

Kiputz IX: a rich sample of reindeer (*Rangifer tarandus* Linnæus, 1758) from the Late Pleistocene of the Iberian Peninsula

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Abstract

Kiputz IX is a Late Pleistocene site that has provided the richest set of complete reindeer remains in the Iberian Peninsula. This paper provides a metric and isotopic study of the postcranial skeleton of the 23 individuals that constitute this exceptional sample. The stage of dental replacement makes evident that the sample is dominated by adult specimens, with a low proportion of juvenile individuals. Application of variability size index on a series of samples from Western Europe and Northern Spain does not permit a model of spatial and temporal variability in the size of the Pleistocene reindeer to be established. Variations in $\delta^{13}\text{C}$ values among reindeer, red deer and steppe bison are related to the specialized consumption of different plant types. The reindeer sample from Kiputz IX constitutes a sound basis for comparative studies of Middle and Late Pleistocene reindeer populations in Europe.

Keywords

Rangifer tarandus, sexual dimorphism, age structure, biometry, isotopes, MIS 2, northern Spain.

Résumé

Kiputz IX: un assemblage significatif de renne (*Rangifer tarandus* Linnæus, 1758) du Pléistocène supérieur final de la péninsule Ibérique.- Kiputz IX est le plus important gisement du Pléistocène supérieur final actuellement recensé pour le renne dans la péninsule Ibérique. Cet article propose une étude métrique et isotopique du squelette postcranien des 23 individus constituant cet échantillon exceptionnel. Le stade de remplacement dentaire montre clairement que l'échantillon est dominé par des adultes, avec une faible proportion d'individus juvéniles. La comparaison des indices de variabilité de la taille sur des échantillons d'Europe occidentale et du nord de l'Espagne ne permet pas de modéliser la variabilité spatiale et temporelle de la taille du renne du Pléistocène. Les variations de valeurs de $\delta^{13}\text{C}$ observées chez le renne, le cerf et le bison des steppes indiquent un lien avec la consommation de différents types de plantes. L'échantillon de rennes du site de Kiputz IX constitue une base solide pour l'étude comparative des populations de rennes du Pléistocène moyen et supérieur en Europe.

Mots-clés

Rangifer tarandus, dimorphisme sexuel, structure d'âges, biométrie, isotopes, stades isotopiques 2, nord de l'Espagne.

1. INTRODUCTION

The genus *Rangifer* probably originated in the Arctic region of North America, Beringia or NE Siberia (Kahlke, 1999) during the Pliocene/Pleistocene transition. Its appearance in Europe occurred around 450 ka BP, at sites in Germany (Süssenborn), France and Great Britain during MIS 12 (Stuart, 1982; Weinstock, 2000). Populations presumably moved to boreal refugia during the Holstenian (MIS 11) and Eemian (MIS 5e) interglacials (Kahlke, 1999). Reindeer became one of the most important prey species for groups of hunter-gatherers in Europe during the Upper Paleolithic. Its

abundant presence and the richness of samples in France and Central Europe (Weinstock, 2000) contrast with the relative scarcity in Spain. Although it is present in 50 sites concentrated mostly in the Cantabrian fringe, most are small samples with less than 25 remains (Gómez *et al.*, 2014). Kiputz IX is the site which to date has provided the richest reindeer sample in the Iberian Peninsula. The aim of this work is to describe the palaeobiological structure (minimum number of individuals, age and sex), the biometry and isotopic analysis of carbon and nitrogen in bone collagen from this rich sample of reindeer. This work is also our small contribution to this tribute to Claude Guérin whose scientific work uniquely shaped

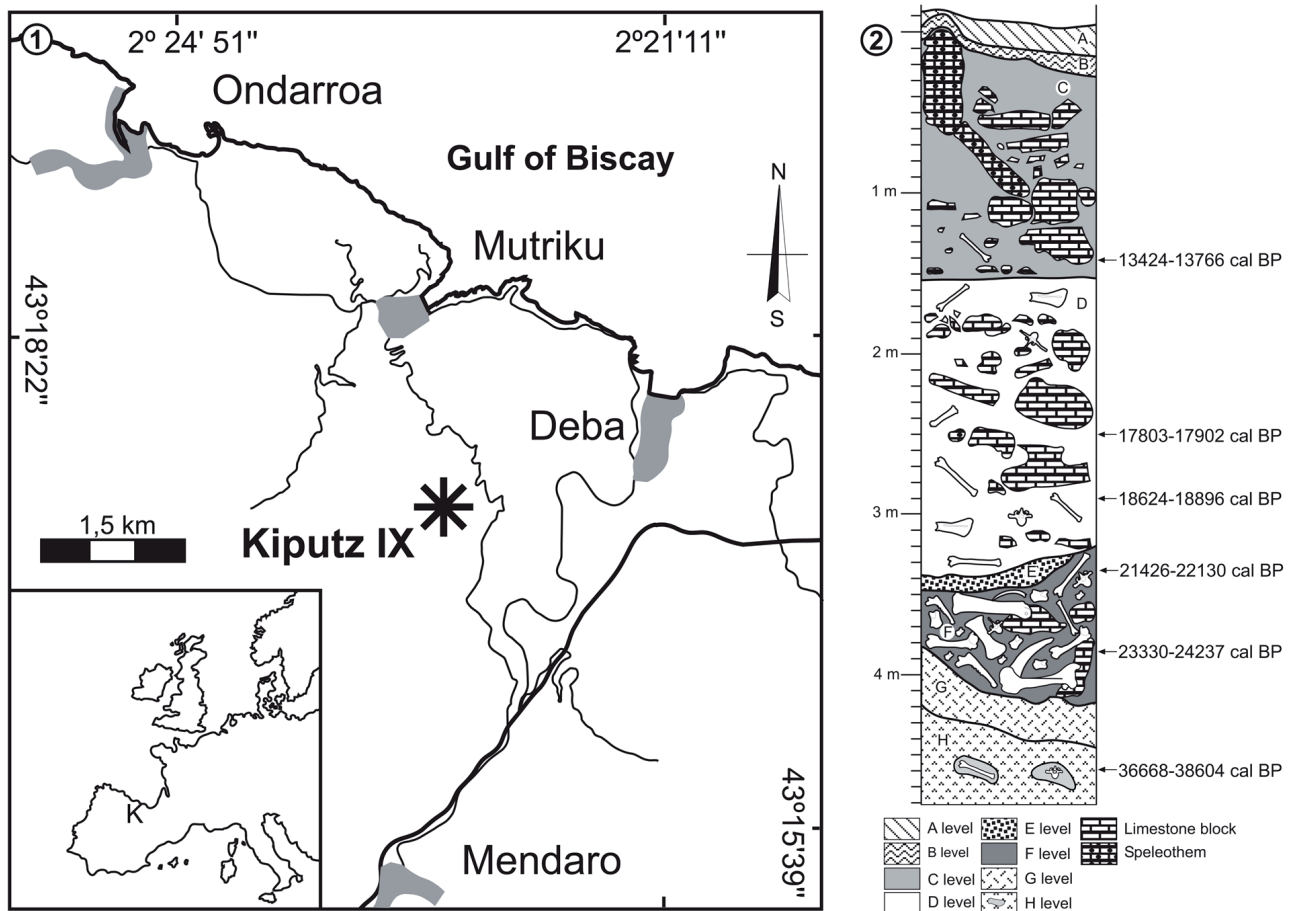


Fig. 1: 1. Geographic location of the Kiputz IX site (Mutriku, Gipuzkoa); 2. Stratigraphic sequence of the Kiputz IX site.

the development of large vertebrate palaeontology and that he studied a rich reindeer sample from the Jaurens site (Valli & Guérin, 2000).

2. SETTING AND CHRONOLOGY

Kiputz IX is a palaeontological site at Mutriku, Gipuzkoa in the Basque Country (northern Iberian Peninsula) (Fig. 1.1). This site was discovered in 2003 and excavated between 2004 and 2007. Kiputz IX is an open karst shaft which functioned as a natural trap where the animals fell and could not escape. The hole is 2 m wide and 2.5 m long, to *circa* 6 m² of floor area and a 4.2 m-thick sediment-filled bottom that has been divided into eight stratigraphic levels (Fig. 1.2).

Large mammal species that accompany the reindeer sample are red deer, steppe bison, horse, chamois, Spanish wild goat, wild pig, brown bear, wolf, red fox, lion, wild cat and European badger (Castaños *et al.*, 2014).

The chronology of the sedimentary fill was obtained from six radiocarbon dates ranging from 36,668-38,604 cal BP to 13,424-13,766 cal BP (Beta Analytic, Florida, USA) (Castaños *et al.*, 2012). This sedimentary sequence

therefore corresponds to late marine isotope stage 3 (MIS 3) to (MIS 2). Stratigraphic levels were classified and divided based on macroscopic sediment descriptions including color, particle size and sorting and morphology of the pebble and cobble fraction (Castaños *et al.*, 2006). Most of the remains of reindeer come from Levels D and F. Therefore they coincide with the Last Glacial Maximum (LGM) (Fig. 1.2).

One of the most important features of the site is the excellent preservation of its fossil samples. Therefore, its characteristic as a trap, combined with the preservation of the site, has provided a representative sample of the species that lived in that ecosystem during the Late Pleistocene (Castaños *et al.*, 2006).

3. MATERIAL AND METHODS

2186 remains of reindeer were recovered from a total of 12683 remains identified at the site. This represents 17.24% of the full sample of large mammals. The remains are spread between Levels C, D and F. The species is absent in level H. The fossils are stored in the "Depósito de materiales arqueológicos y paleontológicos

de Gipuzkoa” (Irún, Spain) under the generic acronym of KI. IX.

The estimation of age at death of reindeer was mostly determined based on the stage of tooth eruption and wear of the last molar according to the methodology of Bouchud (1966). The metric comparison with other samples of reindeer was performed with the index called «Variability Size Index» (VSI) (Uerpmann, 1982). This method allows several samples to be compared, even if they are small and fragmentary, showing changes in size over time or space. For its application it is necessary to choose a standard population with its arithmetic mean (X) and its standard deviation (s) for each measurement of each bone. To compare any isolated measurement or average of a sample with the standard, the index is estimated by using the algorithm: $VSI = 50 (X - m / 2s)$ where m = measurement or mean to compare, X = arithmetic mean of standard population and s = standard deviation of the standard population. This index expresses the positive or negative distance in units of standard deviation of the measurement compared to the standard average. It also allows the comparison of an isolated measurement when the bone is broken. Finally, a statistical set is obtained consisting of all Variability Size Indexes. The values of this set allow us to estimate the degree of coincidence or divergence of the reindeer size across several samples. The measurements of the Spain sites (S. Catalina and Kiputz IX) have been taken by ourselves and those of other European sites come from the literature (Weinstock, 2000; Magniez, 2010).

Extraction of collagen for isotopic analysis was carried out according to the methodology of Bocherens *et al.* (1991). All samples have been analyzed in a mass spectrometer with elemental analyzer of continuous flow (EA-IRMS, Iso-Analytical, Cheshire, UK). Only samples with a value of C/N located within the range 2.7-4.7 and percentages of carbon and nitrogen above 3% and 8% respectively were analyzed (DeNiro, 1985; Ambrose & DeNiro, 1989). To assess collagen preservation, infrared spectroscopy has been performed (Castaños *et al.*, 2010). The non-parametric Kruskal-Wallis test (Kruskal & Wallis, 1952) was applied to compare the differences between the various species since the isotopic data do not follow a normal distribution. Statistical significance was accepted when $p < 0.05$.

The following abbreviations are used for the description of climate events: **B/A**, Bølling/Allerød; Greenland Stadial-3 (**GS-3**), Greenland Interstadial-2 (**GI-2**), Greenland Stadial-2 (**GS-2**), Greenland Interstadial-1 (**GI-1**) (Lowe *et al.*, 2008); **LGM**, Last Glacial Maximum; **OD**, Older Dryas; **YD**, Younger Dryas.

Metric abbreviations: The measurements (in mm) taken on bones and teeth follow the standards of von den Driesch (1976). Measurements abbreviations are: **B**: Breadth; **BA**: Breadth of acetabulum; **BC**: Greatest breadth of caput; **Bd**: Greatest distal breadth; **BG**: Breadth of glenoid cavity; **Bp**: Greatest proximal

breadth; **BPC**: Greatest breadth of proximal articular face; **BT**: Greatest breadth of Trochlea; **DC**: Diameter of *caput femoris*; **Dd**: Distal depth; **DI**: Greatest depth of lateral face; **Dp**: Proximal depth; **DPA**: Depth across *processus anconeus*; **GB**: Greatest breadth; **GL**: Greatest length; **GLP**: Greatest length of the glenoid process; **L**: Length; **LA**: Length of acetabulum; **LG**: Length of glenoid cavity; **LI**: Greatest length of lateral face; **Lm**: Greatest length of medial face; **SD**: Smallest breadth of shaft; **SDO**: Smallest depth of olecranon; **S LC**: Smallest length of *collum scapulae*.

4. SYSTEMATICS

Order Artiodactyla Owen, 1848
Family Cervidae Goldfuss, 1820
Genus *Rangifer* Hamilton Smith, 1827
Type species: *Cervus tarandus* Linnæus, 1758

Rangifer tarandus (Linnæus, 1758)

Anatomy and number of individuals: The anatomical distribution of remains (Table 1) reflects the high degree of fragmentation of the skull, resulting in a large number of isolated teeth detached *postmortem* from the maxillary bones.

The most common bone (talus), taking laterality into account, allows an estimate of a minimum number of 10 individuals in Level D and 13 in Level F. If we consider the two levels together, the total minimum number of individuals is 23. Therefore, the reindeer sample from Kiputz IX is currently the most abundant in the Iberian Peninsula and one of the richest in full long bones in SW Europe, after the Stellmoor (Rust, 1943) in Germany and Kesslerloch (Heierli, 1907) in Switzerland.

Sexual dimorphism: The reindeer, like other cervids, presents some degree of sexual dimorphism that manifests itself in all skeletal elements. In the reindeer, as in most mammals, males are larger and heavier than females. Therefore, the long bones of males are longer and wider. The presence of complete bones in Kiputz IX allows scatterplots with the greatest length and distal breadth of radius, metacarpal and tibia (Fig. 2). The three diagrams present two clouds of points that can be attributed to individuals of each sex as the most likely hypothesis. In all three cases the proportion of males is approximately double that of females. This predominance of males is an interesting fact in the face of the subsequent interpretation of the comparative biometry.

Age structure: The estimation of the age of the individuals follow the methodology of Bouchud (1966) and is based on the tooth replacement state and wear of the lower series. The results allow the sample to be divided into four intervals or age groups (Table 2).

The best represented age group is that of old adults, that represents nearly half (43.5%) of the total sample. The

Table 1: Anatomical distribution of Kiputz IX reindeer remains.

	Level C	Level D	Level F	TOTAL
Horncore		18	58	76
Skull		14	45	59
Maxilla		9	42	51
Upper teeth isoled		24	70	94
Mandible		28	45	73
Lower teeth isoled		15	30	45
Hyoid		2		2
Atlas		4	13	17
Axis		2	6	8
Sacrum		3	12	15
Vertebra		45	373	418
Rib	1	58	117	176
Sternum			3	3
Scapula		9	30	39
Humerus	1	10	43	54
Radius	1	14	26	41
Ulna		4	12	16
Carpal		42	75	117
Metacarpal		13	22	35
Pelvis	2	22	47	71
Femur	2	26	50	78
Patella		8	18	26
Tibia		17	35	52
Calcaneum		17	25	42
Talus		17	24	41
Cubonavicular		11	21	32
Metatarsal		12	32	44
Indet. metapodial		22	19	41
Phalanx I		59	110	169
Phalanx II	1	33	101	135
Phalanx III		18	68	86
Sesamoid		13	17	30
TOTAL	8	589	1589	2186

frequencies of infant (21.7%) and prime adult (26.1%) individuals are respectively slightly below and above a quarter of the total. Juveniles are the scarcest age group with a frequency of 8.7% of the total. These results contrast with the red deer and steppe bison at the site. In these two species immature individuals constitute the largest group among those that fell into the shaft (Castaños *et al.*, 2012, 2014).

Osteometry: The measurements of reindeer remains in levels D and F are very similar. A parametric test of homogeneity of samples was used to compare the data of both levels together with other sites. The maximum length

Table 2: Age distribution of the Kiputz IX reindeer. Abbreviations: + present, - absent, +/- emerging and (0), (+), (++) , (+++) are degrees of wear.

Lower dentition	Age	NMI	Age groups	%
D2-D4(0)	1 month	1		
M1+ M2-	3-13 months	3	infantile	21,7
M2+/-	13 months	1		
M2+M3-	13-24 months	1	juvenile	8,7
M3+/-	24-30 months	1		
M3(+)	3-5 years	6	prime adult	26,1
M3(++)	6-7 years	4	old adult	43,5
M3(+++)	more 8 years	6		

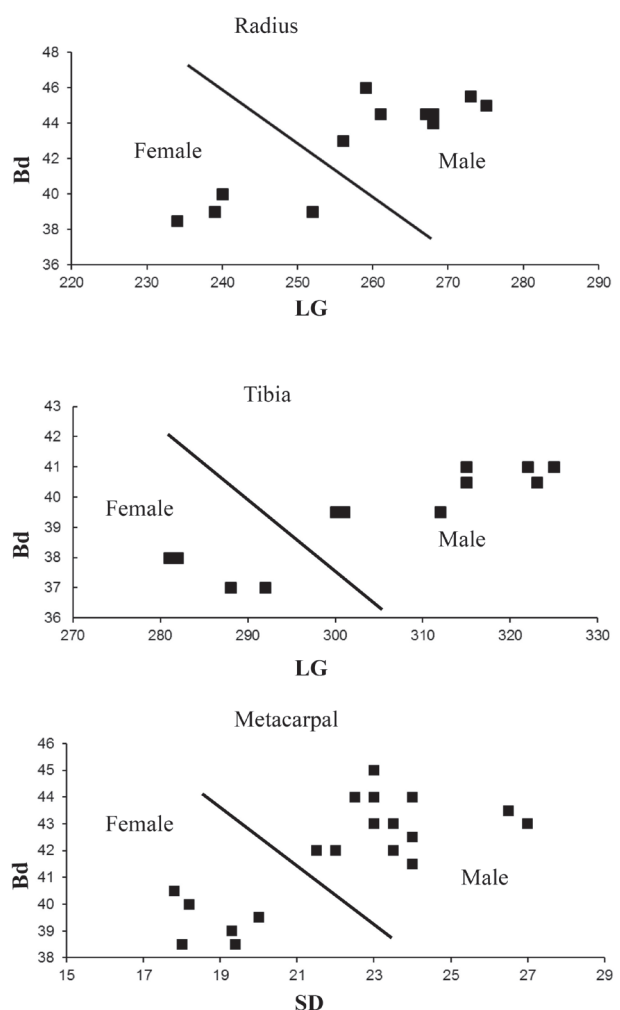


Fig. 2: Kiputz IX; plot of reindeer radius, tibia (greatest length vs. greatest distal breadth) and metacarpal (smallest breadth of shaft vs. greatest distal breadth).

of lateral (Ll) and distal width (Bd) of the most abundant bone (talus) in each of the two levels were chosen for this. The result of a student t-test ($p > 0.05$) confirms that there is no statistically significant difference between the averages of the talus in Levels D and F (Table 3). Therefore, the measurements of the two levels will be used together as if it were a single sample and its metric means have been collated in Table 4.

The Variability Size Index (VSI) was used to compare the mean values of Kiputz IX reindeer measurements with other Late Pleistocene samples in Europe, taking as standard values the average values of the reindeer measurements from Ahrensburgian layer (MIS 2 late) of the German Stellmoor site (Weinstock, 2000) (Table 5). In the Iberian Peninsula, apart from Kiputz IX, there is only one sample of reindeer with sufficient data to carry out a metric comparison: Santa Catalina (Bizkaia, Spain) (Castaños, 2014). Thirteen samples from three regions in Europe were therefore chosen to complete the comparison. Eleven come from eight sites in France: Abri Dufaure (Altuna *et al.*, 1991), Gare de Couze (Prat, 1962), La Madeleine (Weinstock, 2000: 38), Laugerie Haute (Bordes, 1984), Roc de Combe (Bordes, 1984), Combe Grenal (Bordes, 1972), Portel-Ouest and Tournal (Magniez, 2010). Their chronology ranges from the Acheulean to the Magdalenian VI. There are three sets, also Magdalenian, from the South of Germany and Switzerland: Schussenquelle (Schuler, 1991), Petersfels

(Albrecht *et al.*, 1983) and Kesslerloch (Heierli, 1907). This selection is completed with the rich sets of Ahrensburgian and Hamburgian layers from Stellmoor site (Rust, 1943) in the North of Germany. VSI values from all these continental samples are taken from two comprehensive revisions of Western European reindeer (Weinstock, 2000; Magniez, 2010) and are compared with our VSI values from Santa Catalina and Kiputz IX in Table 6.

To study the possible relationship between the size of the reindeer and the geographical distribution of the samples, all sets are ordered according to their latitude. Some authors suggest during Late Glacial a decrease in size of European reindeer following the N-S gradient although this did not remain constant through time (Weinstock, 2000; Álvarez-Laó, 2007). When comparing VSI values, including samples from MIS 3 and MIS 2, this decrease in size is not demonstrated (Fig. 3.1). Sites in high latitudes such as Kesslerloch (Switzerland), Petersfels and Schussenquelle (Germany) show similar VSI values to others at lower latitudes, such as Combe Grenal 60, Laugerie Haute w 7-2, La Madeleine, Gare de Couze G-Gl, Abri Dufaure 4 (SW France) and Santa Catalina (Spain). Some sites such as Combe Grenal 25-23 and Roc de Combe 5, and specially Kiputz IX, have provided VSI values higher than the German samples.

Chronology is another factor that may be related to variation in reindeer body size. The size of the Kiputz IX

Table 3: Descriptive statistics and the results of student t-tests performed on the talus measurements of reindeer from Level D and Level F. Abbreviations: Ll, Greatest length of lateral face; Bd, Greatest distal breadth; n, sample number; Min, minimum; Max, maximum; s.d., standard deviation(%); t, Student's t-test value; p, p-value arising from the Student's t-test.

	Level D					Level F					T student	
	n	Min.	Max.	X	s	n	Min.	Max.	X	s	t	p
Ll	16	42.0	48.0	44.50	1.69	25	41.5	48.0	44.08	1.65	-0.76	0.44
Bd	15	25.0	29.5	28.03	1.16	25	25.5	30.5	27.94	1.35	0.21	0.82

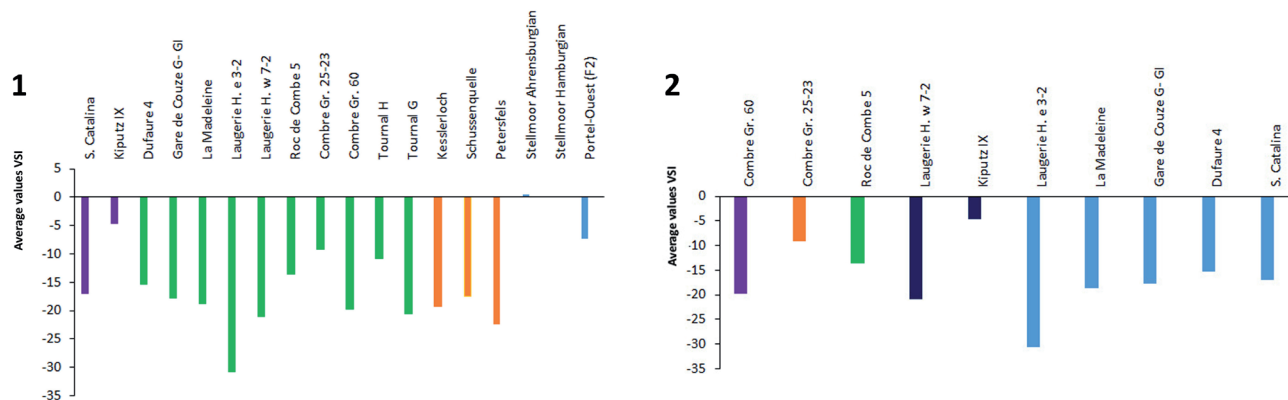


Fig. 3: Spatial (1) and temporal (2) variations of reindeer VSI average values at Late Pleistocene at West Europe. 1: purple (Spain), green (France), orange (Switzerland and S Germany), blue (N Germany); 2: purple (Acheulean MIS 6), orange (Mousterian MIS 4), green (Aurignacian), dark blue (Solutrean), light blue (Magdalenian).

Table 4: Descriptive statistics of the Kiputz IX reindeer measurements.

	n	min.	max.	mean	st.dev.
Mandible					
LP2-M3	16	95.0	114.0	105.84	4.55
LP2-P4	18	41.5	48.0	44.91	1.97
LM1-M3	18	52.0	66.0	62.00	3.31
LM3	26	21.5	26.0	23.59	1.28
BM3	26	9.0	11.9	10.41	0.72
Scapula					
GLP	20	43.5	50.5	47.35	2.16
LG	22	34.0	41.0	37.88	1.77
BG	22	27.5	35.0	32.04	2.09
SLC	22	28.5	40.5	36.20	3.28
Humerus					
GL	10	215.0	258.0	237.30	11.01
Dp	16	59.5	70.0	65.78	3.02
SD	10	21.0	30.0	25.45	2.59
Bd	4	42.0	49.0	45.50	3.25
BT	26	34.0	49.5	44.63	3.85
Radius					
GL	11	234.0	275.0	259.27	12.66
Bp	18	39.0	49.0	45.02	2.66
BPC	18	37.5	46.5	42.75	2.35
SD	11	23.0	29.0	26.36	1.94
Bd	19	37.0	48.0	42.26	3.18
Ulna					
DPA	5	37.5	44.0	41.40	2.47
SDO	5	34.5	40.0	37.20	2.15
BPC	4	23.0	27.5	25.50	2.03
Metacarpal					
GL	18	173.5	207.5	191.00	8.71
Bp	24	30.5	39.0	34.04	2.38
SD	18	17.8	27.0	22.03	2.67
Bd	21	38.5	45.0	41.90	1.97
Dd	21	19.6	24.0	21.57	1.22
Pelvis					
GL	1	312.0	312.0	312.0	-
LA	10	38.0	43.0	40.20	1.76
BA	6	34.5	38.0	36.41	1.13
Femur					
GL	7	263.5	284.0	273.78	9.18
Bp	11	57.0	76.0	68.00	5.19
BC	18	25.5	32.5	29.22	1.60
SD	8	20.0	27.5	23.81	2.51
Bd	21	53.5	63.0	57.57	3.07
Tibia					
GL	12	281.0	325.0	304.66	15.45
Bp	16	54.0	65.0	59.28	3.22
SD	13	22.0	28.0	25.26	2.28
Bd	29	34.5	43.0	39.08	2.14
Calcaneum					
GL	27	86.5	99.5	93.22	3.44
GB	28	26.5	34.0	30.25	1.83
Talus					
Ll	41	41.5	48.0	44.24	1.68
Lm	41	39.0	45.5	41.78	1.58
Dl	41	23.0	27.0	24.78	1.00
BC	40	25.0	30.5	27.97	1.28
Cubo-navicular					
GB	30	31.0	39.0	35.08	2.17
Metatarsal					
GL	8	242.0	284.0	261.75	12.40
Bp	13	26.5	33.5	29.84	2.02
SD	7	18.0	23.5	21.17	1.89
Bd	19	37.5	43.5	40.92	1.64
Dd	19	21.0	25.0	22.57	0.90

reindeer has therefore been compared with eight samples of SW France and Santa Catalina which are at similar latitudes, to avoid the question of geographic variability. The age of the samples range between MIS 2 and MIS 6 with a particular concentration in MIS2 (Fig. 3.2). The VSI values, except Kiputz IX, vary from -9.16 to -19.72 and are smaller than the standard size. Thus, no temporal variability is seen in reindeer during the Late Pleistocene. In the two comparisons, the high values of Kiputz IX stand out over all samples from Western Europe and the most of Central Europe. They are only similar to those of Stellmoor. However, Santa Catalina data are

similar to those from SW France sites. In addition, the high size of the reindeer body is not repeated in other abundant species of the same deposit such as red deer (Castaños *et al.*, 2014) and steppe bison (Castaños *et al.*, 2012). So it seems an exclusive feature of this reindeer sample and it is interesting to raise the possible cause for this peculiarity. It is usually accepted that the factors affecting body size are *ontogenetical* (age and sex) or *ecological* (environmental factors). From the above data, it seems reasonable to rule out spatial or temporal factors as a cause of the high size of the Kiputz IX reindeer. This leads us to raise the role of age and sex in this issue.

Table 5: Descriptive statistics of the Ahrensburgian reindeer measurements from the German Stellmoor site (Weinstock, 2000) used as standard in the comparative VSI method.

	mean	st.dev.	n
Scapula			
GLP	46.32	3.21	215
LG	35.48	2.35	198
BG	30.6	2.72	224
SLC	33.63	4.04	231
Humerus			
BT	43.47	2.37	228
Radius			
Bp	45.41	2.69	176
BPC	42.72	2.15	174
Ulna			
DPA	42.55	3.27	58
SDO	37.60	2.38	57
Metacarpal			
Bp	34.97	2.03	85
Bd	42.97	1.95	165
Dd	22.53	1.02	165
Pelvis			
LA	40.41	1.84	119
Femur			
BC	29.96	1.22	74
Tibia			
Bd	40.09	1.89	133
Calcaneus			
GL	95.72	4.50	113
BG	30.64	1.79	111
Talus			
LI	45.92	1.88	138
Lm	43.43	1.66	138
DI	25.52	1.07	138
BC	28.47	1.42	138
Cubo-navicular			
GB	35.64	1.89	79
Metatarsal			
Bp	30.68	1.27	40
Bd	41.63	1.50	26
Dd	23.31	0.81	26

It is not possible to attribute the big size of Kiputz IX reindeer's to the age because measurements are taken only in adult bones. Therefore, it seems reasonable to relate the reindeer size with the sexual structure in which there is a predominance of males. Therefore, it should

be considered as the most acceptable hypothesis and not a proven conclusion. In the reindeer sample studied, the conditions to establish conclusively the osteometric differences between males and females of this species are not given. The difficulties on this subject in other richer samples like Stellmoor are eloquent in this regard (Weinstock, 2000: 56).

5. STUDY OF STABLE ISOTOPES

In recent years, stable isotope analysis of carbon and nitrogen in bone collagen has been used as a proxy to establish palaeodietary and palaeoclimatic variation (Ambrose & DeNiro, 1989; Iacumin *et al.*, 2000; Stevens *et al.*, 2008; Drucker *et al.*, 2012). The stable carbon isotope ratio ($\delta^{13}\text{C}$) of herbivore tissue is related to factors such as the environment, the photosynthetic pathways of consumed plant matter, water availability, salinity and partial atmospheric pCO_2 (Gannes *et al.*, 1988). It is generally accepted that high $\delta^{13}\text{C}$ values indicate a dry and cold environment and the consumption of some types of plants. On the other hand the stable nitrogen isotope ratio ($\delta^{15}\text{N}$) preserved in animal tissues is related to factors such as diet, climate and water availability (Iacumin *et al.*, 2000; Drucker *et al.*, 2003; Stevens *et al.*, 2008). Low $\delta^{15}\text{N}$ values seem to correspond to humid climate, while high values of $\delta^{15}\text{N}$ are related to aridity (Handley *et al.*, 1999).

This section presents an analysis of the content of stable carbon and nitrogen isotopes in bones of reindeer although it also includes red deer and steppe bison, also from Kiputz IX, as comparative data (Table 7). Nine bone remains of reindeer, six of steppe bison and 33 of red deer have been analyzed. All bones are from the postcranial skeleton and different age-classes have been established, including 14 adult individuals, 19 juvenile and 15 without age assignment.

The bone collagen amount is 0.74-13.5%wt. The Ccoll and Ncoll contents are above 25.6% and 8.2% wt respectively, and the C/N atomic ratio is within the range 3.2-3.6, which corresponds to well-preserved collagen (DeNiro, 1985). The FT-IR absorbance bands of amide II (1600-1500 cm^{-1}) and amide III (1300-1200 cm^{-1}) indicate low collagen deterioration and a lack of significant chemical changes in bone collagen (Greene *et al.*, 2004).

Reindeer show the least negative $\delta^{13}\text{C}$ values, ranging from -20.05‰ to -19.02‰ (average -19.68‰). The red deer $\delta^{13}\text{C}$ values vary between -21.52‰ and -20.25‰ (average -20.98‰), whereas steppe bison $\delta^{13}\text{C}$ values range from -21.21‰ to -20.‰05 (average -21.08), with a strong overlap between the two latter species. $\delta^{13}\text{C}$ values are highly statistically significantly different between reindeer and red deer ($p < 0.0001$) and also between reindeer and steppe bison ($p = 0.004$).

The observed difference in $\delta^{13}\text{C}$ values among the

Table 6: Statistical values VSI calculations for Middle and Upper Paleolithic sites Germany, France and Spain. ¹ Castaños, 2014; ² Weinstock, 2000; ³ Magniez, 2010.

Sites	Level	mean	st.dev.	max.	min.	n
Cantabrian Region						
S. Catalina ¹	Upper Magdalenian	-16.91	23.4	42.77	-86.73	60
Kiputz IX		-4.63	1.34	148.01	-120.29	708
France						
Dufaure 4 ²	Magdalenian	-15.38	25.23	53.91	-101.01	116
Gare de Couze G-GI ²	Magdalenian VI	-17.83	23.89	52.58	-99.84	129
La Madeleine ²	Magdalenian V-VI	-18.69	21.14	31.95	-68.51	205
Tournal H ³	Magdalenian IV	-10.80	27.27	68.90	-93.50	323
Tournal G ³	Magdalenian III	-20.60	22.02	76.50	-111.90	617
Laugerie H. e 3-2 ²	Magdalenian III	-30.71	23.08	28.89	-89.19	206
Laugerie H. w 7-2 ²	Upper Solutrean	-20.99	23.75	42.00	-64.66	136
Roc de Combe 5 ²	Upper Aurignacian	-13.65	20.77	46.47	-50.94	131
Portel-Ouest (F2) ³	Mousterian (MIS 3)	-7.40	27.91	53.6	-102.00	364
Combe Gr. 25-23 ²	Mousterian (MIS 4)	-9.16	30.05	50.28	-74.30	135
Combe Gr. 60 ²	Acheulean (MIS 6)	-19.72	23.57	34.78	-60.90	33
Switzerland						
Kesslerloch ²	Magdalenian	-19.33	25.89	62.24	-113.69	1384
Southern Germany						
Schussenquelle ²	Magdalenian	-17.84	27.68	48.35	-89.20	219
Petersfels ²	Magdalenian	-22.41	28.31	63.29	-103.21	158
Northern Germany						
Stellmolr Ahrensburgian ²	Azilian	0.50	23.29	70.49	-53.21	1803
Stellmoor Hamburgian ²	Magdalenian	-4.11	25.42	77.81	-58.60	330

reindeer and the other two species, although small (1%), may indicate slight differences in the diet. The more positive $\delta^{13}\text{C}$ values for reindeer have been attributed to a lichen consumption since lichens are $\delta^{13}\text{C}$ -enriched compared to other vascular plants in the same ecosystem (Iacumin *et al.*, 2000; Drucker *et al.*, 2003, 2011). These data only allow supposing a peculiarity of the reindeer diet vs the other two herbivores. But the interpretation of steppe bison and red deer $\delta^{13}\text{C}$ values may demand an explanation. Steppe bison are predominantly grazers (Meagher, 1986; Feranec *et al.*, 2009), whereas red deer, from current European specimens, can be classified among the intermediate feeders, with a mixed diet between grazing and browsing (Gebert & Verheyden-Tixier, 2001). The coincidence of steppe bison and red deer $\delta^{13}\text{C}$ values in Kiputz IX may seem to be a contradiction. But these same authors say that red deer diet is composed of 30% of grass and sedges as constant resource and 23% of *Calluna* and *Vaccinium* in some habitats (moorland from Scotland). From these data it is possible to admit that having a mixed diet, some red deer may show a consumption of grasses in open habitats (Iacumin *et al.*, 2000; Drucker *et al.*, 2003, 2011).

Therefore, the simultaneous presence of the red deer with reindeer and steppe bison is not incompatible in an open space as could be the environment of the deposit during the last cold pulsation of the upper Pleistocene. Steppe bison and reindeer $\delta^{15}\text{N}$ values are more positive than red deer nitrogen isotopes. The steppe bison $\delta^{15}\text{N}$ values range between 2.23‰ and 7.98‰ (average 5.7‰), and reindeer $\delta^{15}\text{N}$ values vary between 3.75‰ and about 8‰ (average 5.4‰) whereas red deer nitrogen isotopes range from 2.43‰ to 5.52‰ (average 3.5‰). The Kruskal-Wallis test confirms that red deer values are statistically different from reindeer ($p = 0.007$) and steppe bison values ($p = 0.003$). However, reindeer and bison $\delta^{15}\text{N}$ values show no significant differences ($p = 0.5$). The isotopic deviation between reindeer / steppe bison and red deer is also small (2‰) but statistically significant. This data can support the existence of a slight increase in water in the diet of the red deer with respect to the other two species. It is a fact that the three species shared the same ecosystem (the environment of the chasm). And it can be assumed that while the reindeer and the bison habitually occupied this habitat, the red deer, due to its food preferences, could move around nearby areas

of shrubs and conifers. This assumption is consistent with the dominant environment during the Last Glacial Maximum (Sánchez Goñi *et al.*, 2008).

The isotopic data obtained in the reindeer samples from the Kiputz IX were compared with those obtained

elsewhere in Europe (Iacumin *et al.*, 2000; Drucker *et al.*, 2003, Stevens *et al.*, 2008). $\delta^{15}\text{N}$ values at Kiputz IX during the Late Pleistocene appear to deviate from other European regions. Kiputz IX reindeer nitrogen isotope data are generally higher than those of other continental

Table 7: Results of the isotopic analysis collagen ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) from Kiputz IX red deer (*Cervus elaphus*), reindeer (*Rangifer tarandus*) and steppe bison (*Bison priscus*).

Species	Anatomy	Depth	C (%)	N (%)	C/N	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>Cervus elaphus</i>	Metatarsal	14	39.3	13.4	3.4	-21.05	2.82
<i>Cervus elaphus</i>	Metatarsal	17	50.2	16.9	3.5	-21.42	3.21
<i>Cervus elaphus</i>	Tibia	18	38.00	13.1	3.4	-21.52	2.98
<i>Rangifer tarandus</i>	Metacarpal	18	38.7	13.3	3.4	-19.90	3.75
<i>Cervus elaphus</i>	Phalanx II	19	40.8	13.9	3.4	-21.03	3.49
<i>Rangifer tarandus</i>	Tibia	26	42.2	14.4	3.4	-19.57	7.18
<i>Bison priscus</i>	Tibia	26	35.4	12.0	3.4	-20.05	7.98
<i>Rangifer tarandus</i>	Phalanx I	27	41.4	14.5	3.3	-19.02	5.51
<i>Cervus elaphus</i>	Humerus	28	35.4	12.0	3.4	-20.88	4.09
<i>Cervus elaphus</i>	Metacarpal	29	41.6	14.0	3.5	-20.86	5.52
<i>Cervus elaphus</i>	Phalanx I	29	33.8	11.7	3.4	-21.28	3.50
<i>Rangifer tarandus</i>	Metapodial	29	42.1	14.5	3.4	-19.65	4.86
<i>Cervus elaphus</i>	Metatarsal	30	33.0	11.1	3.5	-20.85	5.52
<i>Cervus elaphus</i>	Metapodial	31	43.4	15.1	3.4	-20.71	2.43
<i>Cervus elaphus</i>	Metatarsal	32	37.0	12.6	3.4	-21.00	3.50
<i>Rangifer tarandus</i>	Metacarpal	32	40.0	13.7	3.4	-20.05	4.69
<i>Cervus elaphus</i>	Metatarsal	32	41.8	13.8	3.5	-21.10	3.68
<i>Cervus elaphus</i>	Metacarpal	33	41.3	14.3	3.4	-21.05	2.73
<i>Bison priscus</i>	Radius	33	40.5	13.9	3.4	-20.68	2.23
<i>Cervus elaphus</i>	Metacarpal	34	40.9	13.7	3.5	-21.22	2.81
<i>Cervus elaphus</i>	Phalanx II	34	45.7	16.0	3.3	-20.25	4.17
<i>Cervus elaphus</i>	Metatarsal	34	35.1	12.0	3.4	-20.91	2.46
<i>Bison priscus</i>	Phalanx I	34	40.2	13.6	3.4	-21.06	5.72
<i>Rangifer tarandus</i>	Metacarpal	35	40.9	14.3	3.3	-19.28	5.41
<i>Rangifer tarandus</i>	Humerus	35	42.2	14.5	3.4	-19.53	6.14
<i>Cervus elaphus</i>	Metacarpal	35	37.5	12.2	3.6	-21.22	2.45
<i>Cervus elaphus</i>	Tibia	36	41.1	14.1	3.4	-20.58	2.45
<i>Cervus elaphus</i>	Phalanx II	37	43.2	14.6	3.4	-20.91	4.81
<i>Cervus elaphus</i>	Humerus	37	41.0	13.7	3.5	-20.91	3.57
<i>Cervus elaphus</i>	Phalanx I	37	43.4	15.0	3.4	-20.91	5.36
<i>Rangifer tarandus</i>	Phalanx I	37	36.8	12.5	3.4	-20.03	7.97
<i>Cervus elaphus</i>	Metapodial	37	36.6	12.4	3.4	-21.49	4.83
<i>Bison priscus</i>	Talus	38	25.6	8.2	3.6	-21.21	5.70
<i>Cervus elaphus</i>	Metacarpal	39	42.6	14.3	3.5	-20.71	3.76
<i>Cervus elaphus</i>	Phalanx I	40	34.7	11.9	3.4	-20.77	3.54
<i>Rangifer tarandus</i>	Tibia	40	40.4	14.0	3.4	-19.75	5.26
<i>Cervus elaphus</i>	Metatarsal	40	42.8	14.8	3.4	-20.64	3.59
<i>Cervus elaphus</i>	Phalanx I	41	40.6	14.0	3.4	-20.66	3.37
<i>Cervus elaphus</i>	Phalanx I	41	41.4	14.2	3.4	-20.69	3.39
<i>Cervus elaphus</i>	Phalanx I	41	35.9	11.6	3.6	-21.11	4.39
<i>Cervus elaphus</i>	Rib	41	42.5	15.3	3.2	-20.68	3.29
<i>Cervus elaphus</i>	Metacarpal	41	43.0	14.8	3.4	-20.91	4.55

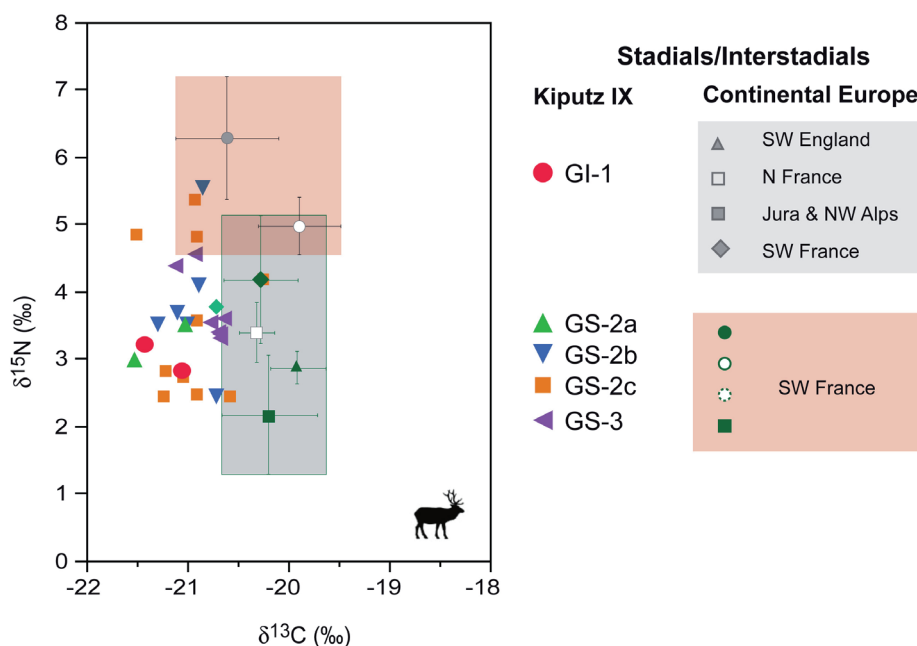


Fig. 4: $\delta^{13}\text{C}_{\text{coll}}$ and $\delta^{15}\text{N}_{\text{coll}}$ values measured on reindeer from Kiputz IX and continental Europe sites (source data in the main text). Vertical and horizontal bars represent standard deviations. GI-2, GS-2, GI-1: climate events.

European values. Only during the Bølling/Allerød period are the isotopic values of Kiputz IX $\delta^{15}\text{N}$ very similar to those in SW France (Iacumin *et al.*, 2000; Drucker *et al.*, 2011). However, there are no significant differences in the carbon isotope values (Fig. 4).

It is well known that herbivores obtain nitrogen from plants and their isotope signatures naturally reflect the plants they consume. In modern ecosystems water availability is the most influential factor affecting plant nitrogen isotope composition, with negative correlations between plant $\delta^{15}\text{N}$ values and precipitation (Austin & Vitousek, 1998; Schulze *et al.*, 1998; Handley *et al.*, 1999; Amundson *et al.*, 2003; Aranibar *et al.*, 2004). $\delta^{15}\text{N}$ values decrease with increasing mean annual precipitation and decreasing mean annual temperature. Therefore, the higher $\delta^{15}\text{N}$ values of Kiputz IX reindeer during the GS-2 stadial suggest a warmer and drier climate condition in the northern Iberian Peninsula than in France and Germany.

6. CONCLUSIONS

The Kiputz IX site has provided the most important ensemble of Late Pleistocene reindeer in the Iberian Peninsula in both the number of remains and their good state of conservation. This sample contains a minimum number of 23 individuals with a clear predominance of males. The best represented age group is old adults followed by prime adults and infants.

There are no metric differences between samples from Level D to Level F. The VSI metric comparison between

the body size of reindeer at Kiputz IX and other European sites indicates that there is no simple relationship between this parameter and spatial or temporal factors.

Variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values show differences between the kinds of plants consumed by red deer, steppe bison and reindeer. These results are consistent with paleoenvironmental conditions attributed to these periods through other proxies. There are also differences between $\delta^{15}\text{N}$ of Kiputz IX reindeer and those of other European sites.

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