
140 follow a predictable route but forages opportunistically (Dingle and Drake, 2007). While these

141 movement behaviors manifest themselves in different ways, ultimately migratory behaviors are a
142 response to ecological stimuli and thus different populations within one taxon can exhibit different
143 behaviors (Dingle and Drake, 2007). Long distance, round-trip migratory behavior in large
144 ungulates has been shown to be selectively advantageous for two main reasons: 1) to enhance
145 temporary access to high quality food in areas that cannot be inhabited year-round (*resource*
146 *tracking*) and 2) to reduce risk of predation (Abraham et al., 2022; Fryxell and Sinclair, 1988;
147 Tyler and Øritsland, 1989). Exposure to insects, other parasites and diseases also drive movement
148 patterns in large ungulates (Downes et al., 1986; Grayson and Delpech, 2005; Russell et al., 1993).
149 Some populations that live in productively poor ecosystems compensate by migrating over vast
150 distances seasonally, such as *Rangifer* (caribou = North American reindeer, reindeer = European
151 *Rangifer*) that live on the open tundra and *Bison* (*Bison bison bison*) of North America (e.g., some
152 grassland environments). The average round-trip migration distance measured among three
153 different herds of barren ground caribou is 1673 ± 491 km, with the longest distance measured at
154 2500 km (Berger, 2004; Bergerud, 1974; Brown et al., 1986). Similarly, *Bison* that occupy habitats
155 that are low in productivity move within areas of 712 km^2 - 1240 km^2 (Berger, 2004; Hanson,
156 1984; Reynolds et al., 2003).

157 Non-migratory ecotypes of *Rangifer* (often referred to as ‘woodland caribou’) live
158 throughout Canada (e.g., north-central British Columbia, northeastern Alberta, Ontario,
159 northwestern Quebec, Labrador) and in the northwestern United States (e.g., Montana, Idaho, and
160 Washington) (Brown et al., 1986; Evans, 1960; Johnson et al., 2002b, 2001; Layser, 1974; Stuart-
161 Smith et al., 1997). The non-migratory ecotype can also be found today in the Norwegian arctic
162 archipelago of Svalbard and in Finland (Kojola et al., 2004; Tyler and Øritsland, 1989). In North
163 America, herds of non-migratory *Bison* (often referred to as wood bison) historically inhabited

164 much of the same habitats as non-migratory *Rangifer* with species ranges extending from
165 northwestern Canada into eastern Alaska (Reynolds et al., 2003). In Europe, non-migratory *Bison*
166 inhabited forests in northern, eastern, and western Europe (Pucek et al., 2004); environments
167 composed of mosaic habitats of pine and spruce woodlands with feather mosses and lichens,
168 shrub/sedge and forb-dominated wetlands, river and lake environments, alpine shrublands and
169 alpine grasslands (Johnson et al., 2002b). In general, the migratory behavior of *Rangifer* and *Bison*
170 appear to be regulated by the temporal and spatial variability of resources, particularly lichen,
171 sedges, and grasses (Johnson et al., 2002a, 2001; Larter and Gates, 1991; Tyler and Øritsland,
172 1989). In southwestern France, relatively positive $\delta^{13}\text{C}$ values of Late Pleistocene *Rangifer* have
173 been measured between 33-15 ka (Drucker et al., 2003) suggesting that lichens were contributing
174 to reindeer diets, although this is not the case for all periods and all regions of France. For example,
175 data from the MIS 3 site of Abri du Maras indicate that lichen consumption was low and that
176 reindeer diets were similar to that of other cervids (Britton et al. 2023).

177 To better understand the diversity of prey animals available to Neandertals in the Dordogne
178 valley over time, three additional species found at Neandertal sites in high abundance are analyzed
179 in this study: horse (*Equus ferus*), red deer (*Cervus elaphus*), and roe deer (*Capreolus capreolus*).
180 Living horse populations have been heavily influenced by domestication, altering modern horse
181 behavior and ecology (Bendrey, 2012). van Asperen (2010) notes that horses from the Middle
182 Pleistocene of northwestern Europe seem to have been less mobile than modern Przewalski's
183 horses (*Equus ferus przewalskii*) and onagers (*Equus hemionus*). Ecomorphological and isotopic
184 dietary studies of caballoid horses from the Middle to Late Pleistocene demonstrate that they were
185 grazers in predominantly open forests and grasslands, though some horse assemblages suggest that
186 they could also forage in more closed habitats (Boulbes and Van Asperen, 2019). Middle to Late

187 Pleistocene horse remains have been found at archaeological sites with paleoenvironmental
188 contexts ranging from open glacial steppes to closed forests (van Asperen, 2010). The strontium
189 isotope analysis conducted here will help clarify how this species behaved in the Pleistocene of
190 southwestern France, as well as adding to information about the availability of Neandertal prey at
191 the sites of RDM and Pech IV.

192 A plethora of research has been conducted on the movement patterns of red deer (*Cervus*
193 *elaphus*) (Albon and Langvatn, 1992; Georgii, 1980; Georgii and Schröder, 1983; Peek, 2003;
194 Pike-Tay, 1991). *Cervus* populations are widely distributed with extant populations ranging
195 throughout western North America, northern Africa, and from western Europe to Siberia (Mahmut
196 et al., 2002; Peek, 2003). Many *Cervus* populations are known to move from lower altitudes in the
197 winter to higher altitudes in the summer (Albon and Langvatn, 1992) and also from coastal to
198 inland areas. These seasonal shifts prolong access to high quality food resources (Albon and
199 Langvatn, 1992). However, as is the case with the other large herbivores studied here, a great deal
200 of variability has been observed in *Cervus* movement patterns (Albon and Langvatn, 1992;
201 Georgii, 1980; Georgii and Schröder, 1983; Peek, 2003; Schmidt, 1993), with some groups
202 (including populations in the Alps) undertaking long distance migrations, while other groups are
203 non-migratory (Georgii, 1980; Georgii and Schröder, 1983; Peek, 2003). Once again, this
204 variability in migratory behavior and home range size appears to be the product of the availability
205 of food resources, difficulty of travel, cover quality, and the presence of insects (Brazda, 1953;
206 Peek, 2003). One study of Pleistocene red deer focused on MIS 6 levels at Lazaret Cave in France.
207 While the red deer showed strong seasonality of movement in their intra-tooth profiles, spatial
208 assignment indicates that both the summer and winter ranges can be found within 20-30 km of the
209 site, and that the migrations were likely to have been altitudinal (summer in the uplands, winter in

210 the lowlands) (Barakat et al. 2023). This highlights that while strontium can reveal seasonal
211 movement patterns in ungulates effectively when combined with serial-sampling, especially in
212 regions of highly variable lithology (e.g., southwest France), those movements may not be
213 occurring over long distances. Similarly, in areas of homogenous lithology, long-distance
214 movements may not be clear from intra-tooth strontium profiles alone, thus detailed analyses are
215 needed.

216 Roe deer (*Capreolus capreolus*) are small cervids (15-35 kg) that live in woodlands,
217 heathlands, and grasslands (Lovari et al., 2017; Saïd et al., 2005; Tufto et al., 1996). *Capreolus*
218 are non-migratory, though snow accumulation has been observed to cause some groups to move
219 short distances seasonally. For example, Ramanzin et al. (2007) tracked radio-collared *Capreolus*
220 in alpine regions of Italy as they moved 12.0 ± 6.2 km from higher-elevation summer ranges to
221 lower elevation winter ranges. Throughout the year median home range size for males is 16.7 ha
222 with a range of 13-31 ha, and 23 ha for females with a range of 13-44 ha (Lovari et al., 2017).
223 Home range size for the species is influenced by plant biomass and reproductive success with more
224 offspring leading to larger home-ranges for females (Saïd et al., 2005). Because *Capreolus* is (and
225 likely was) a non-migratory species with small home range size, they can be used a control species:
226 the radiogenic isotope analysis of the teeth of *Capreolus* will indicate what values we should
227 expect from a local prey species, we can then compare the extent to which isotopic values of other
228 species differ.

229 Knowledge about the environments in which modern populations live and the movement
230 behaviors undertaken by herds living in different types of environments inform us as to how
231 populations of animals would have behaved in the past. Much of the ecological literature has
232 concluded that, during the Pleistocene, areas of southwestern Europe acted as a refugium for trees

233 (e.g., spruce, pine, oak, elm, beech), faunal species and hominins (Barron et al., 2003; de Beaulieu
234 and Reille, 1992; Huntley and Allen, 2003) during cold climatic oscillations. Reconstructed
235 temperature ranges for southern France during MIS 3 (~59-37 ka) appear to have been similar to
236 temperatures observed in modern boreal forests, inhabited by woodland species today (e.g.,
237 modern boreal forest = 5 °C in winter and 17 °C in summer) (Barron et al., 2003; Huntley and
238 Allen, 2003; Pederzani et al., 2021). If these temperature reconstructions are accurate, then
239 mammals living in these environments may have behaved more like extant woodland-dwelling
240 ungulates in undertaking movements within the basins of France (Bouchud, 1966; Delpech, 1983;
241 Lartet and Christy, 1875; Pike-Tay, 1991; White, 1985), effectively creating an environment with
242 dispersed but dense patches of resources (Binford, 1980; Kelly, 1992; Lieberman and Shea, 1994).
243 If this is true, Neandertals would have been able to hunt populations of herbivores year-round
244 within the French basins. In this case a pattern of radiating mobility with sites that served as multi-
245 seasonal base camps, as proposed by many researchers (Binford, 1980; Kelly, 1992; Lieberman
246 and Shea, 1994; Turq et al., 2017), may be supported. In contrast, temperature reconstructions
247 based on oxygen isotopic ratios in equid enamel phosphates suggest stronger temperature
248 seasonality during MIS 3 compared to today in the Rhône Valley at the site of Abri du Maras (as
249 extreme as -10 °C in winter and 31 °C in summer) and – in that phase of the site at least – these
250 conditions are associated with a migratory ecotype of *Rangifer tarandus* (Britton et al., 2023).

251

252 **2.2. Radiogenic isotopic migration studies**

253 Radiogenic Sr isotopic studies have been used to track migration patterns in modern and
254 archaeological animal and human populations (e.g., Britton et al., 2011; 2023; Baraket et al. 2023;
255 Copeland et al., 2016; Ericson, 1985; Hodgkins et al., 2020, 2018; Hoppe et al., 1999; Knudson et

256 al., 2004; Price et al., 1994; Scharlotta et al., 2011), including Neandertals (e.g., Moncel et al.,
257 2019; Richards et al., 2008). To “ground-truth” the method for use in fossil *Rangifer*, Britton et al.
258 (2009) analyzed radiogenic Sr isotope ratios in the teeth of extant *Rangifer* belonging to the
259 Western Arctic Herd in Alaska for which the migratory behavior was known. Results from their
260 analysis showed that the ratios found in the second and third molars of each deer broadly matched
261 the geological ratios throughout the migration route demonstrating that this is an effective method
262 for tracking *Rangifer* migrations, an approach which has since also proven valid when using laser
263 ablation (Le Corre et al. 2023).

264 As summarized in Price et al. (2002), radiogenic Sr ratios are useful for tracking migrations
265 because the bedrock of a particular geological region has a characteristic isotopic signature. That
266 is because different rock types have different initial content of calcium (Ca) and potassium (K),
267 which are substituted for by Sr and rubidium (Rb), respectively. Through time, ^{87}Rb decays to ^{87}Sr ,
268 increasing $^{87}\text{Sr}/^{86}\text{Sr}$ values. Thus, old K-rich rocks (e.g., granite) have higher $^{87}\text{Sr}/^{86}\text{Sr}$ values than
269 young Ca-rich ones (e.g., limestone) (Bentley, 2006). As bedrock is eroded by water, wind and
270 chemical weathering, Sr enters the hydrological system and is taken up by plants, which are
271 ingested by herbivores. Sr is incorporated into herbivore teeth as a substitute for Ca; consequently,
272 the $^{87}\text{Sr}/^{86}\text{Sr}$ signature of an herbivore's teeth is generally indicative of where the animal was as its
273 dentition developed. Thus, if $^{87}\text{Sr}/^{86}\text{Sr}$ within one region is distinct from adjacent areas, measuring
274 $^{87}\text{Sr}/^{86}\text{Sr}$ at multiple loci across the tooth crown that formed over several months can indicate if
275 the animal was moving between those areas (Britton et al., 2009; Lazzerini et al., 2021; Miller et
276 al., 2022). While high-density sampling down the entire length of the crown (either using
277 traditional intra-tooth sampling, or laser ablation) is desirable and likely necessary to observe
278 repeated (i.e., back and forth) movement behaviors, spot sampling at a smaller number of intervals

279 down the crown should be sufficient to identify any potential major shift in $^{87}\text{Sr}/^{86}\text{Sr}$ during tooth
280 formation. This study will employ such an approach – targeting 2-3 sampling points per tooth for
281 low crowned species such as *Rangifer* and *Cervus* and *Capreolus* (closest to the occlusal surface,
282 closest to the enamel-root junction, at the midpoint of the crown), while targeting up to 8 sampling
283 points per tooth on high crowned teeth from species such as *Equus*, to specifically assess whether
284 the herbivores sampled moved between the sedimentary basins in France (i.e. areas with low
285 $^{87}\text{Sr}/^{86}\text{Sr}$ strontium values) or to regions outside of the basins, which have higher $^{87}\text{Sr}/^{86}\text{Sr}$ values.

286

287 **2.3. The sites of Pech de l’Azé IV and Roc de Marsal**

288 Pech de l’Azé IV (Pech IV) is a collapsed cave and part of a larger group of sites in a dry
289 tributary valley of the Dordogne River. The site was discovered and tested in 1952 by François
290 Bordes, and then trenched by an amateur archaeologist between 1953-1956. Bordes directed
291 excavations there between 1970 and 1977, exposing an area of 52 m² and an archaeological
292 sequence with a maximum depth of 4.5 m. For a history of research at Pech IV and neighboring
293 sites see Sandgathe et al. (2018). The lithic artefacts recovered played an important role in
294 Bordes’ definition of several of the Mousterian *facies* (Bordes, 1975). Bordes excavated in 1 m²
295 squares following natural stratigraphy and archaeological features, and piece-plotting finds with
296 tape measurements. More recently, Dibble and McPherron’s 2000-2003 excavations
297 demonstrated good stratigraphic agreement with Bordes’ (Dibble et al. 2018). The specimens we
298 analyzed come from the 1970-1977 campaigns, specifically from Levels I2, Y and Z (the latter
299 being the two lowermost levels in the sequence). All these levels were assigned to the Typical
300 Mousterian (Bordes, 1975). Bordes’ Level I2 corresponds to Dibble and McPherron’s Layer 4C,
301 and Levels Y and Z collectively correspond to Layer 8 and are therefore lumped together here as

302 Level YZ. Layer 4C is characterized by abundant roof spall and occurrence of gelifraction, while
303 Layer 8 is characterized by abundant traces of burning, particularly burned bone, burned lithics,
304 ash, char (gelified organic matter) and reddened sediment (Goldberg et al., 2018). Bordes'
305 (1975) descriptions of Levels I2 and YZ are consistent with these observations. Two
306 thermoluminescence (TL) dates (68.5 ± 6.6 and 71.8 ± 6.7 thousand years [ka] before present
307 [BP]) place Layer 4C in the cold marine isotope stage (MIS) 4 (Richter et al., 2013), consistent
308 with the frost-related features (roof spall and gelifraction) mentioned above. This age is
309 consistent with the weighted mean OSL age of 68 ± 4 (Jacobs et al. 2016; Jankowski, 2018).
310 Layer 8 has a weighted mean age of 94 ± 4 based on OSL (Jacobs et al. 2016; Jankowski, 2018),
311 which is consistent with a TL age of 96 ± 5 ka BP (Richter et al., 2013). Charcoal recovered from
312 Layer 8 comes from temperate woodland taxa including oak, birch, elm and hornbeam (Dibble et
313 al., 2009). Therefore, we assign the specimens from Level YZ to the interglacial MIS 5 (late MIS
314 5c and/or early MIS 5b). The fauna is consistent with these age determinations, being dominated
315 by reindeer in Layer 4C/I2 and by red deer in Layer 8/YZ (Hodgkins et al., 2016; Niven and
316 Martin, 2018).

317 Roc de Marsal (RDM) is located in the valley of a tributary of the Vézère River near the
318 town of Le Bugue. The site was first excavated by Jean Lafille between 1953-1971 (Lafille,
319 1961; Turq et al., 2017), leading to the discovery of a Neandertal child (Bordes and Lafille,
320 1962; Gómez-Olivencia and García-Martínez, 2019; Legoux, 1966). New excavations between
321 2004-2010 recognized 13 layers, with layers 10-2 containing significant Middle Paleolithic
322 remains (Reeves et al., 2019; Turq et al. 2008). Our samples come from layers 4, 7, 8 and 9 of
323 the new excavations. For chronological purposes, the sequence is divided into an upper part
324 dominated by Mousterian Quina technology (layers 4-2) and a lower part dominated by Levallois

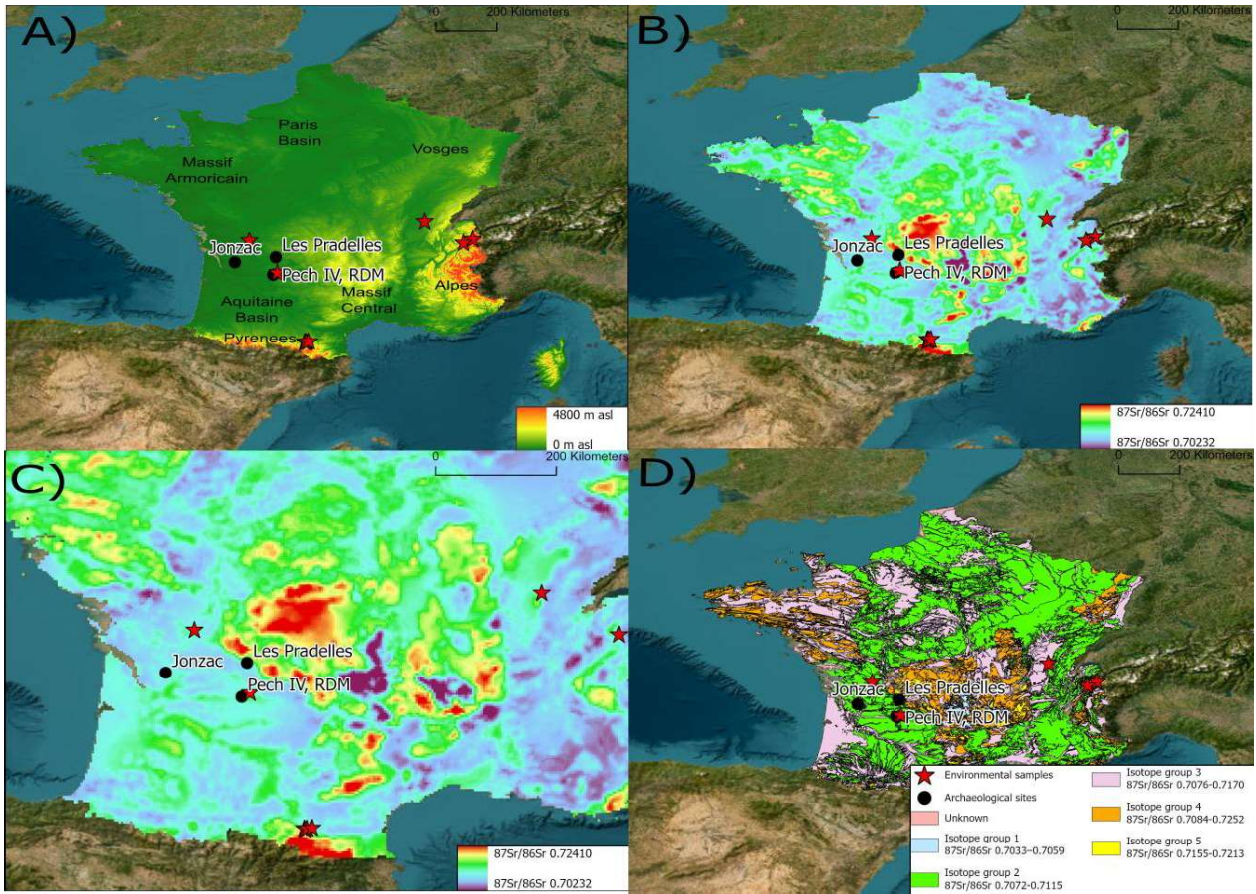
325 technology with the base being richer in denticulates (layers 9-5). The two aggregates have been
326 dated through a combination of TL, OSL and infrared stimulated luminescence to ~ 49 ka BP
327 and ~70-65 ka BP, respectively (Guérin et al., 2017). Therefore, based on the luminescence
328 dating, the upper aggregate, including our samples from Layer 4, are associated with MIS 3,
329 while the lower aggregate, including our samples from layers 7-9, are associated with MIS 4.
330 However, the large mammal remains and phytoliths suggest that the upper aggregate formed
331 during colder conditions and the lower during milder and more humid ones (Hodgkins et al.,
332 2016; Wroth et al., 2019).

333

334 **3. Materials and Methods**

335 Samples for this study include archaeological specimens of *Rangifer*, *Bison*, *Equus*, *Cervus*,
336 *Capreolus* and rodent (*Microtus arvalis*) teeth, which were collected from the sites of Pech IV and
337 RDM. In addition to these samples, wine, soil, water and snail shells (*Helix aspersa*) were also
338 collected following standard protocols for developing baseline datasets for strontium (see Bentley,
339 2006; Evans and Tatham, 2004) throughout France to identify distinct isotopic regions and to
340 establish where herbivores may have been living and/or moving during tooth development (see
341 Table 3 and Figure 1; GPS coordinates available in Supplementary Online Material). One sample
342 location was the town of Les Eyzies, located 10 km from RDM and 30 km from Pech IV, which
343 was used to help establish the range of $^{87}\text{Sr}/^{86}\text{Sr}$ values found close to the sites (Figure 1 Map A).
344 Modern snail shell samples were obtained from Mansle, located 158 km away from the
345 archaeological sites in the northern portion of the Aquitaine Basin (Figure 1 Map A). These
346 samples will be referred to throughout the paper as “local” values. Additional modern samples
347 were taken in the Alps, Pyrénées, and the edge of the Massif Armorican. The values obtained from

348 all samples collected will be compared to values published in Willmes et al., (2018). The geology
 349 of France is complex being characterized by basins (Aquitaine and Paris basins) composed of
 350 young sediments and uplifted hills, plateaus, and mountainous areas composed of older granites.
 351 The presence of these distinctive regions increases the likelihood that mammal movement patterns
 352 can be tracked across the landscape.



353
 354
 355 **Figure 1: A) Topographic map with the major geographic features of France discussed in**
 356 **the text with archaeological sites (black dots shown on all maps) and isotopic sampling sites**
 357 **collect for this paper indicated (red stars shown on all maps). B) Isoscape of bioavailable**
 358 **strontium in France (Willmes et al. 2014; data from IRHUM). C) Zoomed-in isoscape of**
 359 **bioavailable strontium in France focused on the Aquitaine basin. (Willmes et al. 2014; data**
 360 **from IRHUM). D) Isotope groups as determined by Willmes et al. (2018).**

361
 362 Isotope sampling took place in the Archaeological Chemistry Laboratory (ACL) at Arizona
 363 State University (ASU) and in the Facility for Isotope Research and Student Training (FIRST) at
 364 Stony Brook University (SBU). A first set of samples (hereafter Set 1) including all modern *Helix*
 365 shells (n = 7), soils (n = 5), water (n = 8), wine (n = 3), rodent teeth (n = 3) and a portion of
 366 archaeological herbivore teeth (n_{samples} = 63) was prepared for Sr isotope analysis in the Metals,
 367 Environmental and Terrestrial Analytical Laboratory (METAL) at ASU and at the class 100 HEPA
 368 filtered FIRST lab in the Department of Geosciences at SBU. A second set of samples (hereafter
 369 Set 2) including archaeological herbivore teeth (n_{samples} = 44) was prepared in the Picotrace class
 370 ten clean room at the Metal Geochemistry Center of the Department of Earth and Planetary
 371 Sciences at Yale University.

372 The archaeological samples include molars and premolars of herbivores and rodents.
 373 Studies of dental development and eruption in ungulates demonstrate that these teeth develop over
 374 the first few years of life in these animals (see Table 1); thus, linearly-sampling enamel bands at
 375 intervals from each tooth has the potential to gain several ‘snapshots’ into range use during the
 376 period of tooth formation and to compare those data to the local bioavailable values where the
 377 teeth were found.

378

379 Table 1. Tooth crown formation and eruption of relevant teeth in large herbivores

Taxon	Tooth	Enamel mineralization	Crown eruption	References
<i>Rangifer</i>	M1	begins <i>in utero</i>	3-5 months	
	M2	starts <3.5 months	9-12 months	1,2,3,5,7,9
	M3	starts at 9-12 months	< 24 months	
<i>Cervus</i>	M1	begins <i>in utero</i>	3-5 months	3,5
	M2	starts <3 months	10-15 months	
	M3	starts at 9 months	15-29 months	
<i>Equus</i>	M1	birth to 23 months	8-12 months	5,6,7,8,10

	M2	7-37 months	20-26 months	
	M3	21-55 months	~3.5 years	
	P2	13-31 months	~2.5 years	
	P4	19-51 months	~4 years	
<i>Bison</i>	M1	begins <i>in utero</i>	9-12 months	
	M2	birth to 13 months	18 months	4,7
	M3	9-24 months	2.5-3 years	
<i>Capreolus</i>	P4	birth to 10 months	11-15 months	11

380
381 References for Table 1. ¹ Britton et al. (2011); ² Wu et al. 2012; ³ Brown and Chapman, 1991;
382 ⁴ Gadbury et al., 2000; ⁵ Hillson, 2005; ⁶ Hoppe et al., 2004; ⁷ Kelly, 2007; ⁸ Levine, 1982; ⁹ Spiess,
383 1979; ¹⁰ Tomé and Vigne, 2003)
384

385
386 Enamel forms in two waves with different rates and geometry: secretion of a matrix (~20-
387 30% of final mineral weight) and maturation (~70% of final mineral weight) (Green et al., 2017).
388 During maturation, enamel is an open system and diffusion of elements occurs, resulting in
389 averaging of the chemical signal (Balasse, 2003; Bentley, 2006; Fincham et al., 1999; Montgomery
390 et al., 2010; Scharlotta et al., 2011). However, environmental chemistry is still reflected – albeit in
391 attenuated form – throughout the tooth (e.g., Green et al., 2018; Uno et al., 2020).

392 Ideally, strontium isotope analyses would be conducted on individual mandibles or
393 maxillae with all molars present, or at least on second and third molar pairs (Britton et al., 2011);
394 however, it is difficult to find well preserved and associated dentition in archaeological
395 assemblages. At the time this study was undertaken, two partial mandibles were available from
396 RDM layer 4 for sampling, with mostly complete premolar and molar dentitions: specimens J17-
397 2266 a bison, and J18-1379 a *Rangifer*. In these specimens, isotope samples were taken from all
398 available molars. In addition to these specimens, a *Cervus* mandible (F17-2485) was recovered
399 from Pech IV layer YZ that contained the second and third molars, and these teeth were sampled.
400 In order to expand the dataset to help establish whether or not different species were likely to have

401 inhabited ranges that included regions outside of the Aquitaine Basin, it was necessary to also
402 analyze single unassociated teeth. Teeth were chosen that appeared to be well preserved,
403 displaying few cracks in the enamel, and with as little discoloration as possible. Teeth were also
404 chosen based on the extent of wear. Teeth categorized as having no wear to early-wear were
405 prioritized; however, these teeth were not common and nearly half of the specimens sampled were
406 categorized as mid-wear, which means that strontium accumulated in these teeth during the first
407 few months of development could not be sampled due to wear.

408 At Pech IV a total of 11 individuals (12 teeth) were sampled. From layer I2 these specimens
409 included: five *Rangifer* ($M^{1 \text{ or } 2}$, $M^{1 \text{ or } 2}$, M_1 , M_3 , P/M), two *Bison* (M^1 , M_2), and one *Equus* (M^1),
410 which were excavated from units distributed throughout the cave (squares C13, D11, D14, D17,
411 E11, F16). Specimens from layer YZ included: two *Cervus* (one partial mandible with M_2 - M_3 and
412 one isolated M^1) one *Equus* (M_2). These specimens were excavated from a unit located in the
413 mouth of the cave (F16, F17, M15).

414 A total of 18 specimens (20 teeth) were sampled from RDM. From layer 4, these specimens
415 included one bison (partial mandible with M_1 and M_2), five *Rangifer* (one partial mandible with
416 M_1 to M_3 row, and isolated $M^{1 \text{ or } 2}$, M^1 , $M^{1 \text{ or } 2}$, M^3), one *Cervus* (M^1) and two *Equus* (M^2 and P^2)
417 excavated from just inside the cave mouth (squares J16, J17, J18, K16, K17). A single rodent tooth
418 from layer 7 was analyzed. Specimens analyzed from layer 8 included: two *Rangifer* (M_3 , M_1),
419 two *Cervus* (M_1 , M^3), two *Equus* (P_4 , P/M), one *Capreolus* (P_4) and one rodent excavated from
420 squares located just inside the cave mouth and on the terrace just outside the cave (G18, K17,
421 K18,). For layer 9 sampled specimens included two *Cervus* (M^3 , M_1) and one rodent, recovered
422 from just inside and just outside the cave mouth (squares F18, G18, K17).

423 To determine if the teeth analyzed in this study have been diagenetically contaminated over
424 time, major, minor, and trace element analysis (referred to throughout as elemental analysis) was
425 run on a sub-set of herbivore teeth from each site. All archaeological materials are subject to
426 diagenetic processes, but these processes are not uniform over space or time, and therefore
427 specimens buried in different locations within the same site may undergo different chemical and
428 physical changes. A minimum of one specimen from each of the main archaeological layers
429 analyzed in this study (Pech IV layer I2 and YZ, RDM layer 4 and 8) were selected for elemental
430 analysis. An attempt was also made to select specimens from multiple excavation units within each
431 layer. The selected individuals therefore serve as proxies for contamination of other specimens
432 excavated from those same layers and units. In addition, from RDM one specimen from layer 4
433 and one specimen from layer 8 were selected to have both the enamel and the dentin analyzed.
434 This analysis was done to determine the level of contamination that occurred in the more porous
435 dentin portions of specimens as compared to the level of contamination that may have occurred in
436 the enamel.

437

438 ***3.1. Elemental analysis***

439 Enamel or dentin powder was removed from specimens (see section 3.2; n = 12.3 mg
440 each) at METAL, placed in a 15 mL centrifuge tube, and 960 μ L of twice distilled 5M nitric acid
441 was then added to each tube along with 14 mL of Millipore water. All samples were analyzed
442 using a Thermo Electron X-Series (with collision cell technology) Quadrupole Inductively
443 Coupled Plasma Mass Spectrometer (Q-ICP-MS). Calibration standards was a combination of
444 single-element standards designed to be similar in element ratios to bone and enamel. An internal
445 element standard of Sc, Ge, In, and Bi was mixed online with all samples to correct for any

446 change to instrumental sensitivity. A series of solutions with known concentrations (an internal
447 standard CUE-0001, a llama bone, and an external standard NIST-1400, an ashed bovine bone),
448 all of which were matrix-matched for archaeological bone, were measured repeatedly at regular
449 intervals throughout the analysis to monitor the accuracy and precision of the measurements.

450

451 ***3.2. Sample preparation and purification***

452 All teeth (including rodent teeth) and modern snail shells were mechanically cleaned using a
453 Dremel Minimite-750 cordless drill with a tungsten carbide bur (Dremel engraving cutters
454 number 106). These samples were then rinsed with high purity deionized water (Millipore 18.2
455 megaohms) and submerged in an ultrasonic bath of Millipore water for 30 minutes. Due to the
456 potential for diagenetic contamination, the Dremel drill and cleaned carbide burs were used to
457 remove the outer enamel surface of each tooth (Budd et al., 2000; Hoppe et al., 2003). For snail
458 shell samples, each shell was drilled in half and both the outer and inner surface of the shell were
459 removed. Shells and rodent teeth were then placed in 10 ml of 0.8 M acetic acid for five to
460 twenty minutes and then rinsed with Millipore water. Once the teeth of large herbivores were
461 mechanically cleaned, sampling began by drilling horizontal lines into each tooth to collect 4-6
462 mg of enamel powder. Bands were drilled sequentially down the tooth, with the first band drilled
463 close to the occlusal surface and the last band close to the neck of the tooth. After each band of
464 enamel was drilled, the tooth was again placed in an ultrasonic bath of Millipore water for 10
465 minutes so that all powder adhering to the tooth was removed before the next sample was taken.
466 The resulting enamel samples were then analyzed under a light microscope to ensure that no
467 dentin was included. Sampling snail shell and rodent teeth began by placing the mechanically
468 and chemically cleaned specimens into crucibles in a furnace at 800° C for 14 hours and then

469 collecting the ashed samples. Set 1 (processed at ASU), tooth and snail shell samples were
470 dissolved in acid washed 1.5 mL centrifuge tubes with 0.5 mL of twice distilled 5M nitric acid
471 (HNO₃). Set 2 (processed at Yale) tooth samples were dissolved in acid washed Teflon beakers
472 with 1 mL 6.2 M hydrochloric acid (HCl) on a hotplate at 100° C overnight. After dissolution, 50
473 µL of 30% hydrogen peroxide (H₂O₂) were added before evaporation (see below).

474 Soil samples were processed by first grinding each sample with a mortar and pestle. Once
475 ground, 4.0 grams of each sample were ashed in a furnace at 800° C for 14 hours. After ashing,
476 100 mg of each sample were reground with a mortar and pestle and placed in 15 mL centrifuge
477 tubes and dissolved in 5.0 mL of twice distilled 5M HNO₃ and 1.0 mL of hydrofluoric acid (HF).
478 In experiments run by Frank et al. (2022) different methods of soil leaching returned similar
479 ⁸⁷Sr/⁸⁶Sr values, and were consistent to ⁸⁷Sr/⁸⁶Sr values sampled from vegetation at the same
480 sampling site.

481 Water and wine samples were processed by pipetting 20 mL of each water sample and 2 mL
482 of each wine sample into acid washed 20 mL Teflon beakers. Once samples were placed in the
483 beakers, 500 µL of twice distilled 5 M HNO₃ were added to each wine sample.

484 After the steps above, all samples were evaporated on a hotplate. Twice distilled 3M HNO₃
485 (250 µL for Set 1 samples, 500 µL for Set 2 samples) was then added to each sample. Acid
486 washed columns were loaded with Eichrom SrSpec ion-exchange resin (30-50 µL for Set 1
487 samples, ~70 µL for Set 2 samples). Resin was washed multiple times with twice distilled 3M
488 HNO₃ followed by Millipore water. The resin was then conditioned with twice distilled 3M
489 HNO₃. Next, the dissolved samples were loaded into columns, washed with twice distilled 3M
490 HNO₃ (500 µL for Set 1 samples, 1000 µL for Set 2 samples) and eluted with Millipore water
491 (500 µL for Set 1 samples, 1000 µL for Set 2 samples).

492

493 **3.3. $^{87}\text{Sr}/^{86}\text{Sr}$ measurement**

494 Set 1 samples were analyzed with a Thermo-Finnigan Neptune multi-collector inductively
495 coupled plasma mass spectrometer (MC-ICP-MS) at ASU's METAL. Solution concentrations
496 ranged between 3 and 158 ppb. Internal and external standards with varying concentrations were
497 run during analysis demonstrating that for samples with elemental Sr concentrations above 75
498 ppb the error of $^{87}\text{Sr}/^{86}\text{Sr}$ values was less than 0.00004. Sample solutions were diluted to achieve
499 a uniform concentration of 75 ppb Sr for measurement.

500 Set 2 samples were analyzed with a Thermo-Finnigan Neptune Plus MC-ICP-MS equipped
501 with an ESI Apex Omega sample introduction system at the Yale Metal Geochemistry Center.
502 Solution concentrations ranged from below reportable levels to 191 ppb Sr, with a single outlier
503 at 577 ppb Sr. All samples included in this analysis were measured at concentrations of 50 ppb.
504 For set 2, precision was evaluated through duplicate measurements of archaeological samples
505 (± 0.00015 , $n=9$) and accuracy through repeated measurements of an internal matrix-matched
506 standard (modern cow enamel, diluted from a concentrated stock solution and introduced at the
507 same concentration as the samples) with known long-term $^{87}\text{Sr}/^{86}\text{Sr}$ (0.71643, average difference
508 = -0.00010 ± 0.00006 , $n=4$).

509 For both sets, corrections were applied to account for the isobaric interference of $^{86}\text{Krypton}$
510 (Kr) on ^{86}Sr (Kr being present as a trace impurity in the Argon gas used in the plasma) and ^{87}Rb
511 on ^{87}Sr (Rb being present in small amounts after imperfect column purification). The abundance
512 of ^{86}Kr was estimated from the measured abundance of ^{83}Kr , while the abundance of ^{87}Rb was
513 estimated from the measured abundance of ^{85}Rb accounting for instrumental mass fractionation
514 (Horsky et al., 2016; Konter and Storm, 2014). Measurements were corrected for drift using an

515 external intra-elemental correction (*sample-standard bracketing*) with NIST SRM 987 as the
516 bracketing standard.

517

518 **4. Results**

519 **4.1. Elemental analysis**

520 The average calcium-to-phosphorus ratios (Ca/P) measured on NIST-1400 over the course of the
521 analysis were 2.10 ± 0.06 (2σ , $n=9$). This value is accurate and precise when compared to the
522 certified calcium and phosphorus values published by the National Institute of Standards and
523 Technology (Ca/P= 2.13 ± 0.03 , 2σ).

524 Results from elemental analysis demonstrate that most enamel samples were not
525 diagenetically contaminated, since Ca/P from enamel samples (mean Ca/P = 2.14 ± 0.08 , 2σ ,
526 $n=12$) closely match ratios found in modern teeth (~ 2.14) (Table 2) (Burton, 2008;
527 Papageorgopoulou and Xirotiris, 2009; Sillen, 1989). The one exception is a second molar from
528 an *Equus* specimen (F16-3786) from Pech IV, layer YZ, which has an elevated Ca/P ($^{44}\text{Ca}/^{31}\text{P}$
529 =2.24), suggesting some contamination may have occurred in this specimen. As expected from
530 archaeological samples, Ca/P in dentin were elevated demonstrating that dentin is more
531 susceptible to contamination than enamel (Budd et al., 2000). Other tests for diagenetic
532 contamination included measuring concentrations of neodymium (Nd) and uranium (U). Results
533 reveal that none of the enamel samples have undergone contamination by uranium or
534 neodymium as the U/Ca and the Nd/Ca values are within one standard deviation of ratios
535 measured in the NIST 1400 standard. Additionally, U concentrations in all tooth samples were <
536 0.1 ppb, which is within the range that has been reported from modern bones (Burton, 2008;
537 Grimstead et al., 2018; Williams and Marlow, 1987). It has been noted that since U and Nd are

538 universally present in soils, finding low values of these elements in archaeological samples is a
 539 good indication that the samples have largely been resistant to chemical alteration (Burton,
 540 2008). Thus, these results suggest that strontium measured in archaeological teeth from RDM
 541 and Pech IV (with the possible exception of specimen F16-3786) will likely reflect biogenic and
 542 not diagenetic values.

543
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 547

Site, Layer	Specimen	Sample	Ca/P	U/Ca	Nd/Ca
	J18-4657 <i>Equus</i>	ACL-2328 enamel	2.09	1.73E-07	5.19E-07
	K17-1338 <i>Cervus</i>	ACL-2340 dentin	2.79	3.02E-06	3.50E-07
RDM, L4	K17-1338 <i>Cervus</i>	ACL-2340 enamel	2.15	2.55E-07	5.12E-07
	J16-1572 <i>Rangifer</i>	ACL-2337 enamel	2.10	1.46E-07	1.11E-06
	K16-2238 <i>Equus</i>	ACL-2341 enamel	2.15	1.64E-07	1.23E-06
	K17-2382 <i>Rangifer</i>	ACL-2330 dentin	2.35	4.18E-06	4.55E-06
	K17-2382 <i>Rangifer</i>	ACL-2330 enamel	2.11	6.07E-07	7.02E-07
RDM, L8	G18-1882 <i>Rangifer</i>	ACL-2329 enamel	2.17	1.20E-07	3.46E-06
	K17-1418 <i>Equus</i>	ACL-2334 enamel	2.10	1.03E-07	3.03E-07
RDM, L9	G18-6729 <i>Cervus</i>	ACL-3434 enamel	2.13	3.87E-07	3.63E-07

Pech L I2	E11-3125 <i>Rangifer</i>	ACL-2325 enamel	2.14	8.13E-06	2.85E-06
	D11-3951 <i>Rangifer</i>	ACL-2338 enamel	2.15	3.05E-07	9.61E-07
Pech, L YZ	F17-2845 <i>Cervus</i>	ACL-3435 enamel	2.10	1.90E-07	4.58E-07
	F16-3786 <i>Equus</i>	ACL-3436 enamel	2.24	9.60E-07	2.07E-07
CUE-0001 average		n= 5 (2 σ)	2.13 \pm 0.06	2.35E-07 \pm 1.96E-07	2.91E-08 \pm 1.85E- 07
NIST 1400 average		n=9 (2 σ)	2.10 \pm 0.06	1.03E-07 \pm 1.17E-05	5.09E-07 \pm 1.98E-06

548

549 **Table 2: Results from major, minor, and trace element analysis**

550

551

552 **4.2. Radiogenic strontium isotope analysis**

553 For Set 1, data quality was evaluated through repeated measurements of NIST SRM 987, which

554 indicate good precision ($^{87}\text{Sr}/^{86}\text{Sr} = 0.710265 \pm 0.000014$, 2 σ , n=18,) and agreement with

555 accepted (0.71025) and certified (0.71034 ± 0.00026) values for the standard (Faure and

556 Mensing, 2005; Moore et al., 1982). For Set 2, precision was evaluated through duplicate

557 measurements of archaeological samples (± 0.00015 , n=9) and accuracy through repeated

558 measurements of an internal matrix-matched standard (modern cow enamel) with known long-

559 term $^{87}\text{Sr}/^{86}\text{Sr}$ (0.71643, average difference = -0.00010 ± 0.00006 , n=4).

Sample	$^{87}\text{Sr}/^{86}\text{Sr}$ Range	Mean	σ	<i>n</i> Samples
Fossil Herbivore Samples				
All herbivores from Pech IV and RDM	0.7087-0.7138	0.7100±0.0009	1	107
<i>Cervus</i>	0.7097-0.7138	0.7111±0.0013	1	18
<i>Capreolus</i>	0.7096-0.7099	0.7098±0.0001	1	2
<i>Bison</i>	0.7096-0.7108	0.7101±0.0005	1	12
<i>Equus</i>	0.7087-0.7115	0.7197±0.0006	1	38
<i>Rangifer</i>	0.7091-0.7103	0.7097±0.0002	1	37
Modern Samples: soil, water, wine, <i>Helix</i> shells				
Local values for Les Eyzies and Mansle (includes <i>Microtus</i> teeth from archaeological layers)	0.7087-0.7092	0.7090±0.0002	1	7
Alps	0.7072-0.7250	0.7132±0.0067	1	8
Granitoid regions of the Alps: Chamonix Lacs des Gaillands, La Fontaine, Saint Amour	0.7113-0.7250	0.7186±0.0055	1	4
Massif Armorican	0.7137-0.7138	0.7137	1	2
Pyrénées	0.7084-0.7155	0.7108±0.0027	1	8

560

561 **Table 3: Summary of the $^{87}\text{Sr}/^{86}\text{Sr}$ obtained in this study**

562

563 Table 3 summarizes the $^{87}\text{Sr}/^{86}\text{Sr}$ values obtained from soil, water, wine, and snail shells for this

564 study. The $^{87}\text{Sr}/^{86}\text{Sr}$ values obtained from these modern environmental samples are consistent

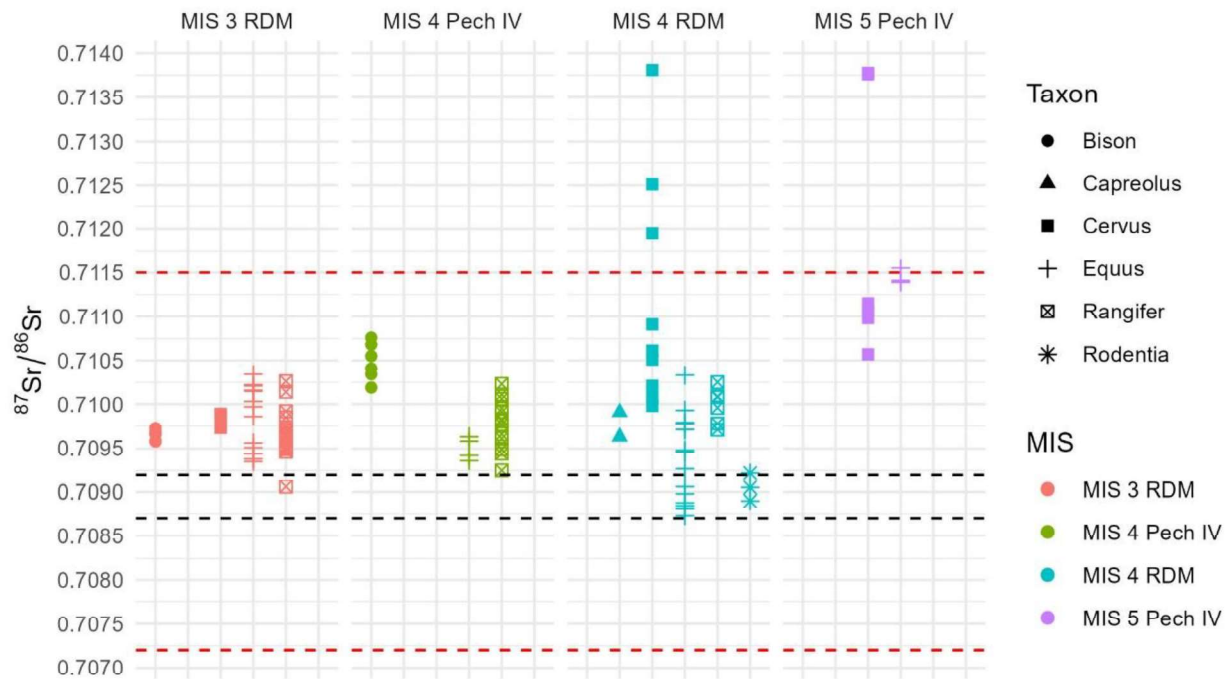
565 with the $^{87}\text{Sr}/^{86}\text{Sr}$ isoscape published by Willmes et al. (2018), which uses lithology to maximize

566 the difference between geological units. This approach averages isotopic values to reduce noise,

567 while sacrificing specificity (see Figure 1, and Table 3). This is a conservative but useful
568 approach for animal movement studies because even non-migratory animals are likely to forage
569 over a variety of lithologies even with a small home range. The local values obtained from Les
570 Eyzies and Mansle (0.7087-0.7092) broadly fall within Willmes and colleagues' Isotope Group
571 2 (0.7072–0.7115), which includes carbonaceous rocks, including those characterizing the
572 Aquitaine and Paris basins; however, some of our local values are compatible with Isotope
573 Group 3 (0.7076–0.7170), including clastic sediments within these basins, although Group 3
574 includes higher values (the group also includes rock types found in the mountains). Values from
575 samples we collected in the Alps (0.7072-0.7250) span Isotope Groups 3 and 4 (0.7084–0.7252),
576 the latter including rock types found in the mountains, most notably granite. Values from the
577 samples we collected from the Massif Armorican (0.7137-0.7138) and the Pyrénées (0.7084-
578 0.7155) span Isotope Groups 3, 4 and 5 (0.7155–0.7213), which collectively include the various
579 rock types found in these mountain ranges.

580 The range of values obtained on herbivore teeth sampled in this study (0.7087-0.7138)
581 spans and exceeds our local values and those of Isotope Group 2 from Williams et al. (2018) to
582 include ratios characteristic of mountainous regions, indicating that at least some taxa or
583 individuals can be confidently labelled as non-local. *Rangifer* values obtained in this study
584 (0.7091-0.7103) overlap (Wilcoxon rank sum test $W = 726, p = 0.51$) with those obtained at
585 Jonzac (0.7095-0.7104, mean $0.7098 \pm 0.0002, 1\sigma, n = 36$; Britton et al., 2011) and both fall
586 within Isotope Group 2 variability, while exceeding the variability of our local environmental
587 samples. Our *Bison* values (0.7096-0.7108) exceed local values as defined here but fall within
588 Isotope Group 2. These values are meaningfully different compared to *Rangifer* from the same
589 sites ($W = 304, p = 0.058$) as well as *Bison* from Jonzac (0.7090-0.7092, mean $0.7091 \pm 0.0001,$

590 1σ , $n = 12$; Britton et al., 2011) ($W = 144$, $p < 0.00001$). *Equus* values (0.7087-0.7115) exceed
 591 local values but fall within Isotope Group 2, and are distinct from those of *Bison* ($W = 137.5$, $p =$
 592 0.04) but not *Rangifer* ($W = 627.5$, $p = 0.43$) at the same sites. *Cervus* yields the largest range of
 593 variation in our sample (0.7097-0.7138, $\Delta = 0.0041$), exceeding the variability of Willmes
 594 Isotope Group 2 (0.7072-0.7115) and indicating with confidence that this taxon was in areas with
 595 older bedrock, which may include the Massif Central, Pyrénées, or perhaps areas in the
 596 Armorican Massif located in northeastern France bordering the Bay of Biscay (Figure 1). *Cervus*
 597 values are statistically different from those of *Rangifer*, *Bison* and *Equus* from the same sites (W
 598 = 605.5, 173.5, 592, respectively, all $p < 0.01$). Finally, two values for *Capreolus* (0.7096 and
 599 0.7099) exceed local variability but fall within Isotope Group 2. Despite the very small sample of
 600 *Capreolus*, this (likely) non-migratory taxon appears indistinguishable from *Rangifer* and *Bison*
 601 in our study.



602

603 **Figure 2. $^{87}\text{Sr}/^{86}\text{Sr}$ measured on archaeological enamel from RDM and Pech IV, grouped**
604 **by age. The black dashed lines mark the boundaries of local baseline as measured in this**
605 **study. The red dashed lines mark the boundaries of Isotope Group 2 as defined by Willmes**
606 **et al., (2018).**

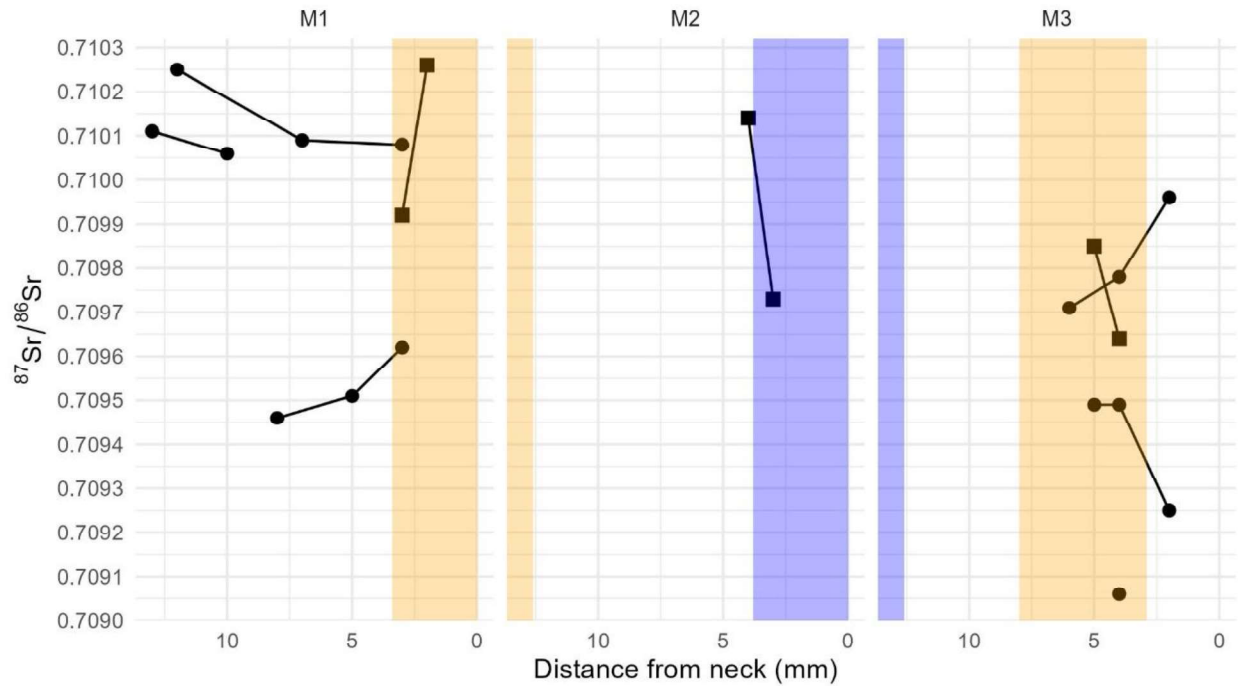
607

608 Breaking down our results by MIS reveals temporal trends in the data (Figure 2). When
609 all taxa are considered together (rodents excluded), there are statistically significant differences
610 across MIS groups (Kruskal-Wallis, $\chi^2 = 22.722$, $p < 0.0001$). These differences are driven by
611 MIS 5 at Pech IV (which has the smallest sample size = 9) being different from all other groups
612 (Pairwise W, $p < 0.001$ [Benjamini and Hochberg FDR correction for multiple testing here and
613 below]). The lack of *Rangifer* samples from the MIS 5 at Pech IV (i.e., layer YZ) is itself
614 meaningful and it is not an artifact of biased sample selection, since the zooarchaeological
615 analysis of layer YZ yielded a single *Rangifer* specimen but a rich assemblage of *Cervus*
616 (Hodgkins et al., 2016).

617 Differences in *Rangifer* values across MIS 4 at Pech IV and RDM and MIS 3 at RDM
618 approach, but do not reach, statistical significance (Kruskal-Wallis, $\chi^2 = 5.4872$, $p = 0.06$). *Bison*
619 values differ between MIS 4 at Pech IV and MIS 3 at RDM ($W = 0$, $p = 0.005$), but in both cases
620 remain well within the variability of Isotope Group 2. MIS 5 *Equus* at Pech IV has clearly high,
621 non-local values, but the other groups show differences as well (Kruskal-Wallis, $\chi^2 = 8.0298$, $p =$
622 0.02), driven by MIS 4 *Equus* at RDM being different from MIS 3 *Equus* at the same site
623 (Pairwise W, $p = 0.02$). MIS 3 *Cervus* at RDM has clearly low, more local values than older
624 individuals, while MIS 4 and 5 *Cervus* at RDM and Pech IV, respectively, are indistinguishable
625 ($W = 16$, $p = 0.22$).

626 Measurements taken at different intervals along the crown heights of each tooth have
627 been plotted in Figures 3-6 for reindeer, bison, horse and red deer respectively. *Rangifer* display
628 some intra-tooth variability (i.e., trends from lower to higher, or higher to lower, values between
629 the two or three points measured in each of the teeth), although all measured values align with
630 bioavailable values determined for the Aquitaine and Paris Basins. While a higher resolution
631 sampling approach including multiple teeth from the same individual would be required to better
632 understand the seasonal movements these animals may have been undertaking, these data from
633 two or three distinct portions of the crown suggest that reindeer range may have been restricted
634 to the basins at this time. This is also the case with the *Bison*, where some intra-tooth variability
635 is displayed, but all values are within the range of values found in the basins. A single horse
636 specimen, and several red deer display some more elevated $^{87}\text{Sr}/^{86}\text{Sr}$ values, with a single *Cervus*
637 M3 (RDM Layer 4, J18-3156) displaying a directionality from high values near the neck
638 (youngest enamel) to lower values near the occlusal surface (oldest enamel) (Figure 6). This
639 pattern shows that this individual moved from a geologically younger substrate to a geologically
640 older substrate. Assuming a late May-early June birth and start of M3 mineralization around nine
641 months of age (Brown and Chapman, 1991), this pattern could be consistent with a springtime
642 movement from winter pastures at lower elevations (lower $^{87}\text{Sr}/^{86}\text{Sr}$) to summer pastures deeper
643 into the mountains (higher $^{87}\text{Sr}/^{86}\text{Sr}$). Higher resolution sampling (i.e. of multiple teeth, with a
644 great number of samples taken at closer intervals) would add clarity to this pattern and
645 determined if these movement patterns were seasonally repeating, as has been highlighted for
646 *Cervus* in the south of France during MIS 6 (Barakat et al. 2023).

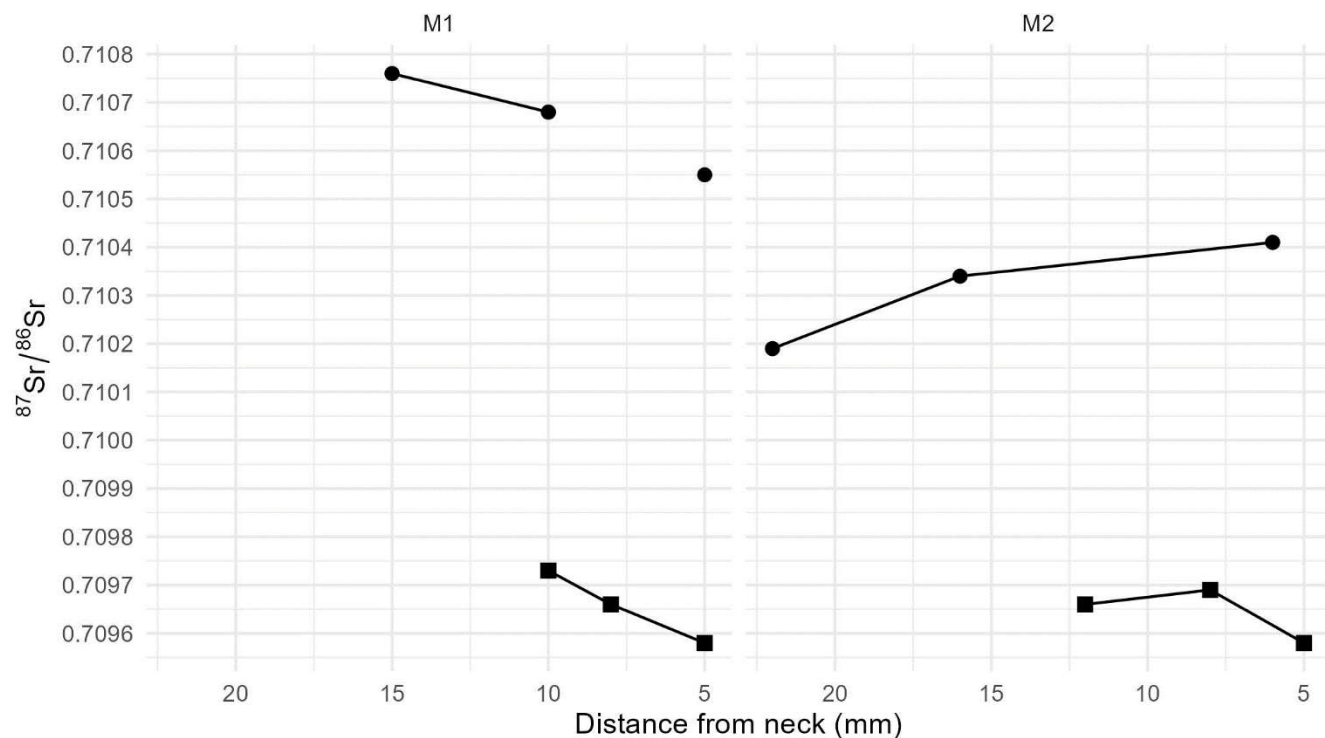
647



648

649 **Figure 3 – Intra-tooth $^{87}\text{Sr}/^{86}\text{Sr}$ measurement in *Rangifer tarandus*. Specimens that could**
 650 **not be confidently assigned to a specific tooth are not represented. Lines connect**
 651 **measurements taken on a single specimen and square symbols denote an individual (RDM**
 652 **Layer 4, J18-1379) for which all three molars were sampled. Orange and blue shading**
 653 **denote estimated summer and winter ranges, respectively, assuming a May-June birth**
 654 **(Geiling et al., 2015), tooth formation times as in Table 1, and a crown height of ~16 mm at**
 655 **the time of full eruption (cf. Pike-Tay et al., 2001). All but one of the *R. tarandus* samples**
 656 **fall outside the range of $^{87}\text{Sr}/^{86}\text{Sr}$ values for the locally collected sample (0.7087-0.7092) but**
 657 **all fall within the Isotope Group 2 range (0.7072-0.7115) of Willmes et al. (2018).**

658



659

660 **Figure 4 – Intra-tooth $^{87}\text{Sr}/^{86}\text{Sr}$ measurement in *Bison*. Lines connect measurements taken**

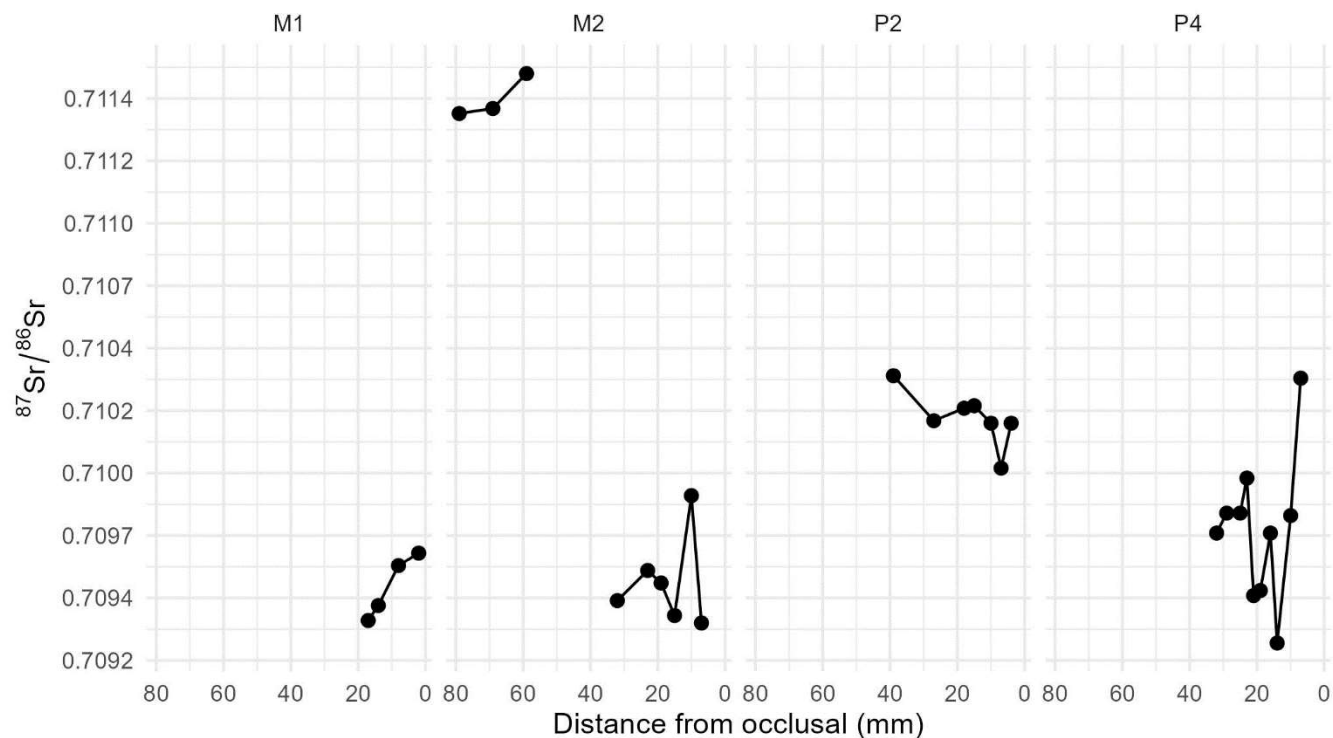
661 **on a single specimen. Square symbols denote an individual (RDM Layer 4, J17-2266) from**

662 **which multiple molars were sampled. The *Bison* samples all fall outside the range of**

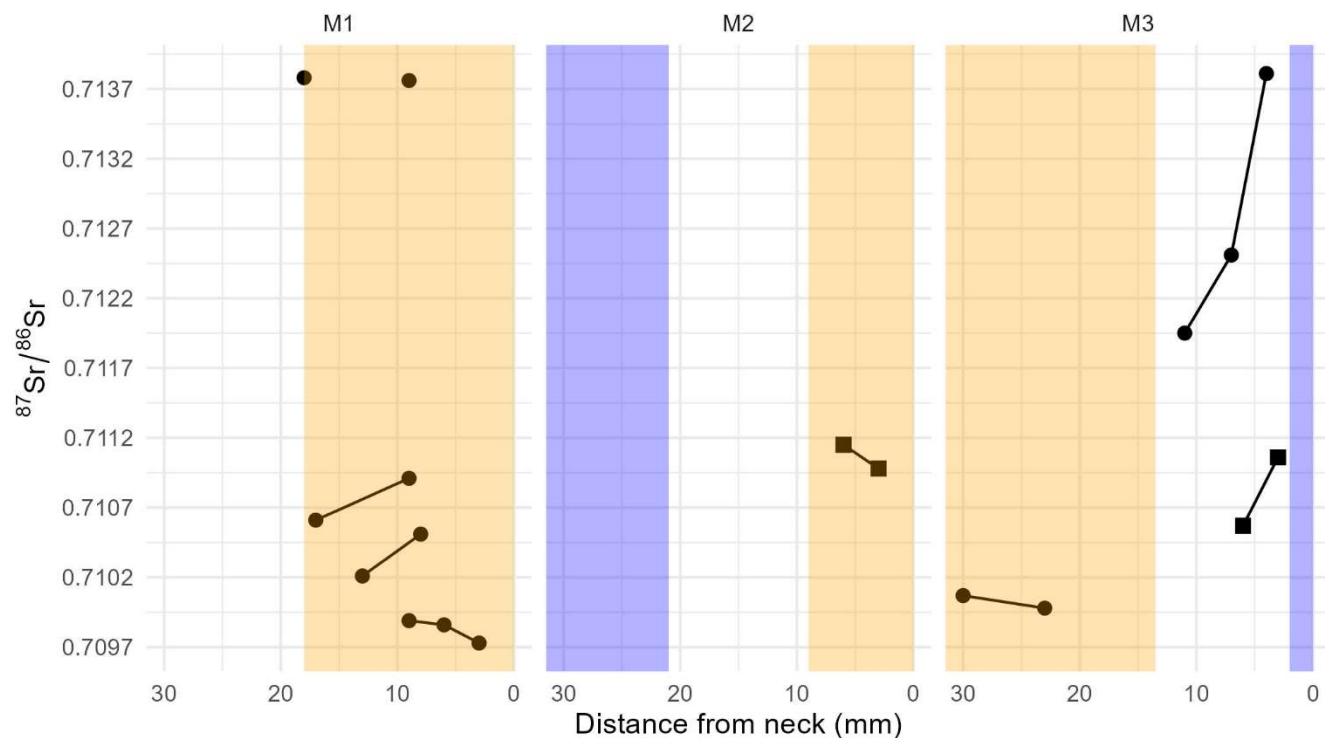
663 **$^{87}\text{Sr}/^{86}\text{Sr}$ values for the local sample (0.7087-0.7092) but within Isotope Group 2 (0.7072-**

664 **0.7115) from Willmes et al. (2018).**

665



666
 667 **Figure 5 – Intra-tooth $^{87}\text{Sr}/^{86}\text{Sr}$ measurement in *Equus ferus*. Specimens that could not be**
 668 **confidently assigned to a specific element are not represented. Lines connect measurements**
 669 **taken on a single specimen. All but one of the *E. ferus* samples fall outside the range of**
 670 **$^{87}\text{Sr}/^{86}\text{Sr}$ values for the locally collected sample (0.7087-0.7092) but all fall within the**
 671 **Isotope Group 2 minimum-maximum range (0.7072-0.7115) of Willmes et al. (2018).**
 672



673
 674 **Figure 6 – Intra-tooth $^{87}\text{Sr}/^{86}\text{Sr}$ measurement in *Cervus elaphus*. Lines connect**
 675 **measurements taken on a single specimen and square symbols denote an individual (F17-**
 676 **2845) for which both M2 and M3 were sampled. Orange and blue shading denote estimated**
 677 **summer and winter seasons respectively, assuming a May birth (Landete-Castillejos et al.,**
 678 **2005), tooth formation times after Brown and Chapman (1991), and unworn crown heights**
 679 **of ~27, ~30 and ~31 mm for M1, M2 and M3, respectively (Steele and Weaver, 2012). All of**
 680 **the *C. elaphus* samples fall outside the range of $^{87}\text{Sr}/^{86}\text{Sr}$ values for the locally collected**
 681 **sample (0.7087-0.7092) and three samples fall above the Isotope Group 2 range (0.7072-**
 682 **0.7115) of Willmes et al. (2018).**

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684

685

686 **5. Discussion**

687 The comparison of $^{87}\text{Sr}/^{86}\text{Sr}$ from archaeological herbivore teeth and the bioavailable
688 $^{87}\text{Sr}/^{86}\text{Sr}$ across France enables a more detailed analysis of the movement of these animals on the
689 landscape. The *Rangifer* sampled here appear to have been moving within the Aquitaine, and
690 perhaps Paris, basins of France. The same applies to *Bison* and the single *Capreolus* studied here,
691 which had the smallest $^{87}\text{Sr}/^{86}\text{Sr}$ range. Interestingly, non-migratory behavior in *Bison* is
692 documented by $^{87}\text{Sr}/^{86}\text{Sr}$ also for a relatively large ($n = 25$) group of individuals from eastern
693 Ukraine, dated to 18.5 ka BP (Julien et al., 2012). *Equus* was also mostly available within the
694 French basins, although a single individual (specimen F16-3786 from Pech IV, layer YZ dating
695 to MIS 5) displays more radiogenic values consistent with ranging in an area between a basin
696 and the mountains, though as noted in the results this individual may have been diagenetically
697 altered because it has an elevated Ca/P ($^{44}\text{Ca}/^{31}\text{P} = 2.24$), so this result should be viewed with
698 caution. Finally, *Cervus* is the only taxon with $^{87}\text{Sr}/^{86}\text{Sr}$ values outside the range observed
699 in *Rangifer*, *Bison*, *Equus*, and *Capreolus*, thus they seem to have had a different foraging
700 pattern than the other species. Higher mobility in *Cervus* compared to sympatric *Equus*
701 *hydruntinus* was inferred from $^{87}\text{Sr}/^{86}\text{Sr}$ at Terminal Pleistocene sites in central Italy, although in
702 that case neither taxon appeared to forage in the mountains (Pellegrini et al., 2008). However, as
703 indicated by the laser ablation data recently obtained for *Cervus* from the site of Lazaret, strongly
704 seasonal strontium signals can be the result of short-distance altitudinal migrations, rather than
705 necessarily long-distance migrations (Barakat et al. 2023). It is also possible that *Cervus* was
706 foraging closer to the coast by the Armorican Massif bordering the Bay of Biscay.

707 While these results do not speak to the distance over which these species were moving
708 (they could have been moving from the Aquitaine basin to the Paris basin), the fact that most do
709 not seem to have spent time in the mountains is at odds with many hypotheses of prey movement

710 patterns in southwestern France. Today, regional movements like this observed in *Rangifer* and
711 *Bison* have been tied to mosaic habitats of pine and spruce woodlands and boreal forests. Thus,
712 these results can be used to assist paleoenvironmental reconstructions of southwestern France.

713 When the radiogenic strontium isotope values measured in *Rangifer* teeth at RDM, Pech
714 IV and from Britton et al.'s (2011) study at Jonzac are compared, the range of values found are
715 nearly identical at all three sites. These results suggest that *Rangifer* were foraging over similar
716 geological units over time and climatic cycles. The intra-tooth sampling conducted by Britton et
717 al. (2011) found that those movements were likely to have been seasonal. The data provided here
718 could be complementary to that study, perhaps reindeer were undertaking seasonal movements
719 between different regions within the basins of France. Further work is needed to characterize the
720 seasonal nature of *Rangifer* behavior in this part of France during the Late Pleistocene and to
721 explore whether this extended into the Paris Basin. Given the common $^{87}\text{Sr}/^{86}\text{Sr}$ values found in
722 both basins, complementary methods such as sulfur or lead isotope analyses may be needed.

723 Britton and coworkers (2011) also analyzed radiogenic strontium isotope ratios from the
724 second and third molars of a bison recovered from Jonzac. Results from this analysis showed that
725 there was little variation across the tooth, suggesting that *Bison* remained within one geological
726 region during tooth development, and unlike the reindeer, did not show evidence of seasonal
727 range use. The mobility pattern inferred from the *Bison* at Jonzac is consistent with the findings
728 of the current study, although one *Bison* from Pech IV does appear to have foraged in a more
729 radiogenic region than other *Bison* at the site. Analyses of *Bison* mobility from all three sites
730 have interesting implications for the Neandertals who would have hunted them. If *Bison* truly
731 were living within more restricted regions, they would have been present for Neandertals to hunt
732 year-round. *Bison* are large herbivores and a valuable resource and may have limited the need

733 for Neandertals to undertake long distance movements. An analysis of dental eruption and wear,
734 as well as aging of fetal animals, throughout the sequence at Pech IV suggests in fact that the site
735 was occupied during multiple seasons (Niven and Martin, 2018).

736 Finally, our data suggests that animals hunted during MIS 5 were either procured farther
737 away from Pech IV and RDM compared to MIS 4 and 3 fauna, or at least lived part of their lives
738 farther from these sites.

739

740 **6. Conclusion**

741 An analysis of variation in the radiogenic Sr isotope ratios of *Bison*, *Equus*, *Rangifer*, and
742 *Capreolus* suggest that all of these animals roamed within the basins of France and would have
743 been available for Neandertals to hunt which is important knowledge for reconstructions
744 Neandertal mobility and strategies. Of course, factors other than availability, could have
745 influenced early hominin hunting behaviors, including the seasonal conditions of animals (both
746 their body mass/fat content) and the condition of their pelts (Britton et al. 2023). For instance, at
747 Abri du Maras, a lack of seasonal movement in *Rangifer* in level 4.1 was combined with a
748 strongly seasonal exploitation pattern – indicating that Neandertals were only either using the
749 site seasonally or that their preference for reindeer at that time was strongly seasonal due to the
750 aforementioned factors (Britton et al. 2023). *Cervus* on the other hand may have ventured further
751 afield, towards the Atlantic coastline or into the mountains, which could indicate that
752 Neandertals ventured into these different ecotones to hunt them during MIS 4 and 5.

753 We hope that this study is useful to future researchers who can utilize methods beyond
754 those applied in this paper to pin down the distances each of these species traveled and/or their
755 seasonal range use within the basins. Higher resolution sampling is necessary to see if subtle

756 repeating isotopic signals exist that could indicate movements within the basins due to their
757 relatively homogenous isotopic profile. In addition, and due to this homogeneity, complementary
758 methods, such as sulfur isotope analysis may still be required to identify range use that spanned
759 across the two basins and differences in total home range size between different species and
760 individuals (e.g., Britton et al. 2023). Given the anomalous pattern of *Cervus* reported in this
761 study, we hope future studies will characterize where summer and winter ranges of *Cervus* may
762 have been, and to determine whether or not these overlapped with the sites during seasonality of
763 site use/procurement in order to assess whether *Cervus* was a seasonally available resource
764 locally or whether Neandertals extended their hunting ranges to exploit this species.

765 The results of this analysis add important information about biogeography of key
766 Neandertal subsistence species and hint at potential changes in their range use over time,
767 contributing important foundational data to future studies and bringing additional understanding
768 to the ecological context of Neandertal subsistence practices.

769

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784 LITERATURE CITED

- 785
- 786 Abraham, J.O., Upham, N.S., Damian-Serrano, A., Jesmer, B.R., 2022. Evolutionary causes and
 787 consequences of ungulate migration. *Nature Ecology & Evolution* 1–9.
- 788 Albon, S.D., Langvatn, R., 1992. Plant phenology and the benefits of migration in a temperate
 789 ungulate. *Oikos* 502–513.
- 790 Arbos, P., 1932. Le rôle économique du renne, in: *Annales de Géographie*. JSTOR, pp. 405–408.
- 791 Bahn, P.G., 1977. Seasonal migration in South-west France during the late glacial period.
 792 *Journal of Archaeological Science* 4, 245–257.
- 793 Balasse, M., 2003. Potential biases in sampling design and interpretation of intra-tooth isotope
 794 analysis. *International Journal of Osteoarchaeology* 13, 3–10.
- 795 Barakat, S., Le Corre, M., Willmes, Malte., Cohen, J., Vuillien, M., Desclaux, E., Britton, Kate.,
 796 2023. Laser ablation strontium isotopes and spatial assignment show seasonal mobility in red
 797 deer (*Cervus elaphus*) at Lazaret Cave, France (MIS 6). *Frontiers in Ecology and Evolution*.
 798 11: DOI=10.3389/fevo.2023.988837
- 799 Barron, E., van Andel, T.H., Pollard, D., 2003. Glacial Environments II: reconstructing the
 800 climate of Europe in the last glaciation., in: *Neandertals and Modern Humans in the*
 801 *European Landscape during the Last Glaciation*. McDonald Institute for Archaeological
 802 Research, Cambridge, pp. 57–78.
- 803 Bendrey, R., 2012. From wild horses to domestic horses: a European perspective. *World*
 804 *Archaeology* 44, 135–157.
- 805 Bentley, R.A., 2006. Strontium isotopes from the earth to the archaeological skeleton: a review.
 806 *Journal of archaeological method and theory* 13, 135–187.
- 807 Berger, J., 2004. The last mile: how to sustain long-distance migration in mammals.
 808 *Conservation Biology* 18, 320–331.
- 809 Bergerud, A., 1974. The role of the environment in the aggregation, movement and disturbances
 810 behavior of caribou, in: Geist, V., Walther, F. (Eds.), *The Behaviour of Ungulates and Its*
 811 *Relation to Management*. International Union for Conservation of Nature, Morges,
 812 Switzerland, pp. 552–582.
- 813 Binford, L.R., 1980. Willow Smoke and Dogs’ Tails: Hunter-Gatherer Settlement Systems and
 814 Archaeological Site Formation. *American Antiquity* 45, 4–20.
 815 <https://doi.org/10.2307/279653>
- 816 Bordes, F., 1975. Le gisement du Pech de l’Azé IV. Note préliminaire. *Bulletin de la Société*
 817 *préhistorique française. Études et travaux* 72, 293–308.
- 818 Bordes, F., Lafille, J., 1962. Decouverte d’un squelette d’enfant mousterien dans le gisement du
 819 Roc de Marsal, commune de Campagne-du-Bugue (Dordogne). *C.R. Hebdomadaires*
 820 *Acad. Sci.* 254, 714.
- 821 Bouchud, J., 1966. Essai sur le renne et la climatologie du Paléolithique moyen et supérieur.
 822 Impr. Magne.
- 823 Boulbes, N., Van Asperen, E.N., 2019. Biostratigraphy and palaeoecology of European Equus.
 824 *Frontiers in Ecology and Evolution* 7, 301.
- 825 Brazda, A.R., 1953. Elk migration patterns, and some of the factors affecting movements in the
 826 Gallatin River drainage, Montana. *The Journal of Wildlife Management* 17, 9–23.
- 827 Britton, K., 2020. Isotope Analysis for Mobility and Climate Studies, in: Britton, K., Richards,
 828 M. (Eds.), *Archaeological Science: An Introduction*, Cambridge University Press,
 829 Cambridge, pp. 99-124.

- 830 Britton, K., Grimes, V., Dau, J., Richards, M.P., 2009. Reconstructing faunal migrations using
831 intra-tooth sampling and strontium and oxygen isotope analyses: a case study of modern
832 caribou (*Rangifer tarandus granti*). *Journal of Archaeological Science* 36, 1163–1172.
- 833 Britton, K., Grimes, V., Niven, L., Steele, T.E., McPherron, S., Soressi, M., Kelly, T.E., Jaubert,
834 J., Hublin, J.-J., Richards, M.P., 2011. Strontium isotope evidence for migration in late
835 Pleistocene *Rangifer*: Implications for Neanderthal hunting strategies at the Middle
836 Palaeolithic site of Jonzac, France. *Journal of human evolution* 61, 176–185.
- 837 Britton, K., Jimenez, E.L., Le Corre, M., Pederzani, S., Daujeard, C., Jaouen, K., Vettese, D.,
838 Tütken, T., Hublin, J.J., Moncel, M.H., Multi-isotope zooarchaeological investigations at
839 Abri du Maras: The paleoecological and paleoenvironmental context of Neanderthal
840 subsistence strategies in the Rhône Valley during MIS 3. *J Hum Evol.* 2023
841 Jan;174:103292. doi: 10.1016/j.jhevol.2022.103292. Epub 2022 Nov 29. PMID:
842 36455403.
- 843 Brown, W.A.B., Chapman, N.G., 1991. Age assessment of red deer (*Cervus elaphus*): from a
844 scoring scheme based on radiographs of developing permanent molariform teeth. *Journal*
845 *of Zoology* 225, 85–97.
- 846 Brown, W.K., Huot, J., Lamothe, P., Luttich, S., Pare, M., Martin, G.S., Theberge, J.B., 1986.
847 The distribution and movement patterns of four woodland caribou herds in Quebec and
848 Labrador. *Rangifer* 43–49.
- 849 Budd, P., Montgomery, J., Barreiro, B., Thomas, R.G., 2000. Differential diagenesis of strontium
850 in archaeological human dental tissues. *Applied geochemistry* 15, 687–694.
- 851 Burch, E.S., 1972. The caribou/wild reindeer as a human resource. *American antiquity* 37, 339–
852 368.
- 853 Burke, A., Pike-Tay, A., 1997. Reconstructing “L’Age Du Renne,” in: Jackson, J., Thacker, P.
854 (Eds.), *Caribou and Rangifer Hunters of the Northern Hemisphere*. Avebury, Aldershot,
855 pp. 69–82.
- 856 Burton, J., 2008. Bone chemistry and trace element analysis, in: Katzenberg, M., Saunders, S.
857 (Eds.), *Biological Anthropology of the Human Skeleton*. John Wiley & Sons, Inc, pp.
858 443–460.
- 859 Copeland, S.R., Cawthra, H.C., Fisher, E.C., Lee-Thorp, J.A., Cowling, R.M., Le Roux, P.J.,
860 Hodgkins, J., Marean, C.W., 2016. Strontium isotope investigation of ungulate movement
861 patterns on the Pleistocene Paleo-Agulhas plain of the Greater Cape floristic region,
862 South Africa. *Quaternary Science Reviews* 141, 65–84.
- 863 Darby, W.R., Pruitt, W.O., 1984. Habitat use, movements and grouping behaviour of woodland
864 caribou, *Rangifer tarandus caribou*, in southeastern Manitoba. *Canadian Field-Naturalist*.
- 865 de Beaulieu, J.-L., Reille, M., 1992. The last climatic cycle at La Grande Pile (Vosges, France) a
866 new pollen profile. *Quaternary Science Reviews* 11, 431–438.
- 867 Delpéch, F., 1983. *Les faunes du Paléolithique supérieur dans le Sud-Ouest de la France*.
868 University of Bordeaux I, Bordeaux.
- 869 Dibble, H. L., S. P. McPherron, P. Goldberg, and D. Sandgathe. 2018. *Excavations at Pech de*
870 *l’Azé IV*. Monograph. Cave and Karst Systems of the World series. Springer.
- 871 Dibble, H.L., Berna, F., Goldberg, P., Mcpherron, S.P., Mentzer, S., Niven, L., Richter, D.,
872 Sandgathe, D., Thery-Parisot, I., Turq, A., 2009. A preliminary report on Pech de l’Azé
873 IV, layer 8 (Middle Paleolithic, France). *PaleoAnthropology* 182, 219.
- 874 Dibble, H.L., Rolland, N., 1992. On assemblage variability in the Middle Paleolithic of Western
875 Europe: History, perspectives, and a new synthesis, in: Dibble, H., Mellars, P. (Eds.), *The*

- 876 Middle Paleolithic: Adaptation, Behavior, and Variability. University Museum Press,
877 Symposium Series, Philadelphia, pp. 1–28.
- 878 Dingle, H., Drake, V.A., 2007. What Is Migration? *BioScience* 57, 113–121.
879 <https://doi.org/10.1641/B570206>
- 880 Downes, C.M., Theberge, J.B., Smith, S.M., 1986. The influence of insects on the distribution,
881 microhabitat choice, and behaviour of the Burwash caribou herd. *Canadian Journal of*
882 *Zoology* 64, 622–629.
- 883 Drucker, D.G., Bocherens, H., Billiou, D., 2003. Evidence for shifting environmental conditions
884 in Southwestern France from 33 000 to 15 000 years ago derived from carbon-13 and
885 nitrogen-15 natural abundances in collagen of large herbivores. *Earth and Planetary*
886 *Science Letters* 216, 163–173.
- 887 Edmonds, E.J., Bloomfield, M., 1984. A study of woodland caribou (*Rangifer tarandus caribou*)
888 in west central Alberta, 1979 to 1983: Alberta Fish and Wildlife Division, unpublished
889 report. Alberta Energy and Natural Resources, Fish and Wildlife Division, Edmonton,
890 Alberta, Canada.
- 891 Enloe, J.G., David, F., 1997. Rangifer herd behavior: seasonality of hunting in the Magdalenian
892 of the Paris Basin, in: Jackson, J., Thacker, P. (Eds.), *Caribou and Rangifer Hunters of*
893 *the Northern Hemisphere*. Avebury, Aldershot, pp. 52–68.
- 894 Ericson, J.E., 1985. Strontium isotope characterization in the study of prehistoric human ecology.
895 *Journal of human evolution* 14, 503–514.
- 896 Evans, H.F., 1960. Preliminary investigation of caribou in northwestern United States.
897 University of Montana, Missoula, Montana.
- 898 Evans, J.A., Tatham, S., 2004. Defining ‘local signature’ in terms of Sr isotope composition using
899 a tenth-to twelfth-century Anglo-Saxon population living on a Jurassic clay-carbonate
900 terrain, Rutland, UK. *Geological Society, London, Special Publications* 232, 237–248.
- 901 Faure, G., Mensing, T.M., 2005. *Isotopes: Principles and applications*, 3rd ed. John Wiley &
902 Sons, Inc, Hoboken.
- 903 Fincham, A., Moradian-Oldak, J., Simmer, J.P., 1999. The structural biology of the developing
904 dental enamel matrix. *Journal of structural biology* 126, 270–299.
- 905 Frank, A.B., Frei, R., Kristiansen, K., Frei, K.M., 2022. A multi-proxy, bioavailable strontium
906 isotope baseline for southern Almería, Spain: Using modern environmental samples to
907 constrain the isotopic range of bioavailable strontium. *Applied Geochemistry*. 144,
908 105405.
- 909 Fryxell, J.M., Sinclair, A.R.E., 1988. Causes and consequences of migration by large herbivores.
910 *Trends in ecology & evolution* 3, 237–241.
- 911 Fuller, T.K., Keith, L.B., 1981. Woodland caribou population dynamics in northeastern Alberta.
912 *The Journal of Wildlife Management* 197–213.
- 913 Gadbury, C., Todd, L., Jahren, A.H., Amundson, R., 2000. Spatial and temporal variations in the
914 isotopic composition of bison tooth enamel from the Early Holocene Hudson–Meng
915 Bone Bed, Nebraska. *Palaeogeography, Palaeoclimatology, Palaeoecology* 157, 79–93.
- 916 Georgii, B., 1980. Home range patterns of female red deer (*Cervus elaphus* L.) in the Alps.
917 *Oecologia* 47, 278–285.
- 918 Georgii, B., Schröder, W., 1983. Home range and activity patterns of male red deer (*Cervus*
919 *elaphus* L.) in the Alps. *Oecologia* 58, 238–248.
- 920 Goldberg, P., McPherron, S.J., Dibble, H.L., Sandgathe, D.M., 2018. Stratigraphy, deposits, and
921 site formation, in: *The Middle Paleolithic Site of Pech de L’Azé IV*. Springer, pp. 21–74.

- 922 Gómez-Olivencia, A., García-Martínez, D., 2019. New postcranial remains from the Roc de
923 Marsal Neandertal child. *PALEO. Revue d'archéologie préhistorique* 164–169.
- 924 Gordon, B.C., 1988. Of men and reindeer herds in French Magdalenian prehistory. *BAR.*
925 *International Series.*
- 926 Grayson, D., Delpech, F., 2005. Pleistocene Rangifer and global warming. *Conservation Biology*
927 557–562.
- 928 Green, D.R., Green, G.M., Colman, A.S., Bidlack, F.B., Tafforeau, P., Smith, T.M., 2017.
929 Synchrotron imaging and Markov chain Monte Carlo reveal tooth mineralization
930 patterns. *PloS one* 12, e0186391.
- 931 Green, D.R., Smith, T.M., Green, G.M., Bidlack, F.B., Tafforeau, P., Colman, A.S., 2018.
932 Quantitative reconstruction of seasonality from stable isotopes in teeth. *Geochimica et*
933 *Cosmochimica Acta* 235, 483–504.
- 934 Grimstead, D.N., Clark, A.E., Rezac, A., 2018. Uranium and vanadium concentrations as a trace
935 element method for identifying diagenetically altered bone in the inorganic phase. *Journal*
936 *of archaeological method and theory* 25, 689–704.
- 937 Guérin, G., Frouin, M., Tuquoi, J., Thomsen, K.J., Goldberg, P., Aldeias, V., Lahaye, C.,
938 Mercier, N., Guibert, P., Jain, M., 2017. The complementarity of luminescence dating
939 methods illustrated on the Mousterian sequence of the Roc de Marsal: A series of
940 reindeer-dominated, Quina Mousterian layers dated to MIS 3. *Quaternary International*
941 433, 102–115.
- 942 Hanson, J.R., 1984. Bison ecology in the Northern Plains and a reconstruction of bison patterns
943 for the North Dakota region. *Plains Anthropologist* 29, 93–113.
- 944 Helle, T., 1979. Observations of group size and composition of wild forest reindeer, *Rangifer*
945 *tarandus fennicus* Lönn., during the calving and summer periods in eastern Finland.
946 *Aquilo Series Zoologica* 19, 5–11.
- 947 Hillson, S., 2005. *Teeth.* Cambridge university press.
- 948 Hodgkins, J., Marean, C.W., Turq, A., Sandgathe, D., McPherron, S.J.P., Dibble, H., 2016.
949 Climate-mediated shifts in Neandertal subsistence behaviors at Pech de l’Azé IV and Roc
950 de Marsal (Dordogne Valley, France). *Journal of Human Evolution* 96, 1–18.
951 <https://doi.org/10.1016/j.jhevol.2016.03.009>
- 952 Hodgkins, J., Marean, C.W., Venter, J.A., Richardson, L., Roberts, P., Zech, J., Difford, M.,
953 Copeland, S.R., Orr, C.M., Keller, H.M., 2020. An isotopic test of the seasonal migration
954 hypothesis for large grazing ungulates inhabiting the Palaeo-Agulhas Plain. *Quaternary*
955 *Science Reviews* 106221.
- 956 Hodgkins, J., Roux, P. le, Marean, C.W., Penkman, K., Crisp, M., Fisher, E., Lee-Thorp, J.,
957 2018. The role of ostrich in shaping the landscape use patterns of humans and hyenas on
958 the southern coast of South Africa during the late Pleistocene. *Multispecies Archaeology*
959 333–346. <https://doi.org/10.4324/9781315707709>
- 960 Hoppe, K.A., Koch, P.L., 2007. Reconstructing the migration patterns of late Pleistocene
961 mammals from northern Florida, USA. *Quaternary Research* 68, 347–352.
- 962 Hoppe, K.A., Koch, P.L., Carlson, R.W., Webb, S.D., 1999. Tracking mammoths and
963 mastodons: reconstruction of migratory behavior using strontium isotope ratios. *Geology*
964 27, 439–442.
- 965 Hoppe, K.A., Koch, P.L., Furutani, T.T., 2003. Assessing the preservation of biogenic strontium
966 in fossil bones and tooth enamel. *International Journal of Osteoarchaeology* 13, 20–28.

- 967 Hoppe, K.A., Stover, S.M., Pascoe, J.R., Amundson, R., 2004. Tooth enamel biomineralization
 968 in extant horses: implications for isotopic microsampling. *Palaeogeography,*
 969 *Palaeoclimatology, Palaeoecology* 206, 355–365.
- 970 Horsky, M., Irrgeher, J., Prohaska, T., 2016. Evaluation strategies and uncertainty calculation of
 971 isotope amount ratios measured by MC ICP-MS on the example of Sr. *Analytical and*
 972 *bioanalytical chemistry* 408, 351–367.
- 973 Huntley, Allen, J., 2003. Glacial Environments III: Palaeo-vegetation Patterns in Last Glacial
 974 Europe, in: Van Andel, T.H., Davies, W. (Eds.), *Neanderthals and Modern Humans in the*
 975 *European Landscape during the Last Glaciation: Archaeological Results of the Stage 3*
 976 *Project.* McDonald Institute for Archaeological Research monographs, Cambridge.
- 977 Jacobs, Z., Jankowski, N.R., Dibble, H.L., Goldberg P., McPherron, S.J.P., Sandgathe, D., Soressi
 978 M., 2016. The age of three Middle Palaeolithic sites: single-grain optically stimulated
 979 luminescence chronologies for Pech de l’Azé I,II,IV in France.
- 980 Jankowski, N.R., 2018. An Absolute Chronological Framework for Pech IV, in: *The Middle*
 981 *Paleolithic Site of Pech de l’Azé IV.* Springer, pp. 75–81.
- 982 Johnson, C.J., Parker, K.L., Heard, D.C., 2001. Foraging across a variable landscape: behavioral
 983 decisions made by woodland caribou at multiple spatial scales. *Oecologia* 127, 590–602.
- 984 Johnson, C.J., Parker, K.L., Heard, D.C., Gillingham, M.P., 2002a. A multiscale behavioral
 985 approach to understanding the movements of woodland caribou. *Ecological Applications*
 986 12, 1840–1860.
- 987 Johnson, C.J., Parker, K.L., Heard, D.C., Gillingham, M.P., 2002b. Movement parameters of
 988 ungulates and scale-specific responses to the environment. *Journal of Animal Ecology*
 989 71, 225–235.
- 990 Julien, M.-A., Bocherens, H., Burke, A., Drucker, D.G., Patou-Mathis, M., Krotova, O., Péan, S.,
 991 2012. Were European steppe bison migratory? ^{18}O , ^{13}C and Sr intra-tooth isotopic
 992 variations applied to a palaeoethological reconstruction. *Quaternary International* 271,
 993 106–119.
- 994 Kelly, R.L., 1992. Mobility/sedentism: concepts, archaeological measures, and effects. *Annual*
 995 *review of Anthropology* 43–66.
- 996 Kelly, T.E., 2007. Strontium isotope tracing in animal teeth at the Neanderthal site of Les
 997 Pradelles, Charente, France. Honours Dissertation, The Australian National University.
- 998 Knudson, K.J., Price, T.D., Buikstra, J.E., Blom, D.E., 2004. The use of strontium isotope
 999 analysis to investigate Tiwanaku migration and mortuary ritual in Bolivia and Peru.
 1000 *Archaeometry* 46, 5–18.
- 1001 Kojola, I., Huitu, O., Toppinen, K., Heikura, K., Heikkinen, S., Ronkainen, S., 2004. Predation
 1002 on European wild forest reindeer (*Rangifer tarandus*) by wolves (*Canis lupus*) in Finland.
 1003 *Journal of Zoology* 263, 229–235. <https://doi.org/10.1017/S0952836904005084>
- 1004 Konter, J.G., Storm, L.P., 2014. High precision $^{87}\text{Sr}/^{86}\text{Sr}$ measurements by MC-ICP-MS,
 1005 simultaneously solving for Kr interferences and mass-based fractionation. *Chemical*
 1006 *Geology* 385, 26–34.
- 1007 Lafille, J., 1961. Le gisement dit “Roc de Marsal”, commune de Campagne du Bugue
 1008 (Dordogne): note préliminaire. *Bulletin de la Société préhistorique française* 58, 712–13.
- 1009 Landete-Castillejos, T., García, A., Gomez, J.A., Berruga, M.I., Gallego, L., 2005. Effects of
 1010 birth date and order in lactation performance of Iberian red deer (*Cervus elaphus*
 1011 *hispanicus*). *Journal of dairy science* 88, 154–158.

- 1012 Larter, N.C., Gates, C.C., 1991. Diet and habitat selection of wood bison in relation to seasonal
 1013 changes in forage quantity and quality. *Canadian Journal of Zoology* 69, 2677–2685.
- 1014 Lartet, E., Christy, H., 1875. *Reliquiae Aquitanicae: Being Contributions to the Archaeology and*
 1015 *Palaeontology of Périgord and the Adjoining Provinces of Southern France; 1865-75.*
 1016 Text. Williams & Norgate.
- 1017 Laysen, E.F., 1974. A review of the mountain caribou of northeastern Washington and adjacent
 1018 northern Idaho. *Journal of the Idaho Academy of Science, Special Research* 1–63.
- 1019 Lazzzerini, N., Balter, V., Coulon, A., Tacail, T., Marchina, C., Lemoine, M., Bayarkhuu, N.,
 1020 Turbat, T., Lepetz, S., Zazzo, A., 2021. Monthly mobility inferred from isoscapes and
 1021 laser ablation strontium isotope ratios in caprine tooth enamel. *Scientific Reports* 11, 1–
 1022 11.
- 1023 Le Corre, M., Grimes, V., Lam, R., Britton, K., 2023. Comparison between strip sampling and
 1024 laser ablation methods to infer seasonal movements from intra-tooth strontium isotopes
 1025 profiles in migratory caribou, *Scientific Reports* 13, 3621.
- 1026 Legoux, P., 1966. Détermination de l'âge dentaire de l'enfant néandertalien du Roc-Marsal.
 1027 *Revue française d'Odontologie Stomatologie.*
- 1028 Levine, M.A., 1982. The use of crown height measurements and eruption-wear sequences to age
 1029 horse teeth. *Ageing and sexing animal bones from archaeological sites* 109, 223–249.
- 1030 Lieberman, D.E., Shea, J.J., 1994. Behavioral differences between archaic and modern humans
 1031 in the Levantine Mousterian. *American anthropologist* 96, 300–332.
- 1032 Lovari, S., Serrao, G., Mori, E., 2017. Woodland features determining home range size of roe
 1033 deer. *Behavioural Processes* 140, 115–120. <https://doi.org/10.1016/j.beproc.2017.04.012>
- 1034 Mahmut, H., Masuda, R., Onuma, M., Takahashi, M., Nagata, J., Suzuki, M., Ohtaishi, N., 2002.
 1035 Molecular phylogeography of the red deer (*Cervus elaphus*) populations in Xinjiang of
 1036 China: comparison with other Asian, European, and North American populations.
 1037 *Zoological science* 19, 485–495.
- 1038 Mellars, P.A., 1985. The ecological basis of social complexity in the Upper Paleolithic of
 1039 southwestern France, in: Price, D., Brown, J. (Eds.), *Prehistoric Hunters-Gatherers.*
 1040 Elsevier, pp. 271–297.
- 1041 Miller, J.H., Fisher, D.C., Crowley, B.E., Secord, R., Konomi, B.A., 2022. Male mastodon
 1042 landscape use changed with maturation (late Pleistocene, North America). *Proceedings of*
 1043 *the National Academy of Sciences* 119, e2118329119.
- 1044 Moncel, M.-H., Fernandes, P., Willmes, M., James, H., Grün, R., 2019. Rocks, teeth, and tools:
 1045 New insights into early Neanderthal mobility strategies in South-Eastern France from
 1046 lithic reconstructions and strontium isotope analysis. *PLoS One* 14, e0214925.
- 1047 Montgomery, J., Evans, J.A., Horstwood, M.S., 2010. Evidence for long-term averaging of
 1048 strontium in bovine enamel using TIMS and LA-MC-ICP-MS strontium isotope intra-
 1049 molar profiles. *Environmental Archaeology* 15, 32–42.
- 1050 Moore, L.J., Murphy, T.J., Barnes, I.L., Paulsen, P.J., 1982. Absolute Isotopic Abundance Ratios
 1051 and Atomic Weight of a Reference Sample of Strontium. *J Res Natl Bur Stand (1977)* 87,
 1052 1–8. <https://doi.org/10.6028/jres.087.001>
- 1053 Morin, E., 2004. Late Pleistocene population interaction in western Europe and modern human
 1054 origins: New insights based on the faunal remains from Saint-Césaire, southwestern
 1055 France (Ph.D. dissertation). University of Michigan Ann Arbor, Michigan.
- 1056 Niven, L., Martin, H., 2018. Zooarcheological Analysis of the Assemblage from the 2000–2003
 1057 Excavations, in: *The Middle Paleolithic Site of Pech de l'Azé IV.* Springer, pp. 95–116.

1058 Papageorgopoulou, C., Xirotiris, N.I., 2009. Anthropological research on a Byzantine population
1059 from Korytiani, west Greece. *Hesperia Supplements* 43, 193–221.

1060 Pederzani, S., Aldeias, V., Dibble, H. L., Goldberg, P., Hublin, J. J., Madelaine, S., ... & Britton,
1061 K. (2021). Reconstructing Late Pleistocene paleoclimate at the scale of human behavior: an
1062 example from the Neandertal occupation of La Ferrassie (France). *Scientific reports*, 11(1), 1419.

1063 Peek, J., 2003. Wapiti, in: Feldhamer, G.A., Thompson, B.C., Chapman, J.A. (Eds.), *Wild*
1064 *Mammals of North America: Biology, Management, and Conservation*. JHU Press,
1065 Baltimore, pp. 877–888.

1066 Pellegrini, M., Donahue, R.E., Chenery, C., Evans, J., Lee-Thorp, J., Montgomery, J., Mussi, M.,
1067 2008. Faunal migration in late-glacial central Italy: implications for human resource
1068 exploitation. *Rapid Communications in Mass Spectrometry: An International Journal*
1069 *Devoted to the Rapid Dissemination of Up-to-the-Minute Research in Mass Spectrometry*
1070 22, 1714–1726.

1071 Pike-Tay, A., 1991. Red deer hunting in the Upper Paleolithic of south-west France: a study in
1072 seasonality. BAR Publishing.

1073 Price, T.D., Burton, J.H., Bentley, R.A., 2002. The characterization of biologically available
1074 strontium isotope ratios for the study of prehistoric migration. *Archaeometry* 44, 117–
1075 135.

1076 Price, T.D., Johnson, C.M., Ezzo, J.A., Ericson, J., Burton, J.H., 1994. Residential mobility in
1077 the prehistoric southwest United States: a preliminary study using strontium isotope
1078 analysis. *Journal of archaeological Science* 21, 315–330.

1079 Pucek, Z., Belousova, I.P., Krasinski, Z.A., Olech, W., 2004. European bison: status survey and
1080 conservation action plan. IUCN, Cambridge.

1081 Ramanzin, M., Sturaro, E., Zanon, D., 2007. Seasonal migration and home range of roe deer
1082 (*Capreolus capreolus*) in the Italian eastern Alps. *Can. J. Zool.* 85, 280–289.
1083 <https://doi.org/10.1139/Z06-210>

1084 Reeves, J.S., McPherron, S.P., Aldeias, V., Dibble, H.L., Goldberg, P., Sandgathe, D., Turq, A.,
1085 2019. Measuring spatial structure in time-averaged deposits insights from Roc de Marsal,
1086 France. *Archaeological and Anthropological Sciences* 11, 5743–5762.

1087 Reynolds, H., Gates, C.C., Glaholt, R., 2003. , in: Feldhamer, G.A., Thompson, B.C., Chapman,
1088 J.A. (Eds.), *Wild Mammals of North America: Biology, Management, and Conservation*.
1089 JHU Press, Baltimore, pp. 1009–1060.

1090 Richards, M., Harvati, K., Grimes, V., Smith, C., Smith, T., Hublin, J.-J., Karkanias, P.,
1091 Panagopoulou, E., 2008. Strontium isotope evidence of Neanderthal mobility at the site
1092 of Lakonis, Greece using laser-ablation PIMMS. *Journal of Archaeological science* 35,
1093 1251–1256.

1094 Richter, D., Dibble, H., Goldberg, P., McPherron, S.P., Niven, L., Sandgathe, D., Talamo, S.,
1095 Turq, A., 2013. The late Middle Palaeolithic in Southwest France: New TL dates for the
1096 sequence of Pech de l’Azé IV. *Quaternary International* 294, 160–167.

1097 Russell, D.E., Martell, A.M., Nixon, W.A., 1993. Range ecology of the Porcupine caribou herd
1098 in Canada. *Rangifer* 1–168.

1099 Saïd, S., Gaillard, J.-M., Duncan, P., Guillon, Nadine, Guillon, Noël, Servanty, S., Pellerin, M.,
1100 Lefevre, K., Martin, C., van Laere, G., 2005. Ecological correlates of home-range size
1101 in spring–summer for female roe deer (*Capreolus capreolus*) in a deciduous woodland.
1102 *Journal of Zoology* 267, 301–308. <https://doi.org/10.1017/S0952836905007454>

- 1103 Sandgathe, D.M., Dibble, H.L., McPherron, S.J.P., Goldberg, P., 2018. Introduction, in: The
 1104 Middle Paleolithic Site of Pech de l'Azé IV. Springer, Cham, pp. 21–74.
- 1105 Scharlotta, I., Weber, A., DuFrane, S., Goriunova, O.I., Creaser, R., 2011. Assessing hunter-
 1106 gatherer mobility in Cis-Baikal, Siberia using LA-ICP-MS: methodological corrections
 1107 for laser interactions with calcium phosphate matrices and the potential for integrated
 1108 LA-ICP-MS sampling of archaeological skeletal materials, in: Black, S. (Ed.), *Laser
 1109 Ablation: Effects and Applications*. Nova Publishers New York, pp. 48–95.
- 1110 Schmidt, K., 1993. Winter ecology of nonmigratory Alpine red deer. *Oecologia* 95, 226–233.
- 1111 Senft, R., Coughenour, M., Bailey, D., Rittenhouse, L., Sala, O., Swift, D., 1987. Large
 1112 herbivore foraging and ecological hierarchies. *BioScience* 37, 789–799.
- 1113 Shoesmith, M.W., Storey, D.R., 1977. Movements and associated behaviour of woodland
 1114 caribou in central Manitoba. Manitoba Department of Renewable Resources and
 1115 Transportation Services.
- 1116 Sillen, A., 1989. Diagenesis of the inorganic phase of cortical bone, in: Price, D. (Ed.), *The
 1117 Chemistry of Prehistoric Human Bone*. Cambridge University Press, New York, pp. 211–
 1118 229.
- 1119 Skogland, T., 1984. Wild reindeer foraging-niche organization. *Ecography* 7, 345–379.
- 1120 Speck, F.G., Eiseley, L.C., 1942. Montagnais-Naskapi bands and family hunting districts of the
 1121 central and southeastern Labrador Peninsula. *Proceedings of the American Philosophical
 1122 Society* 215–242.
- 1123 Spiess, A.E., 1979. *Reindeer and Caribou Hunters; an Archaeological Study*. San Francisco:
 1124 Academic Press.
- 1125 Stardom, R., 1975. Woodland caribou and snow conditions in southeast Manitoba, in: Luick, J.,
 1126 Lent, P., Klein, D., White, R. (Eds.), *Proceedings of the First International Rangifer and
 1127 Caribou Symposium: Biological Papers of the University of Alaska, Special Report No.
 1128 1*. Biol Pap Univ Alaska Spec Rep, pp. 324–334.
- 1129 Steele, T.E., Weaver, T.D., 2012. Refining the Quadratic Crown Height Method of age
 1130 estimation: do elk teeth wear quadratically with age? *Journal of archaeological science*
 1131 39, 2329–2334.
- 1132 Straus, L.G., 1997. Late glacial reindeer hunters along the French Pyrenees, in: Jackson, J.,
 1133 Thacker, P. (Eds.), *Caribou and Rangifer Hunters of the Northern Hemisphere*. Avebury,
 1134 Aldershot, pp. 165–184.
- 1135 Stuart-Smith, A.K., Bradshaw, C.J., Boutin, S., Hebert, D.M., Rippin, A.B., 1997. Woodland
 1136 caribou relative to landscape patterns in northeastern Alberta. *The Journal of wildlife
 1137 management* 622–633.
- 1138 Sturdy, D.A., 1975. Some reindeer economies in prehistoric Europe, in: Higgs, E. (Ed.),
 1139 *Palaeoeconomy*. pp. 55–95.
- 1140 Tomé, C., Vigne, J.-D., 2003. Roe deer (*Capreolus capreolus*) age at death estimates: new
 1141 methods and modern reference data for tooth eruption and wear, and for epiphyseal
 1142 fusion. *Archaeofauna, International Journal of Archaeozoology* 12, 157–173.
- 1143 Tufto, J., Andersen, R., Linnell, J., 1996. Habitat Use and Ecological Correlates of Home Range
 1144 Size in a Small Cervid: The Roe Deer. *Journal of Animal Ecology* 65, 715–724.
 1145 <https://doi.org/10.2307/5670>
- 1146 Turq, A., H. Dibble, J.-P. Faivre, P. Goldberg, S. J. P. McPherron, and D. Sandgathe. “Le
 1147 Moustérien Récent Du Périgord Noir : Quoi De Neuf ?” In *Les Sociétés Du Paléolithique
 1148 Dans Un Grand Sud-Ouest de La France: Nouveaux Gisements, Nouveaux Résultats*,

1149 *Nouvelles Méthodes*, edited by J. Jaubert, J.-G. Bordes, and I. Ortega, 83–94. Mémoire de
1150 la Société Préhistorique Française 48, 2008.

1151

1152 Turq, A., Faivre, J.-P., Gravina, B., Bourguignon, L., 2017. Building models of Neanderthal
1153 territories from raw material transports in the Aquitaine Basin (southwestern France).
1154 Quaternary international 433, 88–101.

1155 Tyler, N.J.C., Øritsland, N.A., 1989. Why don't Svalbard reindeer migrate? *Ecography* 12, 369–
1156 376.

1157 Uno, K.T., Fisher, D.C., Wittemyer, G., Douglas-Hamilton, I., Carpenter, N., Omondi, P.,
1158 Cerling, T.E., 2020. Forward and inverse methods for extracting climate and diet
1159 information from stable isotope profiles in proboscidean molars. *Quaternary International*
1160 557, 92–109.

1161 van Asperen, E.N., 2010. Ecomorphological adaptations to climate and substrate in late Middle
1162 Pleistocene caballoid horses. *Palaeogeography, Palaeoclimatology, Palaeoecology* 297,
1163 584–596.

1164 White, R., 1985. Upper Paleolithic land use in the Périgord: a topographic approach to
1165 subsistence and settlement. *British Archaeological Reports*.

1166 Williams, C.T., Marlow, C.A., 1987. Uranium and thorium distributions in fossil bones from
1167 Olduvai Gorge, Tanzania and Kanam, Kenya. *Journal of Archaeological Science* 14,
1168 297–309.

1169 Willmes, M., Bataille, C.P., James, H.F., Moffat, I., McMorrow, L., Kinsley, L., Armstrong,
1170 R.A., Eggins, S., Grün, R., 2018. Mapping of bioavailable strontium isotope ratios in
1171 France for archaeological provenance studies. *Applied Geochemistry* 90, 75–86.

1172 Willmes, M., McMorrow, L., Kinsley, L., Armstrong, R., Aubert, M., Eggins, S., Falguères, C.,
1173 Maureille, B., Moffat, I., Grün, R., 2014. The IRHUM (Isotopic Reconstruction of
1174 Human Migration) database–bioavailable strontium isotope ratios for geochemical
1175 fingerprinting in France. *Earth System Science Data* 6, 117–122.

1176 Wroth, K., Cabanes, D., Marston, J.M., Aldeias, V., Sandgathe, D., Turq, A., Goldberg, P.,
1177 Dibble, H.L., 2019. Neanderthal plant use and pyrotechnology: phytolith analysis from
1178 Roc de Marsal, France. *Archaeological and Anthropological Sciences* 11, 4325–4346.

1179 Wu, J.P., Veitch, A., Checkley, S., Dobson, H., Kutz, S.J., 2012. Linear enamel hypoplasia in
1180 caribou (*Rangifer tarandus groenlandicus*): A potential tool to assess population health,
1181 *Wildlife Society Bulletin* 36, 554-560.

1182

1183

1184

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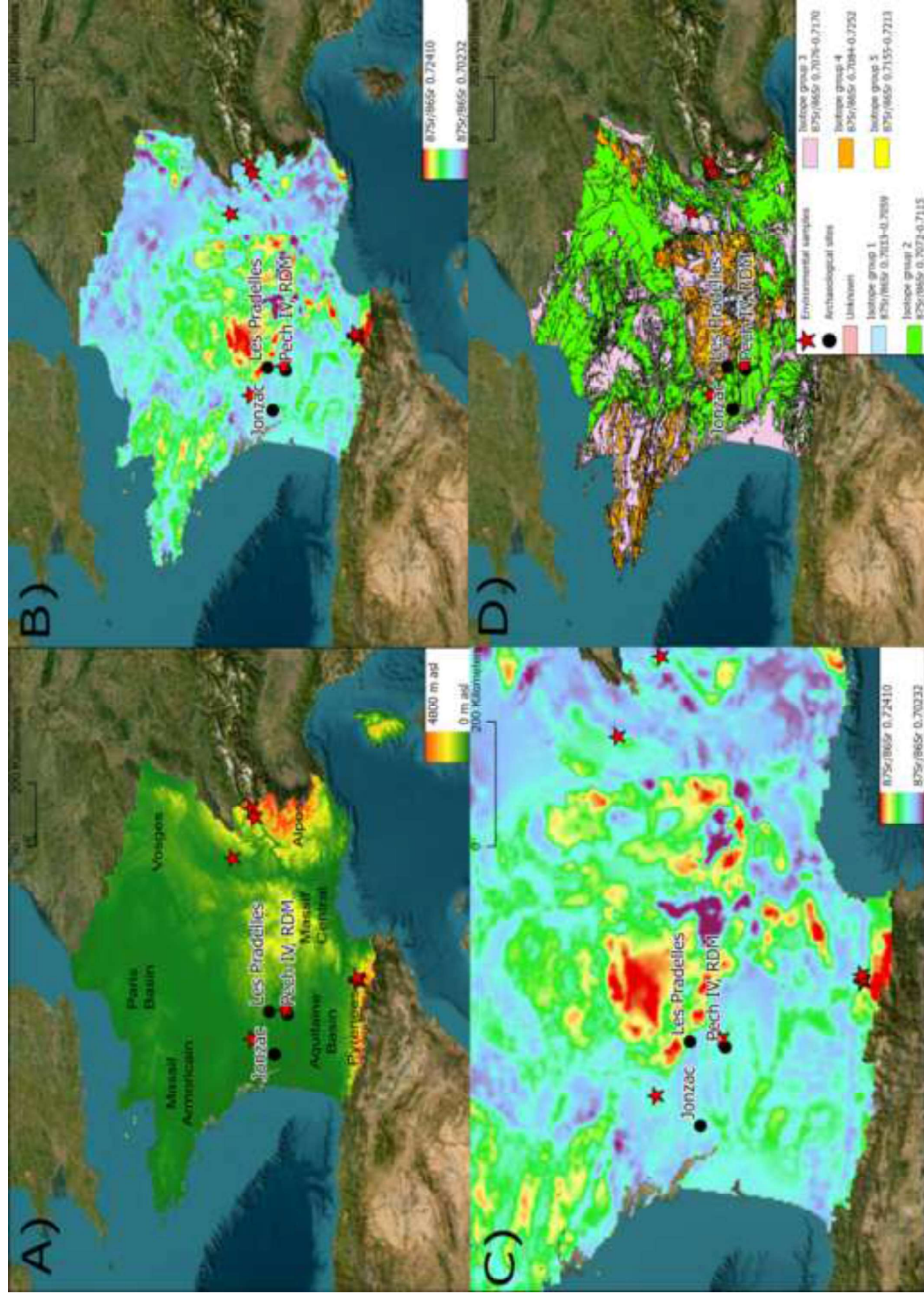
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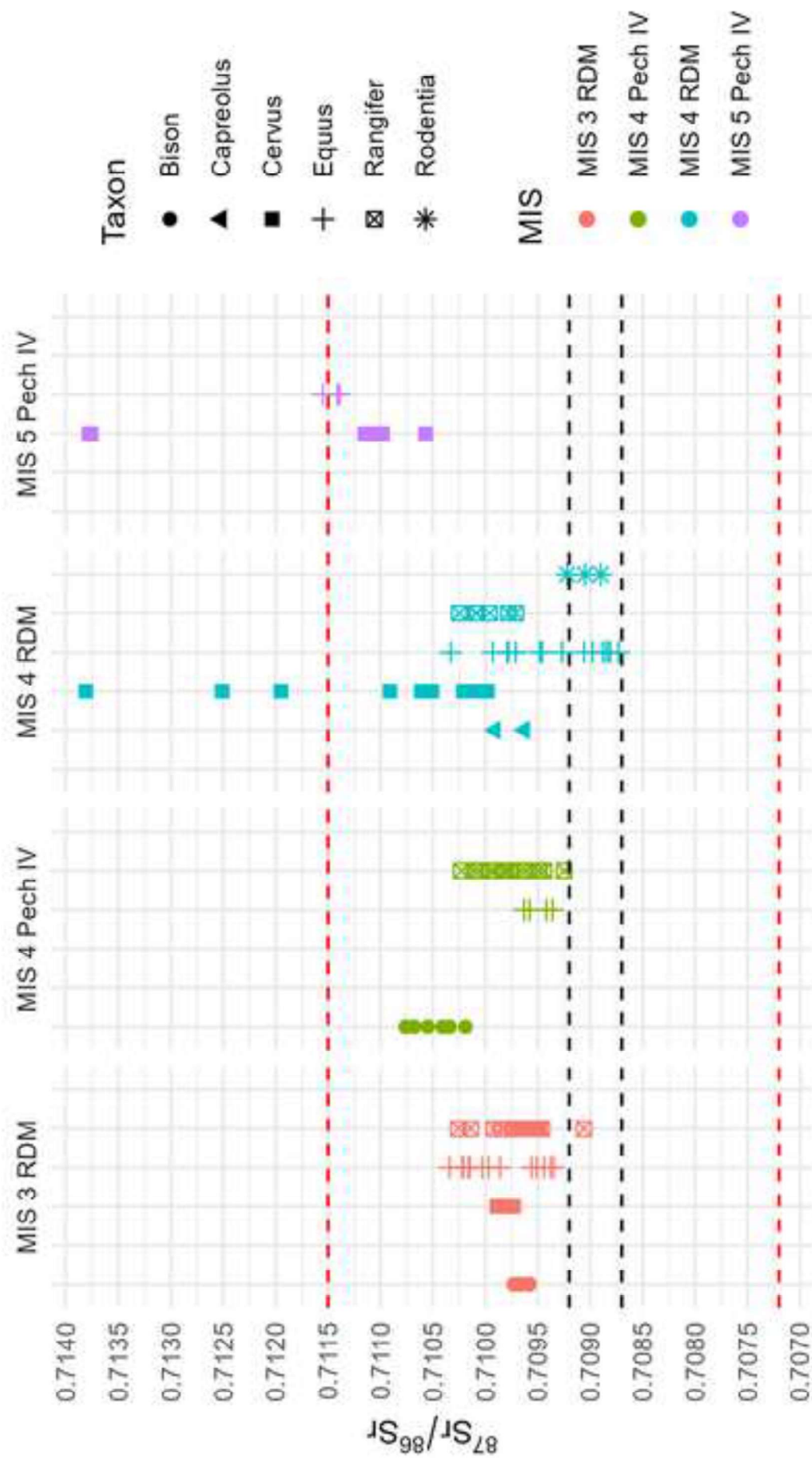
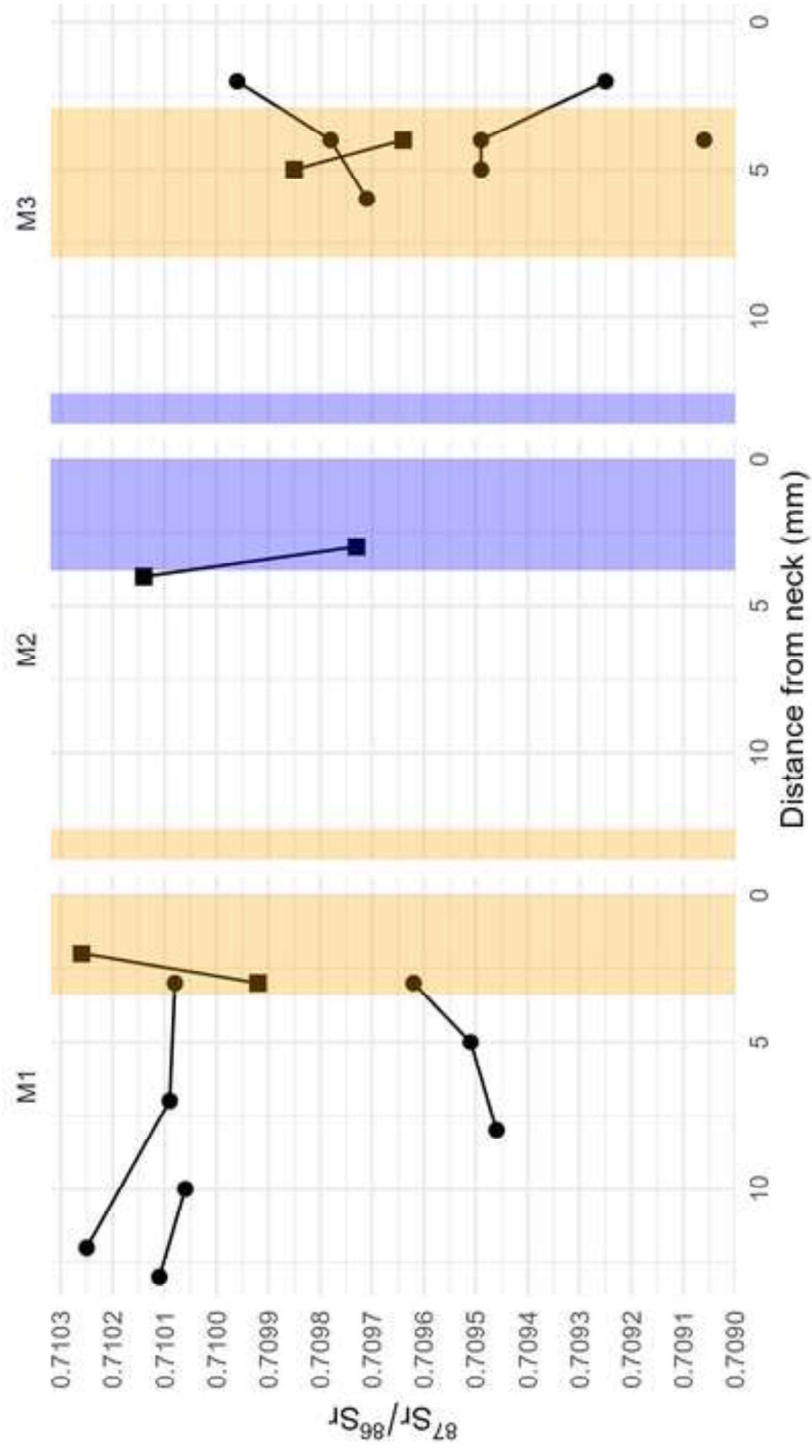


Figure 3

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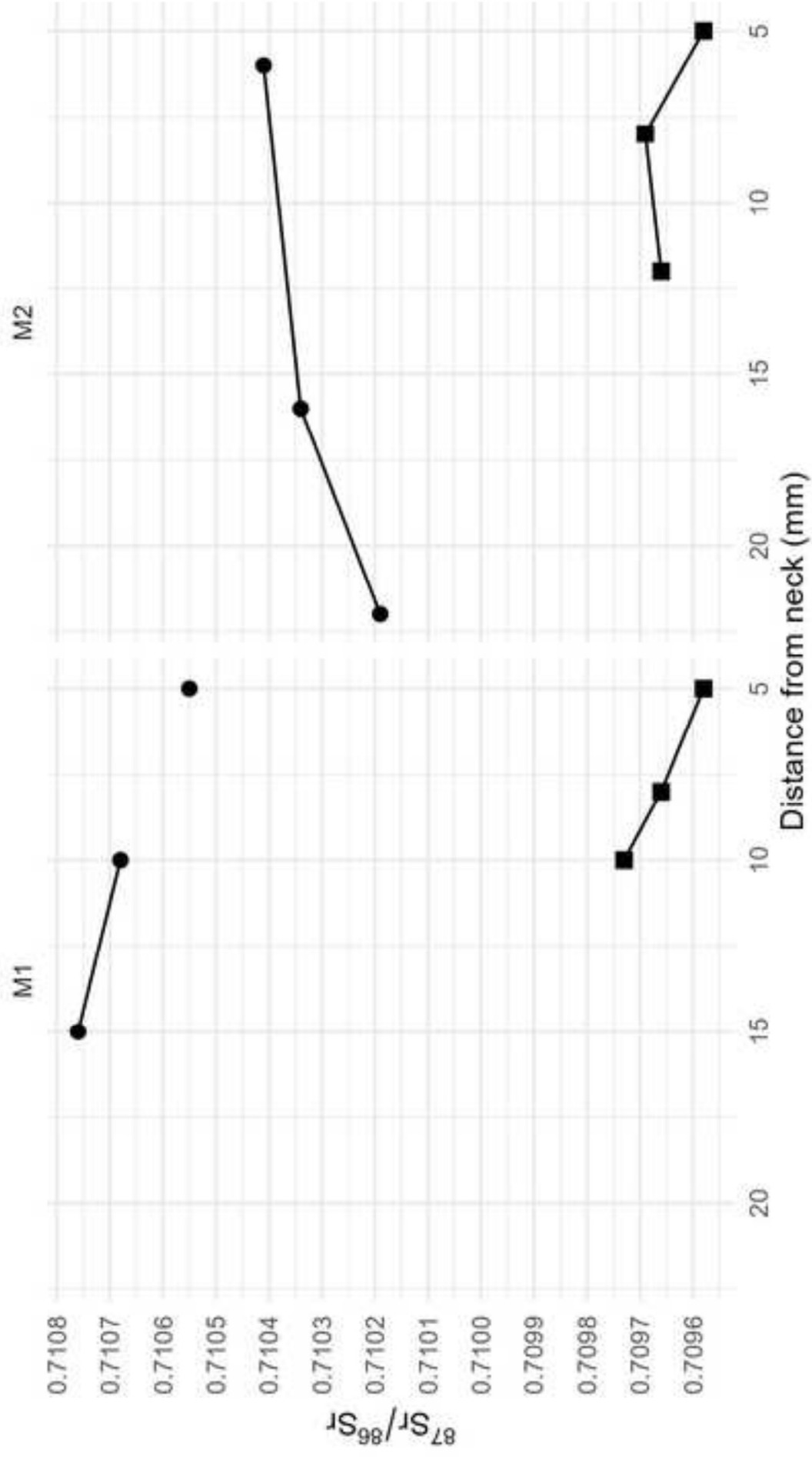


Figure 5

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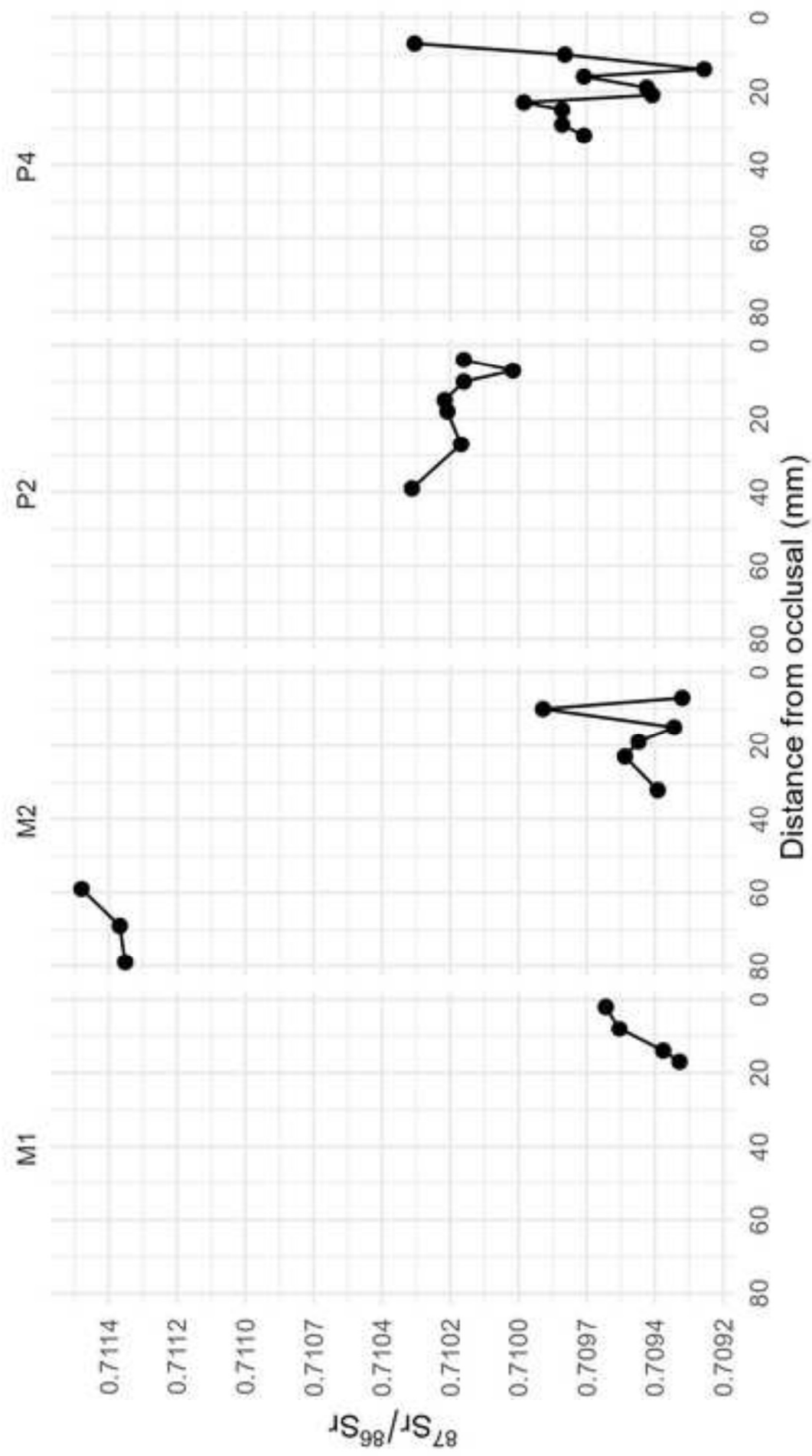
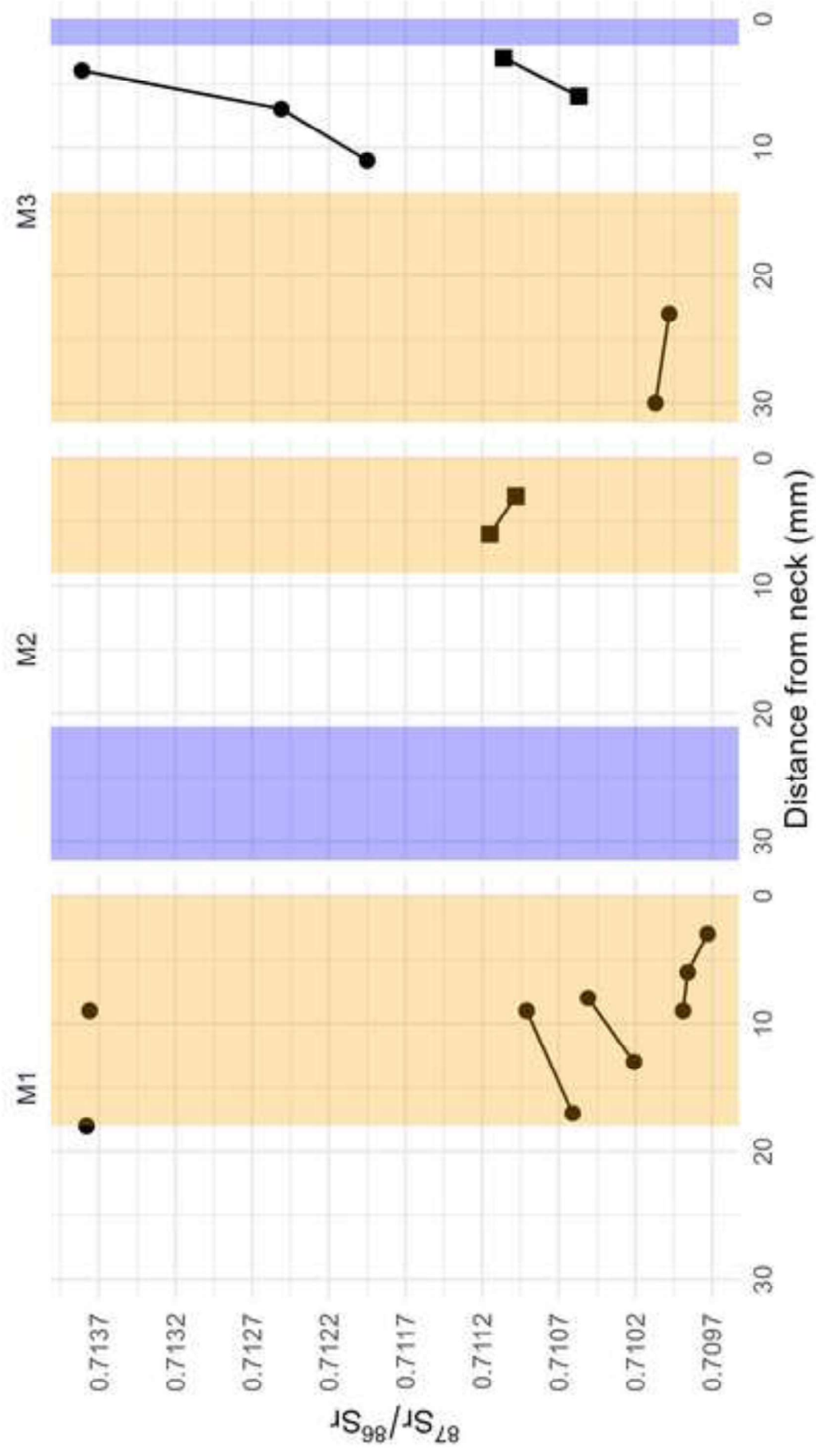


Figure 6

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. The authors did not use any AI programs to write this paper.

Author Contributions

Each of the authors in the author list have contributed in the following ways:

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