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1 The isotope record ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$) of vertical mobility in incremental tissues (tooth enamel, hair)
2 of modern livestock: A reference set from the Mongolian Altai

3

4 N. Lazzerini ^a, A. Coulon ^{b,c}, L. Simon ^d, C. Marchina ^e, D. Fiorillo ^a, Ts. Turbat ^f, N.
5 Bayarkhuu ^f, C. Noûs^g, S. Lepetz ^a, A. Zazzo ^{a,*}

6 ^a Archéozoologie, Archéobotanique: sociétés, pratiques et environnements (AASPE),
7 Muséum national d'Histoire naturelle, Sorbonne université, CNRS, CP 56, 55 rue Buffon
8 75005 Paris, France

9 ^b Centre d'Écologie et des Sciences de la Conservation (CESCO), Muséum national
10 d'Histoire naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, CP
11 135, 57 rue Cuvier 75005 Paris, France

12 ^c CEFE, Univ. Montpellier, Univ. Paul Valéry Montpellier 3, CNRS, EPHE, IRD,
13 Montpellier, France

14 ^d Univ Lyon, Université Claude Bernard Lyon 1, CNRS, ENTPE, UMR 5023 LEHNA, F-
15 69622, Villeurbanne, France

16 ^e Institut Français de Recherche sur l'Asie de l'Est (IFRAE), Inalco, Université de Paris,
17 CNRS, 2 rue de Lille, 75007 Paris, France

18 ^f Institute of Archaeology, Mongolian Academy of Sciences, Mongolia

19 ^g Cogitamus Laboratory, 55 rue Buffon, 75005 Paris, France

20 * Corresponding author

21 E-mail address: antoine.zazzo@mnhn.fr

22

23 **Abstract:**

24 Identifying the isotopic signatures of vertical mobility and alpine meadows exploitation in the
25 teeth of domesticated animals can be a key to understanding the subsistence strategies used by
26 pastoral communities through history. Indeed, the oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) isotopic
27 composition of sequentially sampled tooth enamel, used alone or in combination have been

28 commonly employed to investigate altitudinal mobility and alpine exploitation. However,
29 conflicting interpretations of the outcomes of these analyses exist, due in part to the paucity of
30 modern reference datasets. In this study, we propose a new reference set, composed of GPS
31 monitored sheep, goats and horses from the Mongolian Altai, to investigate the influence of
32 vertical mobility and mean grazing altitude, on the C and O isotopic compositions of
33 sequentially sampled tooth enamel and on the C isotopic composition of horse tail hair. We
34 found that $\delta^{13}\text{C}$ values were negatively correlated with the mean grazing altitude and time of
35 residency of alpine meadows. Although no correlation was found between the average $\delta^{18}\text{O}$
36 values of tooth enamel and mean grazing altitude, vertically mobile livestock had a higher
37 intra-tooth range in $\delta^{18}\text{O}$ values than vertically immobile livestock, possibly reflecting the
38 ingestion of isotopically more diverse sources of water. Moreover, the coefficient of the
39 correlation between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of tooth enamel was - although weakly - negatively
40 correlated with the standard deviation of the animal mean grazing altitude (i.e. reflecting the
41 frequency of altitudinal mobility). These results confirm that $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ analyses of tooth
42 enamel and tail hair can be used to infer animal mobility and land use in modern and ancient
43 times.

44 *Keywords: Sequential isotope analysis; Caprine; Horse; Herding strategy; Plant; GPS*
45 *monitoring*

46 **1. INTRODUCTION**

47 Human-directed mobility of domesticated livestock between different pastures is a key
48 element of the resource management strategy of pastoral systems. It aims to provide access to
49 a continuous source of fresh graze throughout the year for livestock in patchy and low-
50 productivity environments (Little, 2015; Wright and Makarewicz, 2015). Mobile pastoralism
51 is practiced largely in the drylands and highlands of the world, from South America to North-
52 East Asia (e.g. Lynch, 1983; Niamir-Fuller and Turner, 1999; Dong et al., 2011; Stépanoff et
53 al., 2013; Liechti and Biber, 2016; Arbuckle and Hammer, 2018). Pastoral mobility can take
54 various forms such as pasture rotation, transhumance and nomadism, depending on a
55 combination of different parameters such as environmental conditions, species and number of
56 herd animals, economic and political context, social structures, and household life (e.g. for
57 Inner Asia, Fernandez-Gimenez, 2000; Kerven et al., 2006).

58 In mountain areas, where the environment is characterized by a vertical stratification of
59 resources, altitudinal mobility is a common strategy used by herders to maximize the

60 exploitation of pastures situated along an elevation gradient. Not only does it provide a stable
61 buffer against seasonal fluctuations in the quality and quantity of graze, but it also offers
62 protection against winds and snowfalls, especially in extreme continental climatic conditions
63 (Marchina, 2019). In such environments, herds usually graze in low elevation pastures during
64 the cold season and in high elevation pastures during the warm season.

65 Mongolia is a region of particular interest for the study of ancient pastoral societies. Indeed,
66 Mongolia is known as the cultural and geographical center of nomadic empires, from the
67 Xiongnu (3rd century BCE-2nd century CE) to the Mongol Empire (13th century CE). It is
68 recognized that mobile pastoralism may have structured political life, fostered social
69 organization and large-scale political communities (Lynch, 1983; Porter, 2012; Honeychurch,
70 2013; Frachetti et al., 2017). Understanding how and why complex regional organizations
71 emerged among nomadic peoples is one of the most important research questions in
72 Mongolian archaeology today (Honeychurch, 2013; 2015). Knowledge of the mobility
73 strategies and pastoral practices of these peoples is part of the information needed to
74 understand the development of social organizations of these steppe empires. Within
75 Mongolia, the Altai mountains host the oldest record of pastoral occupation (e.g. Kovalev and
76 Erdenebaatar 2009). It is an archaeology-rich area, traditionally considered as the cradle of the
77 Turkic peoples..For millennia, the Altai Mountains were an important transition zone between
78 the Mongolian and Kazakh steppes. Identifying the use of highland pastures, being able to
79 detect the origin and characterize the extent of vertical mobility, is of paramount importance
80 to describe subsistence economies and social interactions in past pastoralist communities of
81 the Altai. However, direct identification of past vertical mobility by archaeologists remains
82 challenging.

83 A promising approach to detect mountainous occupation and altitudinal mobility of ancient
84 herd consists in the isotopic analysis of animal tissues. Indeed, when analysed sequentially in
85 continuously growing tissues (i.e. tooth, hair, horn), carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) stable
86 isotope time series offer a quantitative method to study livestock husbandry strategies,
87 including mobility (e.g. Mashkour, 2003; Balasse and Ambrose, 2005; Pearson et al., 2007;
88 Makarewicz and Tuross, 2012; Dufour et al., 2014; Makarewicz et al., 2017). The oxygen
89 isotopic composition from sequentially sampled tooth enamel has been regularly used to infer
90 altitudinal mobility. Herbivore tooth enamel records the $\delta^{18}\text{O}$ of ingested water, deriving from
91 meteoric water, which is itself influenced by temperature, continental positioning, rainfall
92 amount, humidity and seasonality (Dansgaard, 1964; Rozanski et al., 1993; Gat, 1996; Kohn

93 and Welker, 2005). Altitude also has an important influence on $\delta^{18}\text{O}$ of meteoric water
94 through two parallel phenomena: (1) the progressive rainout along mountain slopes, which
95 preferentially removes ^{18}O -enriched water from clouds; (2) colder temperatures at high
96 altitude. Both result in ^{18}O -depleted precipitation at high altitudes and ^{18}O -enriched
97 precipitation at low altitudes (Gat, 1996; Gonfiantini et al., 2001; Poage and Chamberlain,
98 2001). However, the relationship between altitude and $\delta^{18}\text{O}$ of precipitation varies according
99 to geography, topography, and region-specific conditions (Ambach et al., 1968; Rozanski et
100 al., 1993; Poage and Chamberlain, 2001; Kern et al., 2014; Liu et al., 2014). As a result,
101 identification of animal altitudinal mobility is often based on the interpretation of the
102 amplitude of $\delta^{18}\text{O}$ variations recorded within tooth enamel. Some authors have suggested that
103 because mobile animals avoid climatic extremes, altitudinal mobility will cause a reduction of
104 the isotopic amplitude recorded by tooth enamel compared to animal with low residential
105 mobility (Pellegrini et al., 2008; Britton et al., 2009; Henton et al., 2010; 2017; Henton,
106 2012). This is in contrast with Mashkour (2003) and Mashkour et al. (2005) who proposed
107 that mobile animals exploiting mountain ranges displayed a higher intra-tooth $\delta^{18}\text{O}$ variability
108 than lowland animals due to a wider access of water, outside of the 'local' range. These
109 differences in interpretation may reflect the influence of confounding factors such as the
110 ingestion of buffered water sources (i.e. lakes or groundwater), the variability of drinking
111 behaviour or the ingestion of important proportions of ^{18}O -enriched leaf water in semi-
112 arid/arid environments (Dufour et al., 2014; Makarewicz and Pederzani, 2017; Knockaert et
113 al., 2018). As a consequence, some authors have proposed to focus on the shape of the $\delta^{18}\text{O}$
114 curve instead and developed theoretical models of mobility in order to predict isotopic
115 variations (Henton et al., 2017; Hermes et al., 2017). However, these models only take into
116 account the environmental $\delta^{18}\text{O}$ values and do not consider the dampening of the input signal
117 during enamel mineralization (e.g. Passey and Cerling, 2002; Balasse, 2003; Zazzo et al.,
118 2012). Because of the duration of the mineralization process, only a large and rapid
119 movement between two isotopically distinct areas is able to generate a detectable change in
120 the curve.

121 Carbon isotopes also can be used to infer altitudinal mobility. Indeed, the carbon isotopic
122 composition ($\delta^{13}\text{C}$) of herbivore tissues (i.e. tooth, hair, horn) reflects the $\delta^{13}\text{C}$ value of
123 ingested plants and can be used to track animal dietary changes associated with seasonal
124 changes in pasture composition, mobility or human interference (Balasse et al., 2002; Männel
125 et al., 2007; Barbosa et al., 2009; Fisher and Valentine, 2013; Henton et al., 2017; Ventresca

126 Miller et al., 2017; Winter-Schuh, 2017; Knockaert et al., 2018). Several factors influence the
127 $\delta^{13}\text{C}$ values of terrestrial plants. The dominant influential factor is the photosynthetic pathway
128 used for fixing C. Indeed, plants using the C_3 pathway have an average $\delta^{13}\text{C}$ value of -26‰ ,
129 those using the C_4 pathway exhibit an average $\delta^{13}\text{C}$ value of -12‰ , and those using the CAM
130 pathway show intermediates between the values of the C_3 and C_4 plants (O'Leary, 1988;
131 Kohn, 2010). Other factors are associated with environmental conditions such as water
132 availability. Water-use efficiency increases when water availability decreases, leading to a ^{13}C
133 enrichment in plant carbon (Farquhar et al., 1982; 1989; Stewart et al., 1995; Rao et al.,
134 2017). Generally, plants adapted to dry environments show higher $\delta^{13}\text{C}$ values. Finally,
135 climatic conditions also affect the $\delta^{13}\text{C}$ values of terrestrial plants: an increase in temperature
136 during the hot season induces an increase in plant $\delta^{13}\text{C}$ values due to the reduction of stomatal
137 conductance to decrease water losses (Farquhar et al., 1989; Smedley et al., 1991; Hartman
138 and Danin, 2010). Inversely, plants in wets areas or during wet/growth season tend to have
139 high water losses and thus show lower $\delta^{13}\text{C}$ values (Körner et al., 1991; Smedley et al., 1991;
140 Kohn, 2010). Thus, moving herbivores, sampling the changes in plant communities in space
141 and time, would record the changes in $\delta^{13}\text{C}$ values of plants accordingly. Due to the
142 ecological differences between C_3 and C_4 plants, the relative proportion of C_3 vs C_4 plants
143 increases with altitude, triggering a decrease of the mean $\delta^{13}\text{C}$ value of the plant communities
144 (Tieszen et al., 1979; Cavagnaro, 1988; Li et al., 2009). In C_3 -dominated environments, the
145 range of isotopic variations is more restricted. Nevertheless, several studies have documented
146 an increase in the $\delta^{13}\text{C}$ values of C_3 plants with altitude (Körner et al., 1988; Morecroft and
147 Woodward, 1990; Li et al., 2006; 2007; 2009; Liu et al., 2016) that can be recorded in the
148 $\delta^{13}\text{C}$ values of livestock tissues (Männel et al., 2007). This pattern was explained by the high
149 carboxylation rates relative to stomatal conductance at high altitudes, resulting in lower ^{13}C
150 discrimination (Morecroft and Woodward, 1990; Li et al., 2006, p. 2; 2007; 2009). However,
151 the opposite pattern was reported in SW USA and in China (van de Water et al., 2002; Liu et
152 al., 2016), and was explained by a higher drought stress at lower elevations in these arid and
153 semi-arid regions. Finally, several authors proposed that local climatic factors could modulate
154 the effects of water availability and hence locally complicate the relationship between $\delta^{13}\text{C}$
155 values and altitude (Morecroft and Woodward, 1990; Liu et al., 2007; 2010). The variations in
156 $\delta^{13}\text{C}$ values of plants along altitudinal gradients hence may not be explained by a single factor
157 but rather the result of an interaction between different factors and should be characterized for
158 each site.

159 Given the limits of the O and C isotope systems alone, recent attempts at detecting altitudinal
160 mobility have relied on the combined use of both tracers in tooth enamel. Generally, a co-
161 variation between $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values measured within the same tooth is expected for
162 stationary herbivores in temperate and semi-arid environments (Balasse et al., 2002; 2009;
163 Fraser et al., 2008), with high values during the hot season and low values during the cold
164 season. Anti-covariation, when observed, was interpreted as reflecting animal movements
165 between highland pastures in summer (with less C_4 plants in the diet) and midland/lowland
166 pastures in winter (with more C_4 plants in the diet) (e.g. Fisher and Valentine, 2013; Tornero
167 et al., 2016; 2018; Makarewicz and Pederzani, 2017; Makarewicz et al., 2017). This
168 interpretation has been proposed to describe the mobility patterns of wild (Fisher and
169 Valentine, 2013; Tornero et al., 2016) and domestic caprines (Makarewicz, 2017; Makarewicz
170 et al., 2017; Tornero et al., 2018). In the case of domestic animals, manipulation of the diet by
171 the herders, including winter foddering of livestock with a C_4 -rich diet, cannot be excluded.
172 This was documented for modern domesticated sheep from Mongolia (Makarewicz and
173 Pederzani, 2017) and proposed as an explanation of anti-covariation for archaeological
174 livestock (Makarewicz and Tuross, 2006; Makarewicz, 2017; Winter-Schuh, 2017;
175 Makarewicz et al., 2018). A third explanation was proposed by Chazin et al. (2019) to explain
176 lower summer $\delta^{13}\text{C}$ values recorded in the teeth of domestic animals from Bronze Age
177 Caucasus, involving the increase of ^{13}C -depleted shrubs and forbs in the diet (Smedley et al.,
178 1991; Dodd et al., 1998). This proposition is supported by the observation of the increase of
179 forbs in summer diets of wild and domestic sheep from the desert-steppe of Mongolia
180 (Wingard et al., 2011).

181 These conflicting interpretations are in part due to the paucity of modern reference datasets.
182 Only a few modern reference studies have investigated the origin of this anti-correlation,
183 constraining its origin, either through fodder (Makarewicz and Pederzani, 2017) or vertical
184 mobility (Tornero et al., 2018). In general, these studies involved few individuals and lacked
185 any control group (i.e. non-foddered or sedentary). In this study, we propose a new reference
186 set to investigate the influence of vertical mobility on the C and O isotopic composition of
187 tooth enamel. To do this, we analysed the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ variations in tooth enamel of
188 domestic caprines (sheep and goats) of Kazakh-Mongolian herders from the Altai Mountains
189 of western Mongolia, where nomadic pastoralism is characterized by vertical mobility (Finke,
190 2004). We also included a comparative analysis of previously published $\delta^{13}\text{C}$ variations in tail
191 hair of horses belonging to the same herds. All these animals were fitted with GPS collars to

192 monitor their daily movements for three consecutive years and vegetation was sampled at
193 different localities in order to estimate $\delta^{13}\text{C}$ variations with altitude and the influence of C_4
194 plants in the diet. Our aims were to test the hypothesis that (i) the correlation between $\delta^{18}\text{O}$
195 and $\delta^{13}\text{C}$ values of tooth enamel varies with the altitudinal mobility patterns of livestock in a
196 C_3 -dominated environment (with a positive correlation when livestock has a residential
197 mobility); (ii) the highland pasture exploitation can be tracked by the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of
198 animal tissues, with an expected negative correlation between isotopic values ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$)
199 and mean grazing altitude.

200

201 **2. MATERIAL**

202 ***2.1. Burgast: topography, climate and vegetation***

203 Fieldwork was carried out in the Mongolian Altai (Fig. 1) in the Nogoonnuur district located
204 in the northern part of Bayan - Ölgii Province. The altitudinal profile ranges from 1500 to
205 more than 4000 m.asl with the Türgen Uul summit at 4029 m.asl. A north-south fault splits
206 the landscape in half with the highland of the Altai Mountains to the west and a lowland plain
207 to the east. The climate is strongly continental with cold, long winters (November-March) and
208 hot, short summers (June-August). During the study period (June 2015 to July 2018), monthly
209 temperatures averaged $+18.0^\circ\text{C}$ during summer (June–August) and -12.7°C during winter
210 (December–February) with extremes ranging from $+34$ to -44°C (InfoClimat, 2019). Average
211 annual rainfall is 105 mm with a maximum of precipitation occurring during summer
212 (InfoClimat, 2019).. During winter, there is very little snowfall and most of the time no snow
213 cover at all. Open water is rare, and consists in a few intermittent streams. The vegetation
214 consists of alpine meadows and semi-arid steppes and is mainly composed of grasses, with a
215 few forbs and bushes (*Caragana* sp.) or trees (*Populus laurifolia*) exclusively near rivers in
216 lowlands and valley exits for forbs, shrubs and trees. The steppe vegetation is dominated by
217 plants using the C_3 photosynthetic pathway such Asteraceae, a majority of Chenopodiaceae,
218 Poaceae, or Fabaceae (Pyankov et al., 2000; Ivanova et al., 2019). Some species using the C_4
219 photosynthetic pathway, such *Anabasis brevifolia*, *Eragrostis pilosa*, *Kochia prostrata*, or
220 *Setaria veridis* have also been identified.

221 **2.2 Plant material**

222 Plants were sampled at 246 sites distributed throughout the accessible parts of the study area
223 (Fig. 1), in June 2015, September 2016, November 2017 and July 2018 (see Supplementary
224 Material Table A.1). Sampling localities were chosen to represent the grazing areas of the
225 monitored animals. Some parts of the study area could not be sampled due to difficult access
226 or proximity to the Russian border. The average distance between neighbouring sites
227 (calculated using the 5 nearest neighbours of each site) was 1.7 km. At each site, we collected
228 a handful of plant material in a diameter of 2-3 meters. We collected all the plant specimens
229 visible at these sites, and combined them before analysis. In most cases, most collected plants
230 were grasses, but there were also some forbs and shrubs. The majority of the material was
231 composed of leaves but there were also stems and seeds or fruits if present. All plant material
232 was wrapped in paper then dried in a loosely sealed envelope prior to $\delta^{13}\text{C}$ analysis.

233 **2.3. Animal material**

234 Between June 2015 and July 2018, 17 individuals (6 sheep and 11 goats) were equipped with
235 a GPS collar to track the mobility of the herds of five different families of Kazakh-Mongolian
236 nomadic pastoralists (Table 1). GPS collars were fitted when the animals were around 1-1.5
237 years old, as estimated based on the incisor (I1) development (Schmid, 1972). Animals were
238 equipped with Globalstar© (n=13) or Iridium© (n=4) GPS collars (Lotek Wireless Inc. -
239 <http://www.lotek.com/>). Globalstar© and Iridium© devices were programmed to record
240 animal position every 13 and 2 hours respectively and provided also altitude and temperature.
241 Even if we can assume that one animal represents the entire herd (Moritz et al., 2012), we
242 chose to monitor several animals in each herd to prevent technical failures or loss of GPS
243 collars. Because caprines are led back to the camp every night, GPS monitoring allowed us to
244 infer the location of the different camps and associated pastures. While adult males are only
245 supplemented with fodder during bad years, pregnant females and very young individuals
246 may be winter-foddered for a short period of time. To avoid any potential influence of fodder
247 on the isotopic profiles, we only selected male individuals (Table 1). Interviews with the
248 herders confirmed that the animals did not receive any manufactured food complements. We
249 sampled 20 molars from the 17 caprines (Table 2). Animal slaughter was operated by the
250 herders themselves for their own consumption and was authorized by the ethics committee of
251 the *Muséum national d'Histoire naturelle*.

252 To examine the influence of altitude on isotopic composition on a different animal species, we
253 retrieved the GPS and isotope data obtained on horse tail hair from the same area published in
254 Lazzerini et al (2019). The period of tail hair formation was time-calibrated using the GPS
255 data and $\delta^{13}\text{C}$ values of diet were calculated based on the measured $\delta^{13}\text{C}$ values of tail hair.
256 Our sample also includes 5 molars from 5 non-geolocalized modern horses belonging to
257 herders living in the same area. Depending on the age of the horse, the M1, M2 or M3 was
258 sampled (Table 3). Two of these horses belonged to herder Kb and Kj, who had slaughtered
259 them for their own consumption. As those horses were not equipped with GPS collars, we
260 considered that the occupation pattern was similar to that of the other horses from the same
261 herd whose movements were tracked with GPS collars (Lazzerini et al., 2019). The molars of
262 the other three horses were sampled in skulls that were found in the same area, where they
263 probably died following predator attack or accident. We can assume that they had an
264 important vertical mobility during the year, like the majority of horses from this area. These
265 five horse teeth were used to determine their altitudinal mobility and their occupation of high
266 altitude pastures and to test how they compare with the results obtained on individuals with
267 known mobility. For a summary of the analyses (isotopic and GPS) performed on the animal
268 material see Appendix (Tables B).

269 **3. METHODS**

270 ***3.1 Estimation of tooth formation period and tooth selection***

271 To provide a direct comparison between GPS and isotopic data, it was necessary to estimate
272 the period of growth of the teeth sampled. Date of death was recorded by ourselves for each
273 animal. We then estimated the age at death by combining analyses of tooth eruption stages
274 and tooth wear patterns (Grant, 1982; Jones, 2006) (Table C). According on interviews with
275 herders, the season of birth spreads from February to April with a peak between March and
276 April and with slight variations between years and herders. We hence chose an arbitrary birth
277 date of March 31st for all individuals. Although we are aware of the limits of this arbitrary
278 choice, we argue that an uncertainty of about 1 month is likely to have a minor impact on
279 subsequent comparisons given the duration of the mineralization process which is of ~4
280 months (Balasse, 2003; Zazzo et al., 2010). We calculated an average period of formation of
281 caprine molars for M2 (1.3-13 m.o.) and M3 (10.3-28 m.o.) based on the literature (Weinreb
282 and Sharav, 1964; Milhaud and Nezeit, 1991; Zazzo et al., 2010; Upex and Dobney, 2012)
283 (Table D). We then calculated the proportion of the tooth formed during GPS tracking
284 (Time_{GPS}) using the following formula:

$$Time_{GPS}(\%) = \frac{(T - \Delta d)}{T} \times 100 \quad (1)$$

285 In Eq. 1, T is the total duration of tooth formation (in days) and Δd is the number of days
 286 within this period with no GPS record. Only teeth that grew during the GPS tracking period
 287 were selected. We excluded five teeth with low $Time_{GPS}$ scores (0% - not shown), leaving us
 288 with fifteen teeth ($66\% < Time_{GPS} < 100\%$) (Table 2).

289 **3.2 GPS-based inference of mobility**

290 GPS datasets were cleaned from erroneous GPS fixes. Herder mobility patterns were detected
 291 using the Lavielle's method (Lavielle, 1999; 2005), a method of segmentation of location time
 292 series. This method discriminates series of successive locations ("segments") during which
 293 movements happen at the same spatial scale but between which movements happen at
 294 different spatial scales. This allowed determining changes in animal movement, by identifying
 295 the different pastures and hence discriminating between small-scale movements (within each
 296 pasture) and large-scale movements (among pastures). Due to the nature of the landscape and
 297 after different trials (where segmentation was based on x or y coordinates), we finally based
 298 segmentation on altitude and each inferred segment was considered as a pasture, after visual
 299 validation. The Lavielle's method was implemented in the R package *adehabitatHR* (Calenge,
 300 2006). Camps were identified thanks to the agglomeration of GPS points, since sheep and
 301 goats are led back to camps every night by herders to protect them from wolves. Finally, a
 302 distance matrix in QGIS (version 2.18.14) was used to calculate the distance travelled
 303 between camps by each herd.

304 We then used the GPS data in order to calculate, for each animal during the time of tooth or
 305 tail hair growth, their mean grazing altitude, the altitudinal range of exploited pastures, and
 306 the percentage of time spent at high altitude (above 2000 m.asl.). The limit of 2000 m was
 307 chosen because it represents the minimum altitude of alpine meadows in the mountainous
 308 western part of the study area (Fig. 1). Below this limit, grazing animals are located on the
 309 eastern lowlands. The time spent above 2000 m was calculated as:

$$Time_{Alt}(\%) = \frac{d_{2000}}{(T - \Delta d)} \times 100 \quad (2)$$

310 Where $T - \Delta d$ represents the number of days during tooth growth when the animal was
 311 tracked by a GPS collar and d_{2000} is the number of days spent above 2000 m.

312 For each herder, we compared seasonal differences in pasture elevation using linear mixed
313 models, with animal ID as a random effect (intercept) (Tables E.1).

314 ***3.3 Isotopic analysis of plant material***

315 The 246 plant samples were dried, crushed using a mixer mill, weighed in ultralight tin
316 capsules and combusted in an elemental analyzer (PyroCUBE; Elementar, Hanau, Germany)
317 coupled with an isotope ratio mass spectrometer from Isoprime Ltd (Cheadle Hulme, UK) for
318 C stable isotope analysis at the *Laboratoire d'Ecologie des Hydrosystèmes Naturels et*
319 *Anthropisés* (Lyon, France). In-house standards of sorghum flour calibrated against secondary
320 international standards from the International Atomic Energy Agency, Vienna, Austria
321 (IAEA-CH3, IAEA-CH6, IAEA-N1, IAEA-N2) were analyzed every twelve samples as
322 quality control. The long-term precision (SD) for the internal laboratory standard was better
323 than 0.3 ‰. Isotope data are presented in δ notation [$\delta = (R_{\text{sample}}/R_{\text{standard}}) - 1$], with R the
324 isotope ratio ($^{13}\text{C}/^{12}\text{C}$) of the sample or international standard (V-PDB).

325 ***3.4 Tooth sample preparation and isotopic measures***

326 Tooth enamel surfaces were cleaned by abrasion with a tungsten drill bit. Sequential sampling
327 of modern caprine teeth was performed on the buccal side of the second and third molars, on
328 the anterior lobe of M2 and the middle lobe of M3. The sampling spanned the width of a lobe.
329 Sequential sampling of the horse teeth was performed on the mesial side of molars because
330 this side has a flat surface with a narrow cementum layer and also because it should
331 mineralise faster (Zazzo et al., 2012). For all teeth, enamel was drilled with a diamond bit,
332 perpendicular to the tooth growth axis from the apex to the enamel root junction (ERJ).
333 Samples were taken every 1.5-2mm through the entire thickness of the enamel layer and care
334 was taken to avoid collecting the underlying dentine. Sample position was recorded in terms
335 of their distance (in mm) from ERJ.

336 Samples weighing 3.5-7 mg were chemically treated following the procedure described in
337 Balasse et al. (2002). First, organic matter was removed with a solution of 2-3% NaOCl (24h,
338 0.1 ml solution/ mg of sample) and rinsed several times in distilled water. Then, each enamel
339 sample was reacted with 0.1 M acetic acid (4h, 0.1 ml solution/mg of sample), rinsed in
340 distilled water and dried in an oven at 80°C for 12h.

341 Purified enamel samples were weighted (600 μg approximately) and analyzed on a Kiel IV
342 device connected to a Delta V Advantage isotope ratio mass spectrometer (IRMS) at the

343 *Service de Spectrométrie de Masse isotopique du Muséum national d'Histoire naturelle*
344 (SSMIM) in Paris. Samples were placed into individual vessels to react under vacuum with
345 phosphoric acid [H₃PO₄] at 70°C and purified CO₂ in an automated cryogenic distillation
346 system. In total, 306 enamel samples were analysed over a period comprised between October
347 2016 and October 2018. Analytical precision was 0.04‰ for δ¹³C and 0.05‰ for δ¹⁸O based
348 on the repeated (n= 114) analysis of our internal laboratory carbonate standard (Marbre LM)
349 normalized to NBS 19. Isotope data are presented in δ notation [$\delta = (R_{sample}/R_{standard}) - 1$],
350 with *R* the isotope ratio (¹³C/¹²C and ¹⁸O/¹⁶O) of the sample, reported relative to the
351 international standard V-PDB (Vienna PeeDee Belemnite) and expressed in per mil (‰).

352 δ¹³C values measured in caprine tooth were converted into δ¹³C values of diet (δ¹³C_{diet}) by
353 applying the carbon isotope fractionation between diet and enamel of -15.4‰, determined for
354 sheep raised on C₃ silage (Zazzo et al., 2010) (Table F.1). The δ¹³C_{diet} in horse samples was
355 estimated by applying the carbon isotope fractionation between diet and enamel of -13.7‰
356 proposed for horses (Cerling and Harris, 1999; Tejada-Lara et al., 2018) (Table F.2). These
357 conversions of δ¹³C values of enamel into δ¹³C values of diet allowed us to directly compare
358 them with isotopic data from horse tail hair that had already been converted into δ¹³C_{diet}
359 (Lazzerini et al., 2019).

360 **3.5 Isotopic data analyses**

361 We first explored the isotopic dataset. We compared the isotopic profiles among herders, with
362 one-way ANOVAs followed by Tukey's post-hoc HSD on the average C and O isotopic
363 values of the caprine teeth of the different herders. Then, we compared the isotopic profiles
364 between caprines and horses within the same herd. To do so, we performed one-way
365 ANOVAs on δ¹³C_{diet} of horses and caprines from the same herds using one-way ANOVAs.
366 This analysis was not possible on δ¹⁸O values because of the small number of geolocalized
367 horse.

368 Second, we estimated the proportion of C₄ plants in caprine diet, and its potential influence on
369 the altitudinal signal recorded by δ¹³C values. To do so, we visually compared caprine δ¹³C_{diet}
370 values with the distribution of δ¹³C of our C₄ and C₃ plant samples. We also tested the
371 potential influence of altitude on plant δ¹³C values, using a linear regression with the R
372 function *lm*.

373 We then assessed the effect of animal altitudinal mobility on C and O isotopic values in their
374 tissues. To do so, we performed linear regressions between average grazing altitude (per

375 animal) and (i) average isotopic values ($\delta^{18}\text{O}$ values of caprine tooth enamel, $\delta^{13}\text{C}_{\text{diet}}$ of horses
376 and caprines), (ii) intra-tooth isotopic amplitude. Because the extent of mobility might affect
377 isotopic variability within individuals, we also performed a linear regression between the
378 standard deviation of grazing altitude and intra-tooth isotopic amplitude, with the same
379 method. A one-way ANCOVA was conducted to compare the correlation coefficients
380 between average grazing altitude and average $\delta^{13}\text{C}$ of diet in horses and caprines. We also
381 used linear regressions to assess the relationship between *Time_Alt* (Eq. 2) and the average
382 $\delta^{13}\text{C}$ of diet of horse and caprines and between *Time_Alt* and the average $\delta^{18}\text{O}$ of caprine
383 tooth enamel. A one-way ANCOVA was also performed to estimate the difference between
384 horse and caprine correlations.

385 We tested the existence of a co-variation between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences of each tooth,
386 using Pearson's correlation coefficient. We then tested whether the frequency of altitudinal
387 mobility was responsible for the observed variability among individuals in the patterns of co-
388 variation of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences. To do so, we calculated the linear regression between
389 the standard deviation of mobility and Pearson's correlation coefficients between the $\delta^{13}\text{C}$ and
390 $\delta^{18}\text{O}$ sequences.

391 Finally, equations from significant linear regressions between C and O isotopic values and
392 mobility characteristics were used to infer space use of non-monitored horses.

393 Unless mentioned otherwise, all statistical analyses were conducted using R (version 3.4.4)
394 with a 0.05 threshold of significance.

395 **4. RESULTS**

396 ***4.1 The GPS record of caprine mobility***

397 Four herders (Jk, Kb, Kj, Zk) exploited pastures situated along a large altitudinal range, from
398 the eastern depression (around 1400-1500 m.asl) to the western mountain pastures (up to 3000
399 m.asl) while herder Dl exploited essentially high altitude pasture (Fig. 2). The standard
400 deviation of the average exploited altitude ranged from 131 (Dl) to 351 (Kj), reflecting the
401 altitudinal mobility of herds. The distance travelled by year ranged from 38km (Dl) to 291 km
402 (Zk). For all herders, the summer residency was located at a higher altitude than winter
403 residency, with a difference between summer and winter pastures ranging from 94 m (Dl) to
404 412 m (Zk) (Tables E.1; G.1 and Figures E.2)

405 **4.2 Plant $\delta^{13}\text{C}$ values**

406 Plant $\delta^{13}\text{C}$ values ranged from -31.2 to -13.2‰, with an average value of $-27.1 \pm 2.3\text{‰}$ (Fig.
407 3). Although the vast majority of samples had $\delta^{13}\text{C}$ values lower than -25 ‰, six plant
408 samples had $\delta^{13}\text{C}$ values higher than -20‰, indicative of a C4 photosynthetic pathway. These
409 samples were identified as *Anabasis brevifolia* (B. Oyuntsetseg, pers. comm.). They were
410 found in the lowland pastures below 1950 m.asl (for more details see Table A.1), which
411 explains the higher variability in $\delta^{13}\text{C}$ values observed at low altitudes. Plant $\delta^{13}\text{C}$ values were
412 negatively correlated with altitude (Pearson's correlation: $r = -0.16$; $r^2 = 0.02$; $P\text{-value} = 0.01$
413 – Fig. A.1). The correlation between plant $\delta^{13}\text{C}$ values and altitude no longer exist when the
414 six C4 plant samples are excluded from the dataset ($P\text{-value} = 0.8$ – Fig. A.2) and we did not
415 find any significant correlation between plant $\delta^{13}\text{C}$ values and altitude when looking at the
416 summer and fall data separately (Fig. A.3 and A.4).

417 **4.3 Variations of $\delta^{18}\text{O}$ values in tooth enamel**

418 Summary results from stable isotope analyses are presented in Table 4 and complete data are
419 available in Table F. Oxygen isotope profiles of caprines and horses followed a sinusoidal
420 pattern (Fig. 4 and 5) reflecting seasonal changes in the oxygen isotopic composition of
421 ingested water. In the continental Mongolian steppe environment, maximum values reflect
422 high summer temperatures with ingestion of ^{18}O enriched water and minimum values reflect
423 low winter temperatures with ingestion of ^{18}O depleted water. On average, caprines had a
424 $\delta^{18}\text{O}$ value of $-7.9 \pm 3.6\text{‰}$, with values ranging from -14.6‰ to -0.1‰. Intra-tooth amplitude
425 in $\delta^{18}\text{O}$ value ranged from 9.2 to 12.2 ‰, except for 2018-63B-M2 which showed a lower
426 amplitude of 6.5‰ due to an incomplete record of the seasonal cycle (Fig. 4). On average, DI
427 caprines exhibited lower intra-tooth variability (Table 4). There were no statistically
428 significant differences in the average $\delta^{18}\text{O}$ values of the different herds.

429 We found no correlation between the average $\delta^{18}\text{O}$ value and average altitude ($r = -0.37$; $r^2 =$
430 0.13 , $P\text{-value} = 0.18$; Fig. H.1), but we found a negative correlation between the intra-tooth
431 $\delta^{18}\text{O}$ amplitude and altitude ($r = -0.62$; $r^2 = 0.38$; $P\text{-value} = 0.01$ - Fig. H.2) and between
432 average $\delta^{18}\text{O}$ value and the relative amount of time spent above 2000 m.asl ($r = -0.81$; $r^2 =$
433 0.65 ; $P\text{-value} = 3e^{-04}$ - Fig 6). We also found a positive correlation between the intra-tooth
434 $\delta^{18}\text{O}$ amplitude and the standard deviation of the mean grazing altitude ($r = 0.54$; $r^2 = 0.29$; $P\text{-}$
435 $\text{value} = 0.04$ –Fig. 7).

436 On average, the teeth of the non-geolocalized horses had a $\delta^{18}\text{O}$ value of $-10.8 \pm 2.6\text{‰}$, with
 437 values ranging from -5.0 to -16.1‰ . Intra-tooth amplitude in $\delta^{18}\text{O}$ value ranged from 6.5 to
 438 9.5‰ (Table 4). The average $\delta^{18}\text{O}$ value of horse teeth was significantly lower than that of
 439 caprines ($p\text{-value} = 7e^{-14}$). Similarly, the intra-tooth amplitude in $\delta^{18}\text{O}$ value of horse was
 440 significantly lower than that of caprines ($p\text{-value} = 0.005$).

441 **4.4 Variations of $\delta^{13}\text{C}$ values of horses and caprines**

442 On average, caprine enamel $\delta^{13}\text{C}$ value was $-11.2 \pm 0.9\text{‰}$, with values ranging from -13.7‰
 443 to -9.4‰ . For each herd, the average $\delta^{13}\text{C}$ values ranged from $-12.4 \pm 0.5\text{‰}$ (Dl) to $-10.6 \pm$
 444 0.7‰ (Kj) (Table 4). Dl caprine $\delta^{13}\text{C}$ values were significantly lower than those of all the
 445 other herders ($P\text{-value} < 0.01$). The estimated average (\pm s.d.) $\delta^{13}\text{C}_{\text{diet}}$ was $-26.6 \pm 0.9\text{‰}$ (Fig.
 446 3). This variability is within the range of C_3 plant $\delta^{13}\text{C}$ values (-20 to -37‰ , (O’Leary, 1988;
 447 Kohn, 2010), indicating that the caprines of the study area consumed a diet that included no or
 448 very little C_4 plants. Caprine $\delta^{13}\text{C}_{\text{diet}}$ was significantly higher ($P\text{-value} = 0.04$) than that of the
 449 geolocalized horses studied in Lazzarini et al. (2019) ($-27.5 \pm 0.8\text{‰}$).

450 For both groups of animals, there was a significant negative relationship between the average
 451 $\delta^{13}\text{C}_{\text{diet}}$ value of the diet consumed by the animals and the average grazing altitude ($Elev_{\text{avg}}$ in
 452 meters):

$$453 \text{Caprines: } \delta^{13}\text{C}_{\text{diet}} = -2.576e^{-03}(\pm 7.655e^{-04}) \times Elev_{\text{avg}} - 21.331(\pm 1.606) \quad (3)$$

$$(r^2 = 0.46, P\text{-value} = 0.005 - \text{Fig. 8}).$$

$$454 \text{Horses: } \delta^{13}\text{C}_{\text{diet}} = -1.449e^{-03}(\pm 3.074e^{-04}) \times Elev_{\text{avg}} - 24.140(\pm 0.709) \quad (4)$$

$$(r^2 = 0.85, P\text{-value} = 0.001 - \text{Fig. 8}).$$

455 The slopes of the two equations were not significantly different ($F_{1, 19} = 0.89$, $P\text{-value} = 0.36$),
 456 and neither were the Y intercepts ($F_{1, 19} = 1.4$, $P\text{-value} = 0.25$). Combining data of all
 457 livestock, we obtained the following equation between $\delta^{13}\text{C}_{\text{diet}}$ and the average grazing
 458 altitude ($r = -0.76$; $r^2 = 0.57$; $P\text{-value} = 7e^{-5}$ – Fig. 8):

$$\delta^{13}\text{C}_{\text{diet}} = -2.519e^{-03}(\pm 4.985e^{-04}) \times Elev_{\text{avg}} - 21.520 (\pm 1.076) \quad (5)$$

459 The slopes of the linear regressions between plant $\delta^{13}\text{C}$ (i.e C_4 included) value and altitude,
 460 caprine $\delta^{13}\text{C}_{\text{diet}}$ value and altitude, and horse $\delta^{13}\text{C}_{\text{diet}}$ value and altitude were not significantly
 461 different (one-way ANCOVA - $F_{2, 265} = 0.14$; $P\text{-value} = 0.87$). The Y intercepts were not
 462 significantly different either ($F_{2, 265} = 0.2$; $P\text{-value} = 0.85$).

463 We also found a negative relationship between the $\delta^{13}\text{C}_{\text{diet}}$ values of the diet consumed by the
 464 animals and the relative amount of time spent above 2000 m asl (Fig. 9):

$$\begin{aligned} \text{Caprines: } \delta^{13}\text{C}_{\text{diet}} & & (6) \\ &= -2.272e^{-02}(\pm 5.658e^{-03}) \times \text{Time_Alt}(\%) - 25.555(\pm 0.314) \\ & & (r^2 = 0.55, P\text{-value} = 0.001). \end{aligned}$$

465

$$\begin{aligned} \text{Horses: } \delta^{13}\text{C}_{\text{diet}} &= & (7) \\ &= -1.163e^{-02}(\pm 2.906e^{-03}) \times \text{Time_Alt}(\%) - 26.728(\pm 0.197) \\ & & (r^2 = 0.80, P\text{-value} = 0.02). \end{aligned}$$

466

467 The slopes of these two equations (Fig. 9) were not significantly different ($F_{1, 19} = 1.5$., $P\text{-}$
 468 $\text{value} = 0.24$), unlike the Y intercepts ($F_{1, 19} = 5.7$, $P\text{-value} = 0.03$).

469 Finally, enamel $\delta^{13}\text{C}$ value of non-geolocalized horses was $-12.8 \pm 1.1\text{‰}$ on average, with
 470 values ranging from -16.4 to -10.6‰ (Table 4). Intra-tooth amplitude in $\delta^{13}\text{C}$ value ranged
 471 from 1.2 to 4.4‰ , with average amplitude of $2.7 \pm 1.6\text{‰}$. These non-geolocalized horses
 472 displayed an average $\delta^{13}\text{C}_{\text{diet}}$ of -26.5 ± 1.1 , not significantly different ($P\text{-value} = 0.6$) from
 473 the average $\delta^{13}\text{C}_{\text{diet}}$ of caprines, but significantly higher ($P\text{-value} = 0.02$) than the average
 474 $\delta^{13}\text{C}_{\text{diet}}$ of the monitored horses. Using equation 4 we estimated a mean grazing altitude of
 475 1584 ± 376 m, ranging from 1246 to 2012 m (Table 5), significantly lower ($p\text{-value} = 0.03$)
 476 than the average grazing altitude of the monitored horses (2298 ± 208 m; Table 2), with a
 477 mean difference of 714 m. Using equation 7, we estimated that these horses spent 10% of
 478 their time above 2000 m (Table 5), significantly less ($P\text{-value} = 0.002$) than the monitored
 479 horses (64%; Table 2).

480 **4.5 Co-variations between $\delta^{13}\text{C}$ vs. $\delta^{18}\text{O}$ values**

481 The relationships between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for all the individuals are shown in Figures I.
 482 DI caprines showed a positive correlation for one individual and no significant correlation for
 483 the others. For Jk, Kj and Zk caprines all significant correlations were negative (Table 4).

484 Finally, Kb caprines exhibited both positive and negative correlations between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$
485 intra-tooth values (Table 4 and Fig. 4). We found a marginally significant negative
486 relationship (P -value = 0.08) between the standard deviation of the mean grazing altitude and
487 the Pearson's correlation coefficients between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of the sheep and goat
488 teeth (Fig. 10).

489 For non-monitored horses, tooth enamel individual $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values were negatively
490 correlated (r coefficient from -0.88 to -0.26) and this relationship was statistically significant
491 (P -value < 0.05), except for 2017-104-M2.

492 **5. DISCUSSION**

493 ***5.1 Influence of altitudinal residency on $\delta^{18}\text{O}$ values***

494 We did not find any relationship between the average $\delta^{18}\text{O}$ values of caprine tooth enamel and
495 mean grazing elevation. However, we found a negative relationship between the average $\delta^{18}\text{O}$
496 values and the percent of time spent grazing at high altitude (Fig. 6). This result supports the
497 hypothesis that tissues of animals grazing at higher elevation should record lower $\delta^{18}\text{O}$ values
498 than animals grazing at lower elevation (Poage and Chamberlain, 2001; Pederzani and
499 Britton, 2019). The lack of correlation between average $\delta^{18}\text{O}$ values and mean grazing
500 elevation could be explained by the fact that in our study area the water sources available for
501 drinking mainly consist in streams (resulting from snow melt), which are the products of
502 various enrichment and transport processes (e.g. Gibson et al., 2002; Barbour, 2007; Halder et
503 al., 2015) and may not directly reflect $\delta^{18}\text{O}$ values of meteoric water, especially given the low
504 amount of rainfall in this semi-arid region.

505 In addition, we noticed that range of altitudinal mobility is positively correlated with the
506 (range in intra-tooth $\delta^{18}\text{O}$ values (Fig. 7). This is in agreement with the prediction of
507 Mashkour et al. (2005) who stated that transhumant animals should record larger intra-tooth
508 $\delta^{18}\text{O}$ variability due to the ingestion of isotopically more diverse sources of water and isotopic
509 analyses of modern caprines in the eastern Pyrenees (Knockaert et al., 2018).

510 ***5.2 Influence of altitudinal residency on $\delta^{13}\text{C}$ values***

511 We found a significant negative correlation between average tissue $\delta^{13}\text{C}$ values and mean
512 grazing altitude for caprines and horses (Fig. 8). Because tissue $\delta^{13}\text{C}$ values derive from that
513 of the animal's diet, it is reasonable to assume that the altitudinal effect is caused by plant
514 $\delta^{13}\text{C}$ values, which also exhibit this negative correlation with altitude (Figure A.1). The

515 negative relationship between $\delta^{13}\text{C}$ of plants and altitude is similar to that observed in several
516 mountainous areas like the Spanish Pyrenees (Tornero et al., 2018), central China (Liu et al.,
517 2016), or central Mongolia (Makarewicz and Tuross, 2006). The correlation we found seems
518 to be influenced by the rare presence of C_4 plants with high $\delta^{13}\text{C}$ values ($> -20\text{‰}$) in low
519 altitude (Figure A.2). The absence of correlation between $\delta^{13}\text{C}$ of C_3 plants and altitude in
520 arid regions was described before and seems to be partly caused by a balance between the
521 positive effect of temperature and precipitation and the negative effect of atmospheric
522 pressure (Chen et al., 2017). It is noteworthy that the correlation found between $\delta^{13}\text{C}$ of plants
523 (C_3 & C_4) and altitude is in apparent contradiction with Lazzerini et al. (2019) who did not
524 find any correlation between high-resolution time series in horse tail hair $\delta^{13}\text{C}$ value and
525 altitude. This apparent discrepancy, obtained on the same dataset analyzed at two different
526 scales (sequential vs. bulk), could be due to the fact that frequent (daily) changes in altitude
527 by horses increase the noise to signal ratio and make any relationship between altitude and
528 $\delta^{13}\text{C}$ difficult to detect at a daily to weekly resolution.

529 It is also interesting to note that $\delta^{13}\text{C}_{\text{diet}}$ values of geolocalized horses were significantly lower
530 than those of caprines, similar to what was also observed in the northern Kazakh steppe
531 (Ventresca Miller et al., 2018). This can be interpreted as the result of different dietary
532 preferences by the two species. While horses prefer to feed in wetter grasslands, near streams
533 (King, 2002; Menard et al., 2002) caprines can reach steep slopes in high altitude pastures to
534 find fresh grass (Negi et al., 1993 and own field observations). These slope pastures are
535 potentially dryer than valley bottoms and this may explain the higher $\delta^{13}\text{C}$ diet values of
536 sheep and goats.

537 Our results also show that there is a negative relationship between average $\delta^{13}\text{C}_{\text{diet}}$ of caprine
538 and horse tooth enamel and average amount of time spent above 2000 m.asl (Fig. 9). For
539 caprines, $\delta^{13}\text{C}_{\text{diet}}$ values $\leq -27\text{‰}$ are indicative of preferential residency ($\geq 66\%$) above 2000
540 m asl whereas $\delta^{13}\text{C}_{\text{diet}}$ values $\geq -26\text{‰}$ are indicative of preferential residency ($\geq 90\%$) below
541 2000 m asl. For horses (Fig. 9), $\delta^{13}\text{C}_{\text{diet}}$ values $\leq -27.5\text{‰}$ would reflect preferential
542 exploitation ($\geq 66\%$) of high altitude pastures, whereas average $\delta^{13}\text{C}_{\text{diet}}$ values $\geq -26.8\text{‰}$
543 would indicate preferential exploitation ($\geq 90\%$) of lowland pastures. When used in
544 combination with other information, these results might help to differentiate between animals
545 found in mountainous zones. However, it is important to note that the sensitivity of this
546 altimetric proxy is low (Eq. 3 to 7) and may limit the applicability of this approach to the
547 estimation of altitudinal occupation for modern and archaeological animals whose mobility

548 pattern is unknown. Moreover, it is essential to emphasize that the equation may not be
549 directly transferable to other study areas as the specificity of the local conditions (climate,
550 vegetation) may impact its characteristics (slope, intercept).

551 Finally, it is important to discuss the difference of 700 m in grazing elevation estimated for
552 monitored (derived from the hair dataset) versus non-monitored horse (derived from the tooth
553 enamel dataset). The average altitude estimated for the non-monitored horse (1250m) is lower
554 than the lowest elevation of the study area. This discrepancy probably results from (1) the low
555 sensitivity of the altimetric proxy (2) uncertainty in the enamel-diet fractionation factor used
556 for horses. We used the enamel-diet enrichment factor of +13.7 proposed for the horse by
557 Cerling and Harris (1999). This value is based on uncontrolled animals and is associated with
558 an uncertainty of 1.9‰. Shifting this enrichment factor by 1 ‰ only would reconcile the
559 $\delta^{13}\text{C}_{\text{diet}}$ values calculated for monitored and non-monitored horses. It would lead to an average
560 grazing altitude of 2264 ± 376 m, and a 59% occupation of pasture above 2000 m for the non-
561 monitored horses (Table 5). An enrichment factor between diet and enamel of 14.7 ‰ for
562 horses seems reasonable as it remains within the uncertainty proposed by Cerling and Harris
563 (1999) but also corresponds to that of zebras (*Equus burchelli*), close relatives of domestic
564 horses (Cerling and Harris, 1999; Tejada-Lara et al., 2018).

565 **5.3 Relationship between $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ and altitudinal mobility**

566 We found that carbon and oxygen isotope values were negatively correlated for animals
567 which exploited a large altitudinal range of pastures (i.e. Jk and Kj animals), whereas a
568 positive correlation was found for more residential animals (i.e. DI). As a result, the
569 correlation between carbon and oxygen isotope values of caprine tooth enamel (Pearson's r)
570 displayed a marginally significant decrease with the standard deviation of the animal
571 altitudinal residency (SD-Altitude – Fig. 10). This result suggests that the anti-correlation
572 between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences can indeed be interpreted as evidence for vertical mobility,
573 as proposed by several authors (Fisher and Valentine, 2013; Tornero et al., 2016; 2018;
574 Makarewicz, 2017; Makarewicz et al., 2017). It is noteworthy that this relationship was found
575 in a C_3 -dominated environment and might be slightly different in a mixed C_3/C_4 environment.
576 Moreover, this anti-covariation was also found for horse (Fig. 5) which, even if not
577 monitored, most likely followed the herds in their altitudinal mobility. This anti-covariation
578 can be explained in two different ways: (i) a complete reversal of the $\delta^{18}\text{O}$ cycle with low
579 $\delta^{18}\text{O}$ during summer (Hermes et al., 2017), or (ii) higher $\delta^{13}\text{C}$ values during winter. The first
580 hypothesis is purely theoretical and remains to be tested with real animals. In our case, we

581 showed that this model is unlikely because O isotope values are positively correlated with air
582 temperatures thus high $\delta^{18}\text{O}$ values recorded in enamel correspond to summer (Lazzerini et
583 al., 2020). Therefore, the absence or presence of covariation between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ profiles
584 should be due to differences in seasonal variations of $\delta^{13}\text{C}$ values between residential and
585 mobile animals. The lower summer $\delta^{13}\text{C}$ values could be explained by the higher water-
586 availability of alpine meadows during summer due to increased precipitation and snow
587 melting during this period, allowing access to rich pasture for herds. The increase in $\delta^{13}\text{C}$
588 values during winter can be explained by hydric stress. As the growing season is very short
589 and restricted to the summer period (Eisma, 2012), plants ingested by animals during winter,
590 mainly in the lowlands, grew during summer and would be ^{13}C -enriched due to the higher
591 temperature and water stress in the lowlands compared to the uplands. Alternatively, it could
592 be explained by a diet switch. Sheep and goats of desert-steppe in Mongolia have been
593 observed to increase the proportion of shrub and forbs in their diet during summer (Wingard
594 et al., 2011; Chazin et al., 2019). Shrubs and forbs are relatively ^{13}C -depleted relative to grass
595 and thus an increase in proportion in the diet would lead to lower $\delta^{13}\text{C}$ values (Smedley et al.,
596 1991; An and Li, 2015). Forbs, as *Caragana* sp., are found only in valley bottoms and
597 lowland areas in our study area (Figure J). However, Jk, Kb, Kj and Zk's herds did not remain
598 at high altitude during the whole summer. They exhibited important altitudinal mobility and
599 often stood at low altitude during spring/early summer and late summer (Fig. 2 and J).
600 Therefore, a seasonal preference for forbs and shrubs in the summer vs grass in the winter
601 could well explain the summer minimum and winter maximum measured in enamel $\delta^{13}\text{C}$
602 values. D1 animals, with a permanent residency at high altitude, had probably less access to
603 forbs which resulted in higher $\delta^{13}\text{C}$ values during summer compared to the other animals.

604 **6. CONCLUSION**

605 The Altai region hosts Mongolia's oldest record of pastoral occupation (e.g. Kovalev and
606 Erdenebaatar 2009). Our aim was to propose a toolkit for understanding and interpreting
607 archaeofauna from Bronze and Iron Age burials and archaeological sites in the region, in
608 order to understand the emergence of pastoral societies. To do this, we combined detailed
609 isotope data with careful life-history control in order to clarifying the relationship between
610 livestock stable isotope composition and mobility patterns.

611 Our study demonstrates that $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ analyses of tooth enamel and $\delta^{13}\text{C}$ of tail hair can
612 be used to make inferences regarding animal mobility and land use in mountainous regions.

613 We showed that average $\delta^{13}\text{C}$ values of livestock recorded mean grazing altitude and could be
614 used to calculate the amount of time spent in alpine meadows. Vertical mobility in modern
615 livestock from western Mongolia may also be identified through sequential sampling of $\delta^{13}\text{C}$
616 and $\delta^{18}\text{O}$ of sheep tooth enamel. The comparison of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values was very
617 informative to reveal variation in the altitudinal pattern of animals: individuals displaying a
618 large range of altitudinal residency also showed a negative correlation between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$
619 sequences, whereas individuals with a more restricted mobility displayed a positive
620 correlation between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values. This pattern seems to be controlled by
621 environmental factors, such as changes of water availability/aridity with altitude, seasonal
622 precipitation in summer and could also be influenced by ecological factors such as the
623 seasonal and altitudinal dependence of the relative proportion of forbs versus grasses in the
624 diet.

625 It is important to note, however, that mobility patterns can be quite complex and that
626 methodological advancements (e.g. modelling, higher sampling resolution) will be needed to
627 more fully picture this complexity. This is important to keep in mind when interpreting
628 mobility patterns in archaeological specimens. We also stress that directly applying our results
629 to identify altitudinal mobility of livestock in other climatic regions may not be
630 straightforward and will require to establish similar modern reference datasets in order to
631 determine isotopic markers of altitudinal mobility. Finally, further investigations are needed
632 to decipher between the influence of foddering practices (Makarewicz and Pederzani, 2017)
633 and vertical mobility.

634

635 **Credit author statement**

636 Conceptualization: A.Z, S.L., A.C. and C.N. Methodology: N.L, A.C, and A.Z. Software: N.L. and
637 A.C. Validation: N.L., A.C., L.S., D.F., A.Z. Formal analysis: N.L. Investigation: N.L., A.Z., A.C.,
638 C.M., C.N. Resource: D.F., L.S., Ts.T., B.N. Writing (original draft): N.L., A.Z., and A.C. Writing
639 (review and editing): N.L., A.Z., A.C., Ts.T., C.M., S.L., N.B. and L.S.. Funding acquisition: A.Z.,
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641

642 **Data availability statement**

643 The data that supports the findings of this study are available in the supplementary materials of this
644 article.

645

646 **Declaration of competing interest**

647 The authors declare that they have no known competing financial interests or personal relationships
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649

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985

986 **Figure captions**

987 **Figure 1:** Map of the study area and its location in Mongolia (bottom right) with the location
988 of the campsites of the five Kazakh-Mongolia households whose animals were tracked by
989 GPS. Black crosses represent plant sampling sites (n = 246).

990 **Figure 2:** Temporal altitudinal variations of GPS-monitored caprine herds from the five
991 Kazakh-Mongolian households, based on the locations monitored by one selected GPS collar
992 for each of the three periods. Each panel represents a different herder (A =Dl; B = Jk; C = Kb;
993 D = Kj; E = Zk). For individual Alt16-283-M3 (B) only altitudinal mobility that differs from
994 that of the other individuals of Kb, between 31/01/2016 and 04/05/2016, has been represented
995 (red line). The different rectangles represent the estimated growth periods of the fifteen teeth
996 used in the study.

997 **Figure 3:** Histograms showing (A) The distribution (in black) and mean (red dashed line) of
998 local $\delta^{13}\text{C}$ values from the 246 plant samples from the study area, on top of the $\delta^{13}\text{C}$
999 distribution values of global C_3 (white) and C_4 (grey) plants after O'Leary (1988). Note that
1000 because raw data of O'Leary (1988) were not available and the original y-axis was not
1001 preserved, the C_3 and C_4 areas only show the relative frequency of $\delta^{13}\text{C}$ values of plants. (B)
1002 The distribution of $\delta^{13}\text{C}$ values of sheep and goat diet calculated from enamel $\delta^{13}\text{C}$ values
1003 based on a carbon isotope fractionation ratio between diet and tooth enamel bioapatite of -
1004 15.4‰ (Zazzo et al., 2010). The red dashed line represents the mean $\delta^{13}\text{C}_{\text{diet}}$ value.

1005 **Figure 4:** Sequential variations of $\delta^{18}\text{O}$ (white circles) and $\delta^{13}\text{C}$ (black squares) along the
1006 tooth crown from the fifteen molars of sheep and goat (M2 and M3) belonging to Dl (A), Jk
1007 (B), Kb (C), Kj (D) and Zk (E). Samples are located in the tooth crown using the distance
1008 from enamel-root junction (ERJ) in mm

1009 **Figure 5:** Oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) isotopes values along the tooth crown of modern
1010 horse molars. ERJ is the distance between the sample and the enamel-root junction. White and
1011 black circles represent measured $\delta^{18}\text{O}$ (‰) and $\delta^{13}\text{C}$ (‰) respectively, with analytical error
1012 inside the square.

1013 **Figure 6:** Mean $\delta^{18}\text{O}_{\text{enamel}}$ (‰) of sheep (triangle) and goat (circle) plotted against the
1014 percentage of time, during tooth formation, spent grazing at high altitude (> 2000 m.asl) with
1015 the corresponding linear regression (dashed black line). Shaded areas are the 95% confidence

1016 interval of each linear regression. Each herder is represented with a different color. Vertical
1017 bars indicate the standard deviation of the calculated average

1018 **Figure 7:** Intra-tooth amplitude of $\delta^{18}\text{O}$ (‰) of sheep (triangle) and goat (circle) plotted
1019 against the standard deviation of the mean grazing altitude during tooth formation with the
1020 corresponding linear regression (dashed black line). Shaded areas are the 95% confidence
1021 interval of each linear regression. Each herder is represented with a different color.

1022 **Figure 8:** (1) Mean $\delta^{13}\text{C}_{\text{diet}}$ (‰) of sheep (triangle) and goat (circle) (calculated from enamel
1023 $\delta^{13}\text{C}$ values with carbon isotope fractionation of -15.4‰) plotted against the mean grazing
1024 altitude during the tooth formation with the corresponding linear regression (dashed black
1025 line). Compared with (2) Mean $\delta^{13}\text{C}_{\text{diet}}$ (‰) of horses (square) from the same study area
1026 (Lazzerini et al.; 2019), plotted against the mean grazing altitude with the corresponding
1027 linear regression (dot dashed line). Shaded areas are the 95% confidence interval of each
1028 linear regression. Each herder is represented with a different color. Red line represents the
1029 linear regression including all caprine and horse data. For better readability, the error bars
1030 have been removed and are visible in Figure H.3 in Supplementary material.

1031 **Figure 9:** (1) Mean $\delta^{13}\text{C}_{\text{diet}}$ (‰) of sheep (triangles) and goats (circles) (calculated from
1032 enamel $\delta^{13}\text{C}$ values with carbon isotope fractionation of -15.4‰) plotted against the
1033 percentage of time, during tooth formation, spent grazing at high altitude (> 2000 m.asl), with
1034 the corresponding linear regression (dashed black line). Compared with (2) Mean $\delta^{13}\text{C}_{\text{diet}}$ (‰)
1035 of horses (square), from the same study area, plotted against the percentage of time, during
1036 tooth formation, spent grazing at high altitude (> 2000 m.asl) with the corresponding linear
1037 regression (dot dashed line). Shaded areas are the 95% confidence interval of each linear
1038 regression. Each herder is represented with a different color. Vertical bars indicate the
1039 standard deviation of the calculated average.

1040 **Figure 10:** Correlation coefficient (Pearson's r) between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of enamel of sheep
1041 (triangle) and goats (circle) plotted against the standard deviation of the mean grazing altitude
1042 during tooth formation, with the corresponding linear regression (dashed black line). Shaded
1043 area is the 95% confidence interval of the linear regression. Colors represent the different
1044 herders.

1045

1046 **Table captions**

1047 **Table 1:** Information about animals equipped with GPS collars (Gb = Globalstar; Ir =
1048 Iridium) during the three study periods. * = GPS 38766 was equipped on the same individual
1049 during periods 1 & 2. ** = sampling of an animal from the same herd that did not have a GPS
1050 collar. † GPS out of service before the field mission during which the animal was sampled
1051 and the GPS collars reclaimed.

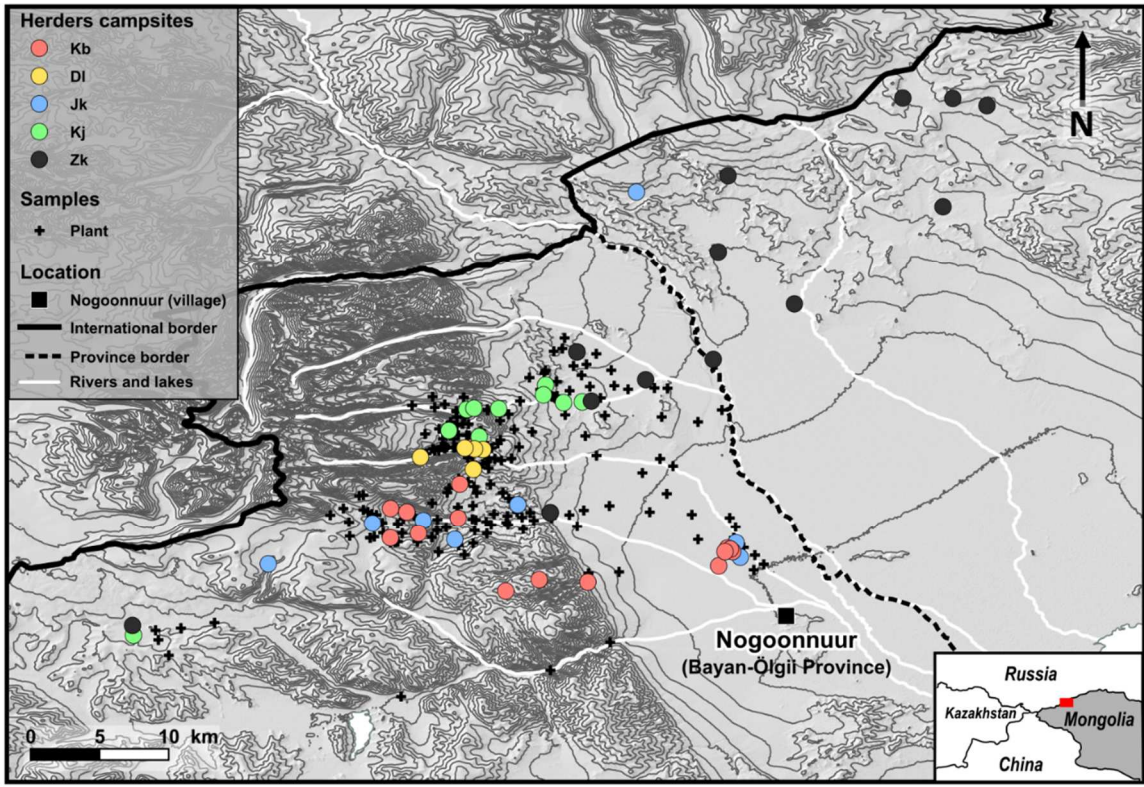
1052 **Table 2:** Characteristics of the geolocalised reference set of animal tissues used in the
1053 analyses with altitude data corresponding to the period of tooth formation. DOB = date of
1054 birth. The start and the end of formation of each tooth were calculated from the average dental
1055 development rate. ¹ Time-GPS represents the percentage of the period of formation covered
1056 by GPS tracking. ² Time-Alt represents the proportion of time, during the period of tooth
1057 formation, spent at high altitude (> 2000 m.asl). A = amplitude. * All data concerning tail hair
1058 of horses are from Lazzerini et al. (2019).

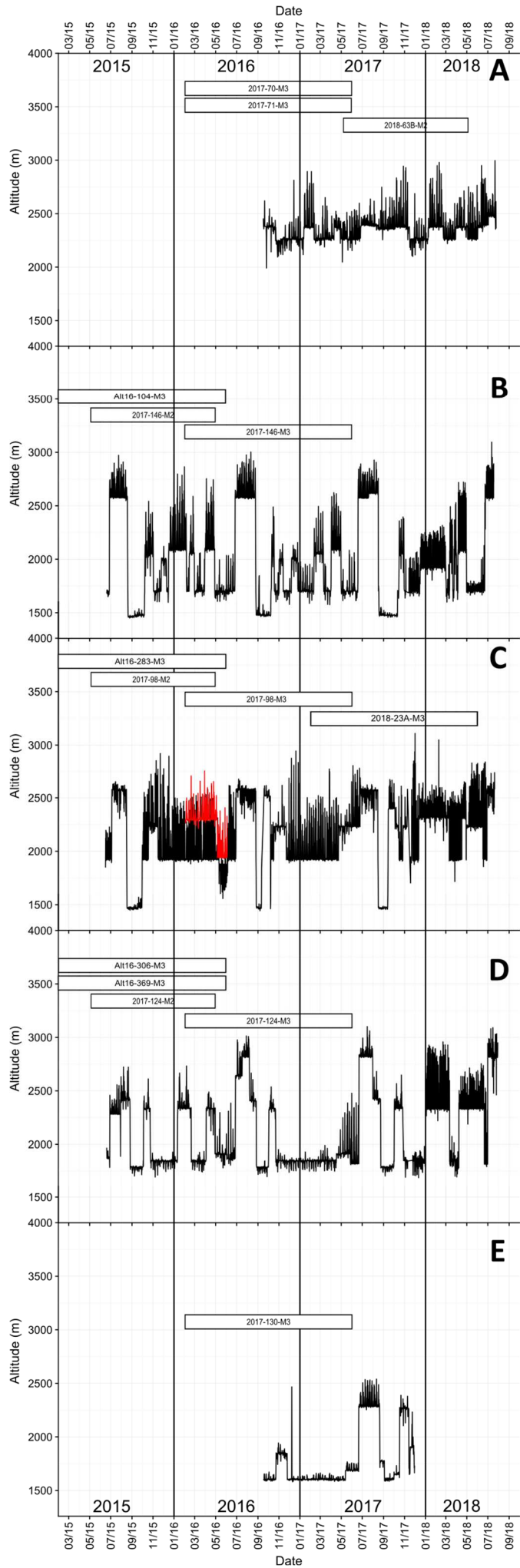
1059 **Table 3:** Characteristics of the non-geolocalised modern horses sampled for this study. DOB
1060 = date of birth. DOD = date of death. Subscript and superscript indicate that the molar was
1061 taken from the lower or upper jaw, respectively.

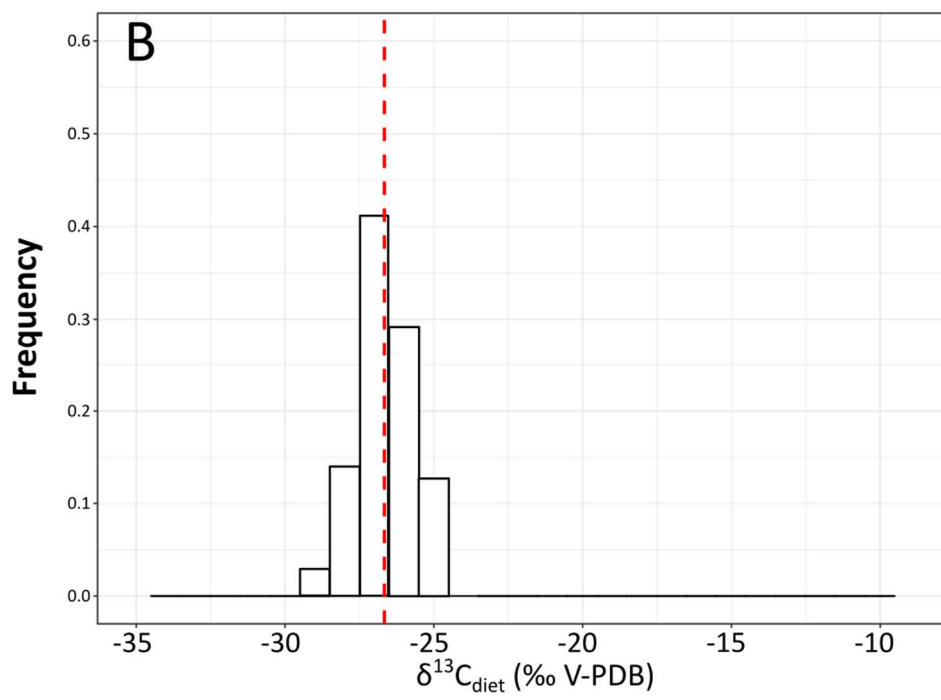
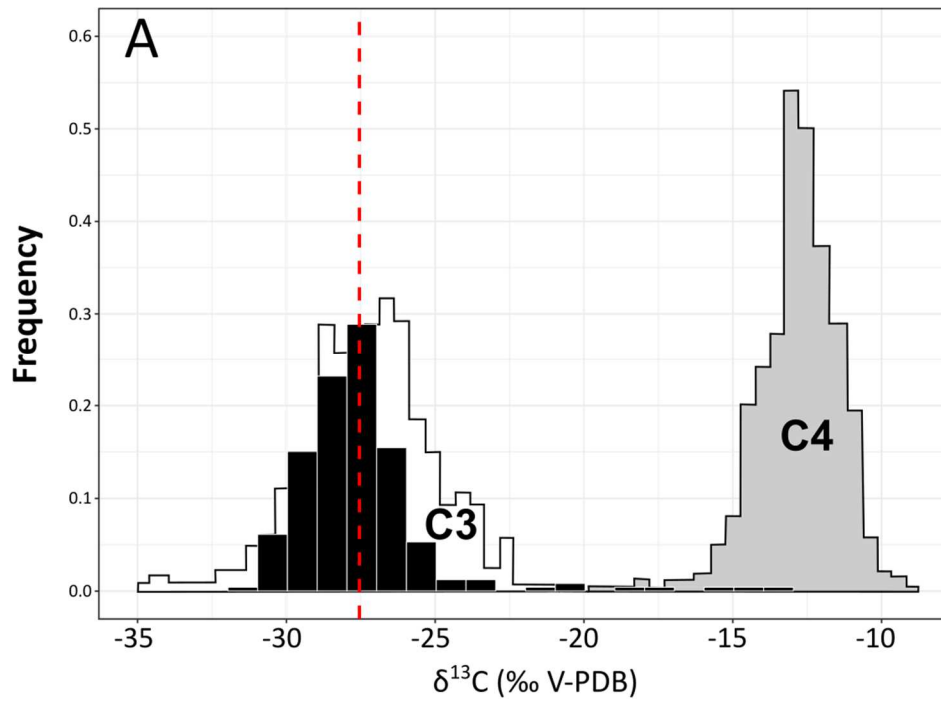
1062 **Table 4:** Summary statistics of the isotopic values of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences of enamel
1063 bioapatite samples. ¹: $\delta^{18}\text{O}$ values from Lazzerini et al. (2020). ²: $\delta^{18}\text{O}$ values from this study.
1064 N = number of samples by tooth. Pearson's r = correlation coefficient between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$
1065 sequences, df = degree of freedom of the correlation, *p-value* = significance level.

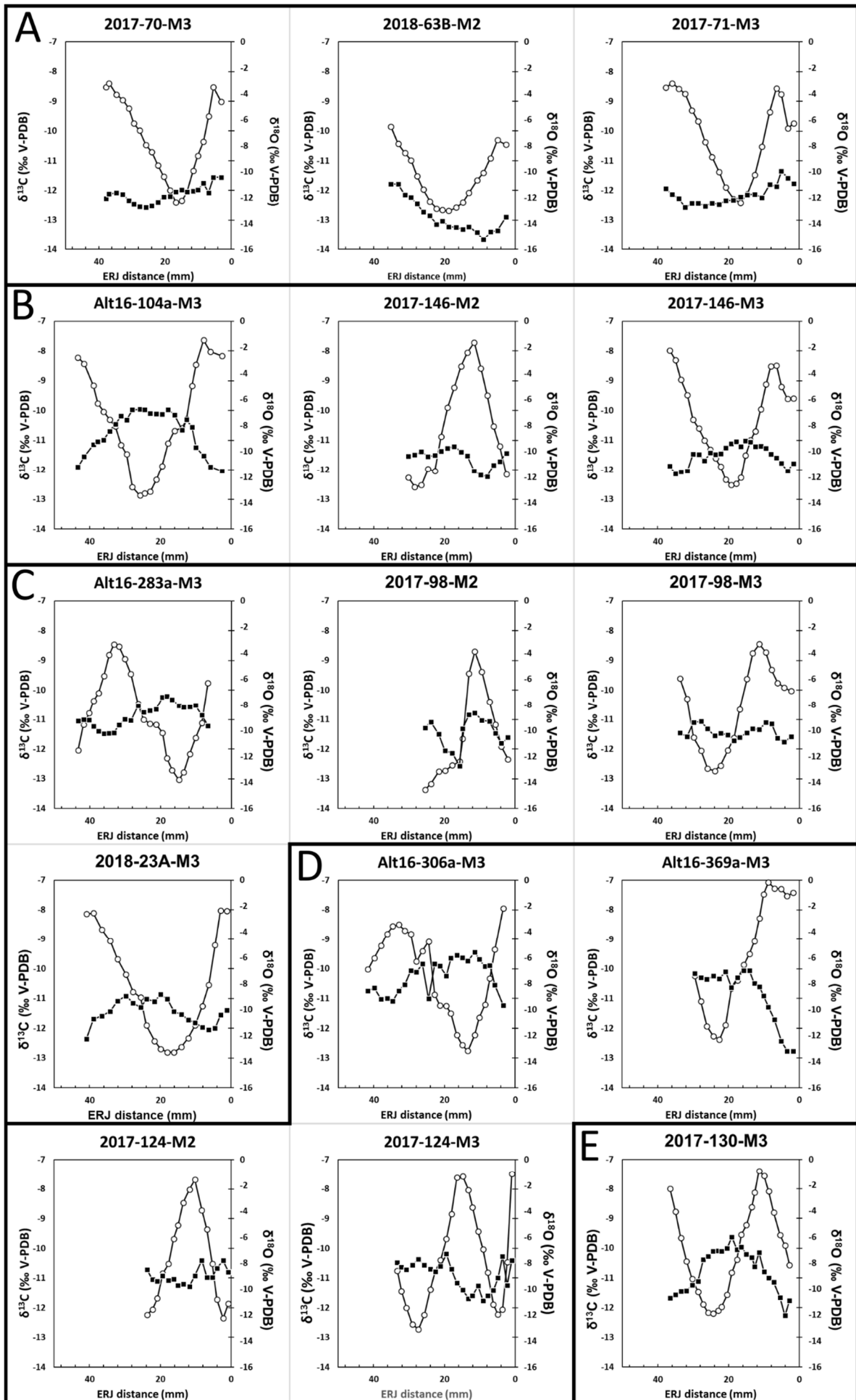
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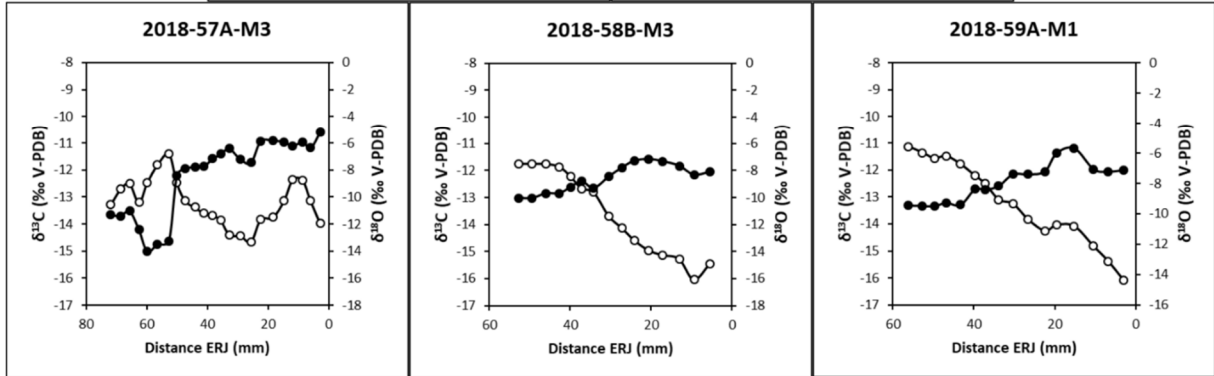
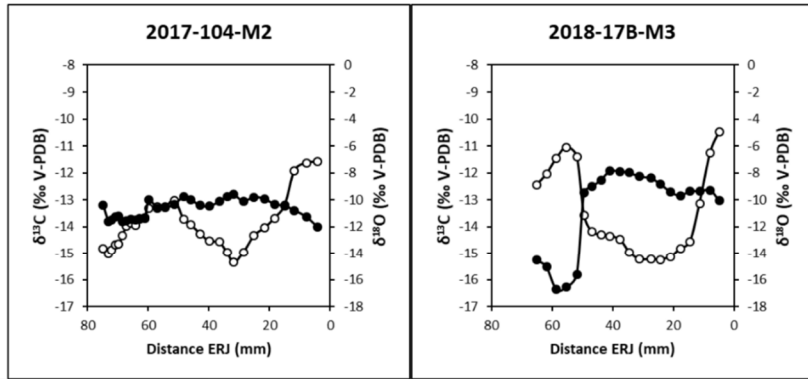
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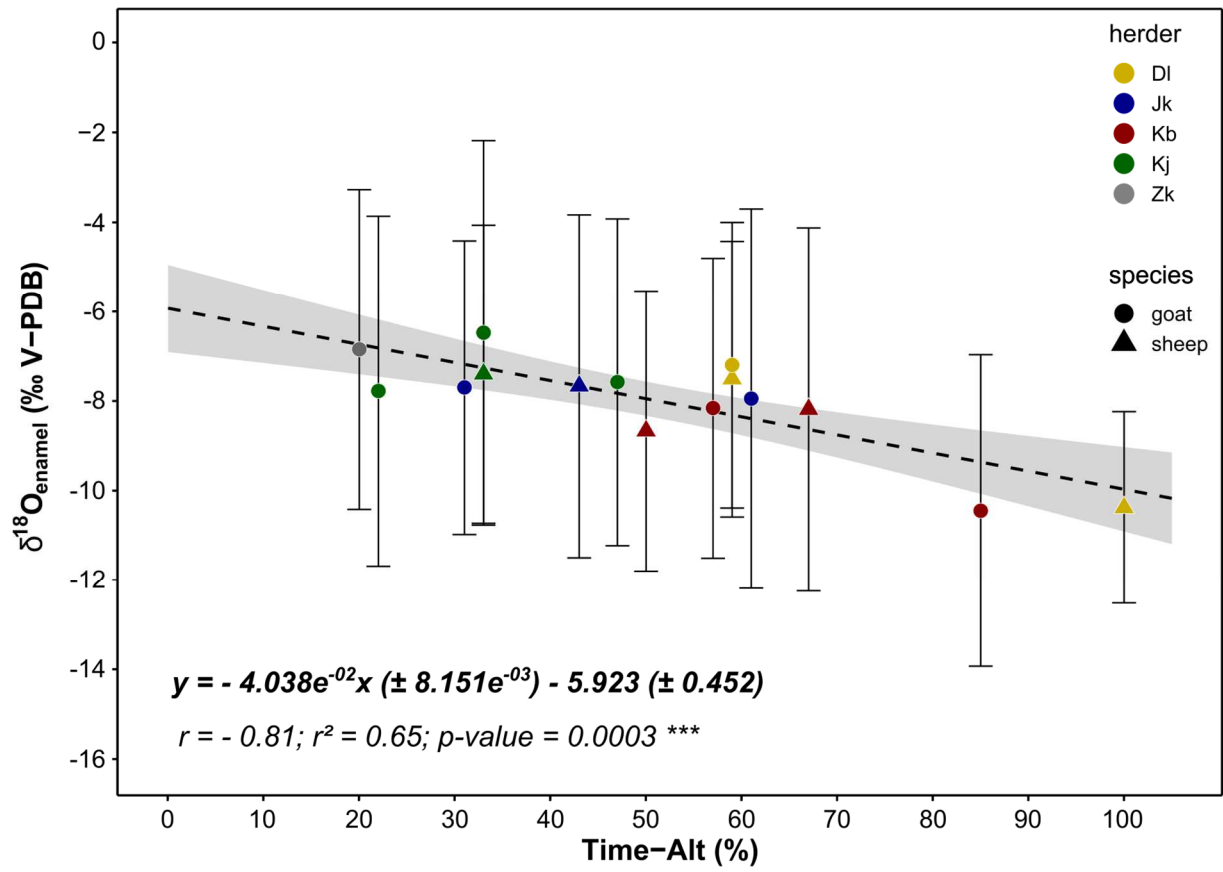


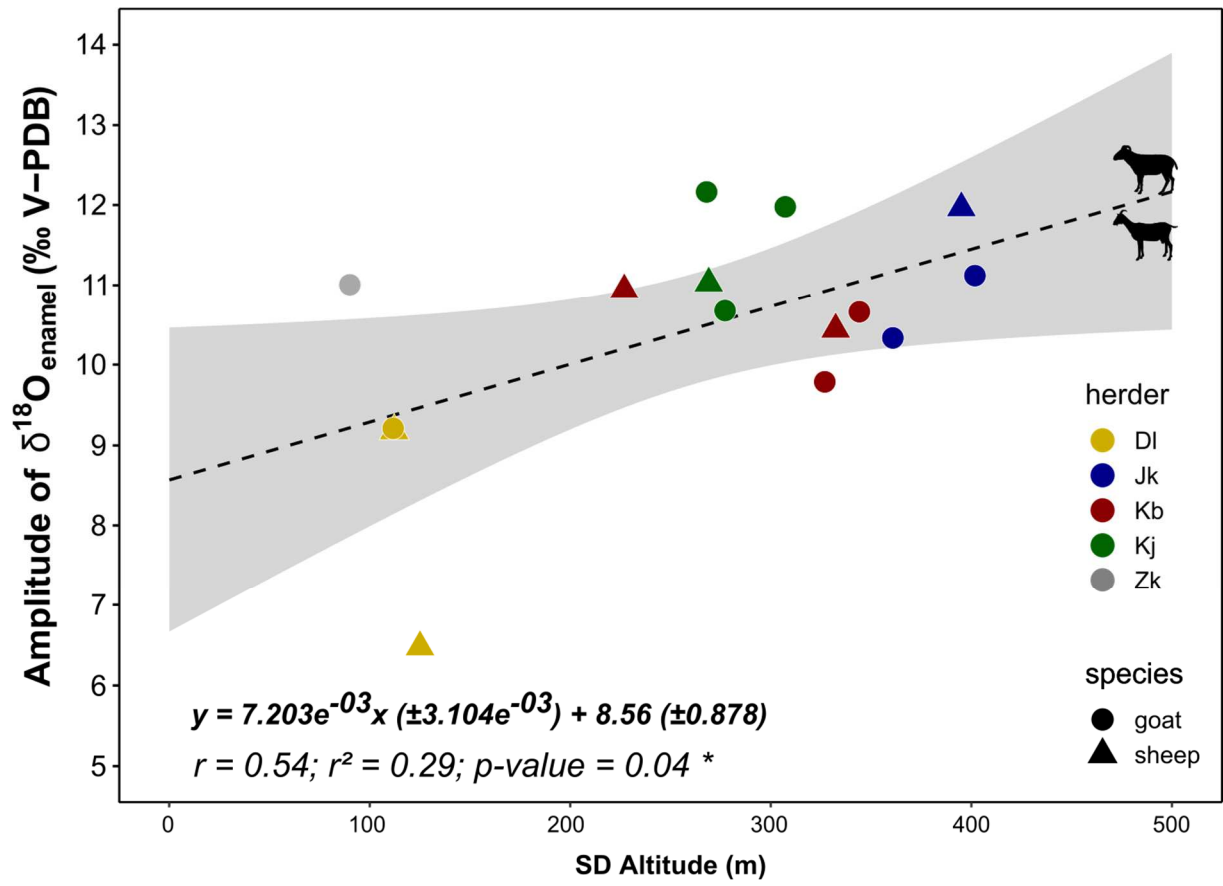


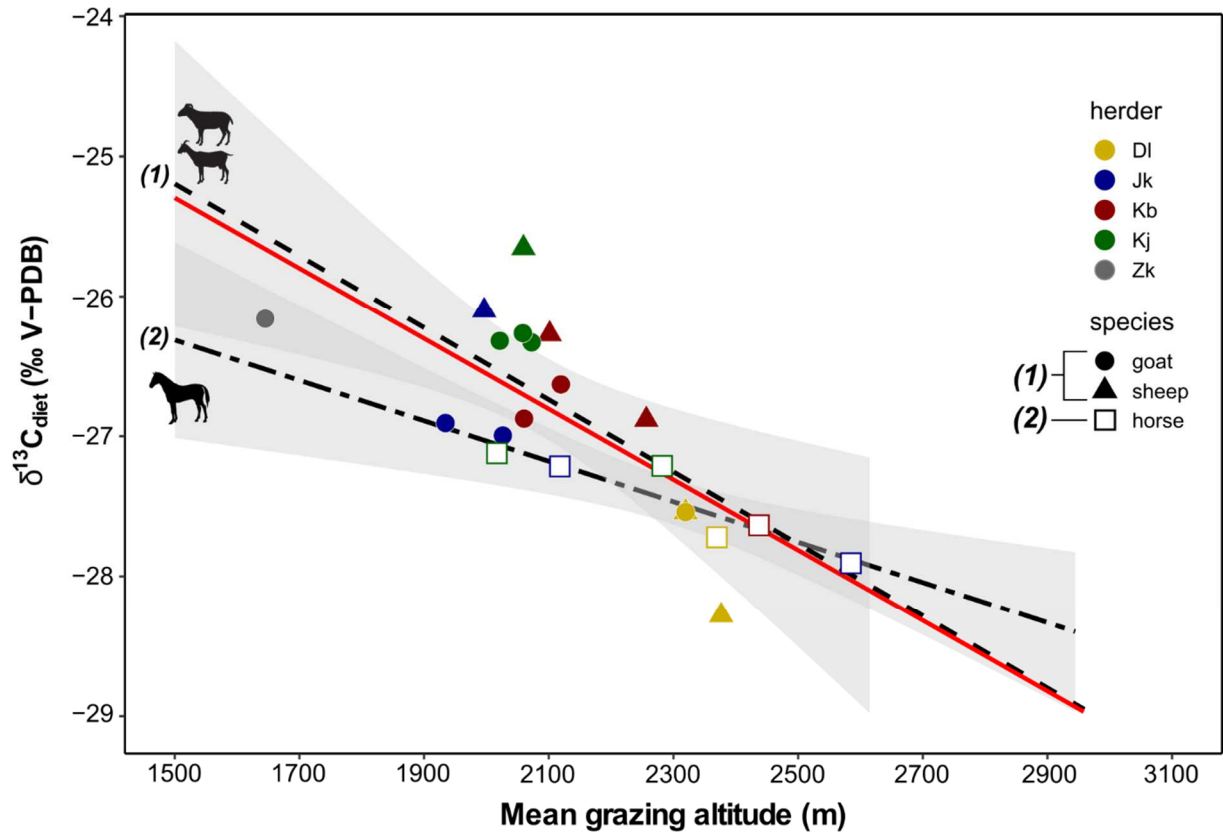






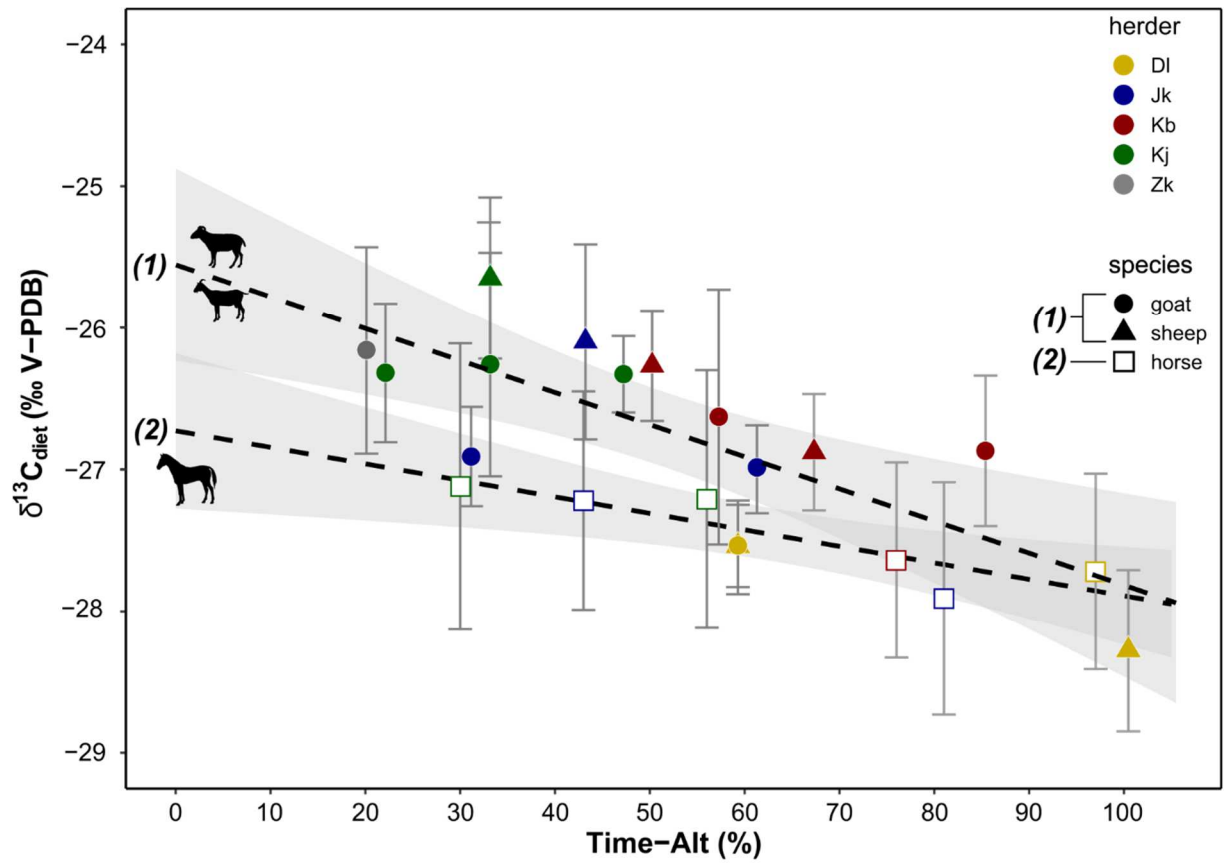






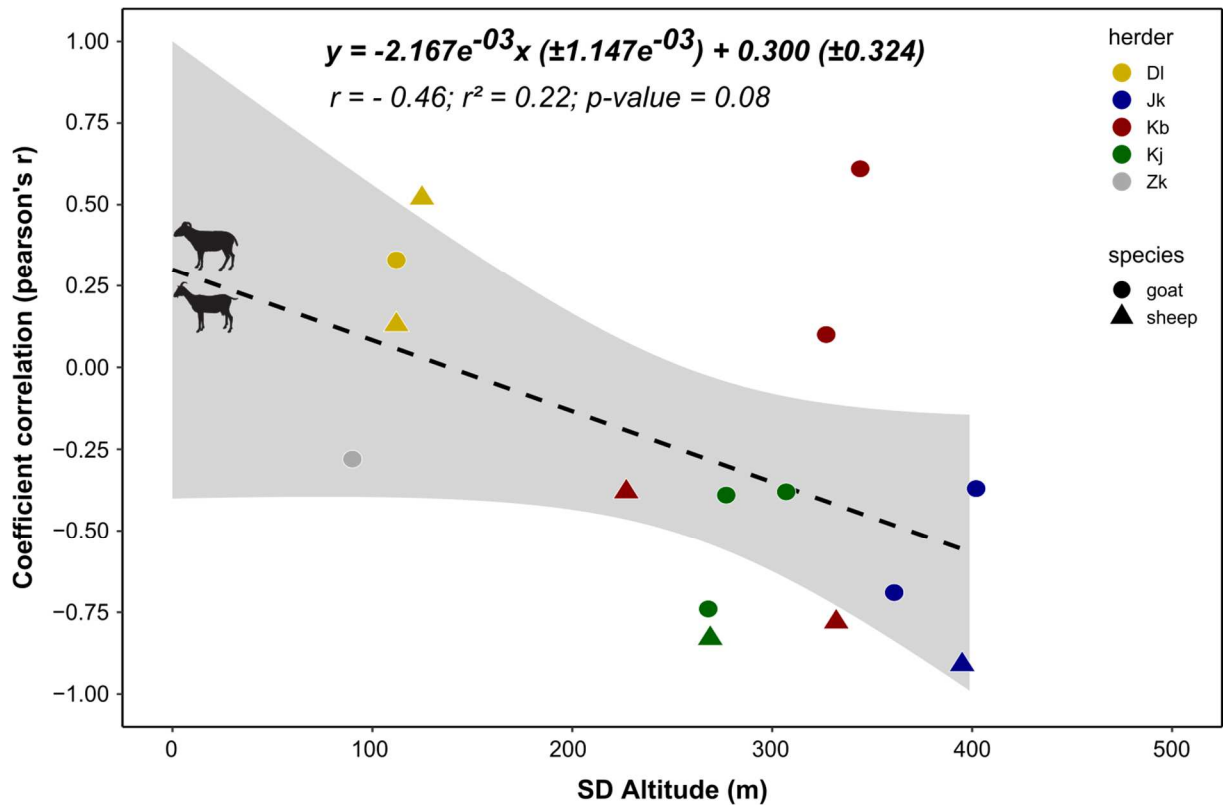
1) $y = -2.576e^{-03}x (\pm 7.655e^{-04}) - 21.330 (\pm 1.606)$
 $r = -0.68; r^2 = 0.47; p\text{-value} = 0.005^{**}$

2) $y = -1.449e^{-03}x (\pm 3.074e^{-04}) - 24.140 (\pm 0.709)$
 $r = -0.92; r^2 = 0.85; p\text{-value} = 0.001^{***}$



1) $y = -2.272e^{-02}x (\pm 5.658e^{-03}) - 25.555 (\pm 0.314)$ $r = -0.74; r^2 = 0.55; p\text{-value} = 0.001^{**}$

2) $y = -1.163e^{-02}x (\pm 2.906e^{-03}) - 26.728 (\pm 0.197)$ $r = -0.89; r^2 = 0.80; p\text{-value} = 0.02^*$



Animal & Tooth sample ID	GPS type	Species (Sex)	Start GPS	End GPS	Herder
Period 1: June 2015 – Sept. 2016					
Alt16-103	Ir	<i>Capra (M)</i>	17/06/2015	03/09/2016	Jk
Alt16-104	Gb	<i>Ovis (M)</i>	19/06/2015	07/09/2016	Jk
Alt16-156	Gb	<i>Capra (M)</i>	19/06/2015	05/09/2016	Jk
Alt16-258	Ir	<i>Capra (M)</i>	16/06/2015	11/09/2016	Kb
Alt16-285	Gb	<i>Capra (M)</i>	17/06/2015	12/09/2016	Kb
Alt16-283	Gb	<i>Ovis (M)</i>	16/06/2015	12/09/2016	Kb
Alt16-306	Ir	<i>Ovis (M)</i>	19/06/2015	14/09/2016	Kj
Alt16-362	Gb	<i>Capra (M)</i>	19/06/2015	07/10/2017 *†	Kj
Alt16-369 **	Gb	<i>Capra (M)</i>	19/06/2015	20/09/2016	Kj
Period 2: Sept 2016 – Nov. 2017					
2017-70	Gb	<i>Ovis (M)</i>	16/09/2016	17/11/2017	Dl
2017-71	Gb	<i>Capra (M)</i>	16/09/2016	17/11/2017	Dl
2017-146	Gb	<i>Capra (M)</i>	05/09/2016	03/05/2017 †	Jk
2017-98	Gb	<i>Capra (M)</i>	18/09/2016	09/11/2017	Kb
2017-124	Gb	<i>Capra (M)</i>	21/09/2016	09/11/2017	Kj
2017-130	Gb	<i>Capra (M)</i>	17/09/2016	29/11/2017	Zk
Period 3: Nov. 2017 – July 2018					
2018-63	Gb	<i>Ovis (M)</i>	17/11/2017	24/07/2018	Dl
2018-23 **	Ir	<i>Ovis (M)</i>	18/11/2017	20/07/2018	Kb

Caprine tooth sample	Sampled tooth	Herder	Individual DOB	Start formation	End formation	Time _{GPS} ¹	Altitude (m)				Time-Alt ₂
							Mean ± sd	Max	Min	A	
2017-70-M3	M ₃ left	DI	31/03/2015	05/02/2016	30/05/2017	66%	2319 ± 112	2895	1991	904	59%
2017-71-M3	M ₃ left	DI	31/03/2015	05/02/2016	30/05/2017	66%	2319 ± 112	2895	1991	904	59%
2018-63B-M2	M ₂ left	DI	31/03/2017	08/05/2017	30/04/2018	100%	2376 ± 125	2980	2100	880	100%
Alt16-104a-M3	M ₃ left	Jk	31/03/2014	05/02/2015	30/05/2016	77%	1996 ± 361	2973	1450	1523	43%
2017-146-M2	M ₂ left	Jk	31/03/2015	08/05/2015	29/04/2016	88%	2026 ± 402	2973	1450	1523	61%
2017-146-M3	M ₃ left	Jk		05/02/2016	30/05/2017	100%	1934 ± 361	3003	1463	1540	31%
Alt16-283a-M3	M ₃ left	Kb	31/03/2014	05/02/2015	30/05/2016	77%	2101 ± 332	3132	1454	1678	50%
2017-98-M2	M ₂ left	Kb	31/03/2015	08/05/2015	29/04/2016	88%	2060 ± 344	3024	1437	1587	85%
2017-98-M3	M ₃ left	Kb		05/02/2016	30/05/2017	100%	2119 ± 327	2964	1444	1520	57%
2018-23A-M3	M ₃ right	Kb	31/03/2016	31/05/2017	29/06/2016	100%	2256 ± 227	3348	1455	1893	67%
Alt16-306a-M3	M ₃ left	Kj	31/03/2014	05/02/2015	30/05/2016	77%	2059 ± 269	2734	1686	1048	33%
Alt16-369a-M3	M ₃ left	Kj	31/03/2014	05/02/2015	30/05/2016	77%	2059 ± 269	2734	1686	1048	33%
2017-124-M2	M ₂ left	Kj	31/03/2015	08/05/2015	29/04/2016	88%	2072 ± 277	2734	1686	1048	47%
2017-124-M3	M ₃ left	Kj		05/02/2016	30/05/2017	100%	2021 ± 307	3014	1690	132	22%
2017-130-M3	M ₃ left	Zk	31/03/2015	05/02/2016	30/05/2017	66%	1645 ± 90	2468	1581	887	0.2%
Hair sample of horses *				Start formation	End formation	Time-GPS ¹	Mean ± sd	Max	Min	A	Time-Alt ₂
	DI 1	DI	-	05/02/2016	03/11/2017	64%	2366 ± 138	2814	1698	1116	97%
	Jk 1	Jk	-	19/04/2015	16/11/2017	94%	2115 ± 476	2916	1450	1466	43%

Jk 2	Jk	-	14/02/2017	18/07/2018	44%	2580 ± 477	3216	1447	1769	81%
Kb 1	Kb	-	12/09/2014	06/11/2017	68%	2433 ± 432	3157	1205	1952	76%
Kj 1	Kj	-	22/04/2015	26/08/2016	88%	2278 ± 459	3154	1468	1686	56%
Kj 2	Kj	-	23/03/2016	06/007/2018	80%	2014 ± 356	3103	1429	1674	30%

Horse tooth sample	Herder	Sex	DOB	DOD	Estimated age (years)	Sampled tooth
2017-104 M2	Kb	F	April–May 2013	10 November 2016	2.5	M ₂ right
2018-17B M3	?	M	2013–2014?	early July 2017	4	M ³ right
2018-57A M3	?	M	2003?	late February 2007	3-4	M ³ left
2018-58B M3	Kj	M	2015?	20–25 April 2018	3	M ³ right
2018-59A M1	?	F	2016?	January 2018	1.5	M ₁ right

Herder	Tooth sample	N	$\delta^{13}\text{C}$ (‰ V-PDB)				$\delta^{18}\text{O}$ (‰ V-PDB)				Pearson's r	df	p-value
			Mean \pm sd	Max	Min	A	Mean \pm sd	Max	Min	A			
Dl	2017-70-M3 ¹	21	-12.14 \pm 0.29	-11.6	-12.6	1.0	-7.50 \pm 3.08	-3.2	-12.4	9.2	0.13	19	>0.05
	2017-71-M3 ¹	20	-12.15 \pm 0.33	-11.4	-12.6	1.2	-7.19 \pm 3.19	-3.2	-12.4	9.2	0.33	18	>0.05
	2018-63B-M2 ¹	18	-12.88 \pm 0.57	-11.8	-13.7	1.9	-10.37 \pm 2.14	-6.5	-13.0	6.5	0.52	16	<0.05
	All	59	-12.37 \pm 0.53	-11.4	-13.7	2.3	-8.27 \pm 3.15	-3.2	-13.0	9.8			
Jk	Alt16-104a-M3 ¹	24	-10.70 \pm 0.69	-10.0	-12.1	2.1	-7.66 \pm 3.83	-1.5	-13.4	12.0	-0.91	22	<0.001
	2017-146-M2 ²	16	-11.60 \pm 0.31	-11.2	-12.2	1.0	-7.94 \pm 4.24	-1.6	-12.8	11.1	-0.37	14	>0.05
	2017-146-M3 ¹	24	-11.51 \pm 0.35	-11.0	-12.1	1.1	-7.69 \pm 3.28	-2.3	-12.6	10.3	-0.69	22	<0.001
	All	64	-11.23 \pm 0.64	-10.0	-12.2	2.3	-7.74 \pm 3.59	-1.5	-13.4	12.0			
Kb	Alt16-283a-M3 ¹	24	-10.87 \pm 0.39	-10.2	-11.5	1.3	-8.66 \pm 3.13	-3.5	-13.8	10.4	-0.78	22	<0.001
	2017-98-M2 ²	14	-11.47 \pm 0.53	-10.8	-12.6	1.8	-10.44 \pm 3.48	-3.9	-14.6	10.7	0.61	12	<0.05
	2017-98-M3 ¹	18	-11.23 \pm 0.90	-11.1	-11.8	0.7	-8.15 \pm 3.35	-3.3	-13.1	9.8	0.10	16	>0.05
	2018-23A-M3 ¹	21	-11.48 \pm 0.41	-10.9	-12.4	1.5	-8.18 \pm 4.06	-2.3	-13.3	10.9	-0.38	19	>0.05
All	77	-11.46 \pm 0.39	-10.8	-12.6	1.8	-8.77 \pm 3.75	-2.3	-14.6	12.2				
Kj	Alt16-306a-M3 ¹	24	-10.25 \pm 0.57	-9.4	-11.2	1.8	-7.39 \pm 3.33	-2.2	-13.2	11.0	-0.83	22	<0.001
	Alt16-369a-M3 ¹	18	-10.86 \pm 0.79	-10.1	-12.8	2.7	-6.47 \pm 4.29	-0.1	-12.3	12.2	-0.74	16	<0.001
	2017-124-M2 ²	16	-10.93 \pm 0.27	-10.4	-11.3	0.9	-7.57 \pm 3.65	-1.6	-12.3	10.7	-0.39	14	>0.05
	2017-124-M3 ¹	23	-10.92 \pm 0.49	-10.2	-11.8	1.6	-7.77 \pm 3.91	-1.1	-13.1	12.0	-0.38	21	>0.05
All	81	-10.57 \pm 0.70	-9.4	-12.8	3.3	-7.38 \pm 3.80	-0.1	-13.4	13.2				
Zk	2017-130-M3 ¹	25	-10.76 \pm 0.73	-9.6	-12.3	2.6	-6.84 \pm 3.57	-0.9	-11.9	11.0	-0.28	23	>0.05
Kb	2017-104 M2	30	-13.4 \pm 0.4	-12.8	-14.0	1.2	-11.8 \pm 1.9	-7.2	-14.7	7.5	-0.26	28	>0.05
?	2018-17B M3	20	-13.3 \pm 1.6	-11.9	-16.4	4.4	-10.9 \pm 3.3	-5.0	-14.5	9.5	-0.72	18	<0.001
?	2018-57A M3	23	-12.2 \pm 1.4	-10.6	-15.0	4.4	-10.4 \pm 1.7	-6.8	-13.3	6.5	-0.60	21	<0.01
Kj	2018-58B M3	20	-12.3 \pm 0.5	-11.6	-13.0	1.4	-11.2 \pm 3.1	-7.5	-16.1	8.6	-0.88	13	<0.001
?	2018-59A M1	16	-12.5 \pm 0.7	-11.2	-13.3	2.1	-9.2 \pm 2.7	-5.6	-14.4	8.8	-0.82	14	<0.001