

# Subsistence behavior during the Initial Upper Paleolithic in Europe: site use, dietary practice, and carnivore exploitation at Bacho Kiro Cave (Bulgaria)

Article

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3	Europe: Site use, dietary practice and carnivore exploitation at
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#### 22 Abstract

23 The behavioural dynamics underlying the expansion of *Homo sapiens* into Europe remains 24 a crucial topic in human evolution. Due to poor bone preservation, past studies have 25 strongly focused on the Initial Upper Palaeolithic (IUP) stone tool record. Recent 26 excavations and extensive radiocarbon dating at Bacho Kiro Cave (Bulgaria) pushed back 27 the arrival of IUP Homo sapiens into Europe to ca. 45,000 years ago. This site has 28 exceptional bone preservation and we present the study of 7431 faunal remains from 29 across two IUP layers (I and J) and one Middle Palaeolithic layer (K). We identified a shift in 30 site use and occupation intensity through time, marked by increased find density and 31 human modifications in Layer I. Alongside a decrease in carnivore presence and 32 seasonality data demonstrating human presence in all seasons, this indicates a more 33 frequent or prolonged occupation of the site by IUP groups. Contrary, the dietary focus 34 across the IUP and MP layers is similar, centred on the exploitation of species from a range 35 of habitats including wild cattle, bison, deer, horse and caprines. While body parts of large herbivores were selectively transported into the site, the bears remains suggest that these 36 37 animals died in the cave itself. A distinct aspect of the IUP occupation is an increase in 38 carnivore remains with human modifications, including these cave bears but also smaller 39 taxa (e.g., wolf, fox). This can be correlated with their exploitation for pendants, and 40 potentially for skins and furs. At a broader scale we identified similarities in subsistence 41 behaviour across IUP sites in Europe and western Asia. It appears that the first IUP 42 occupations were less intense with find densities and human modifications increasing in

43 succeeding IUP layers. Moreover, the exploitation of small game appears to be limited
44 across IUP sites while carnivore exploitation seems a recurrent strategy.

45 **Keywords**: Bacho Kiro Cave; Initial Upper Palaeolithic; Zooarchaeology; Middle-Upper
46 Palaeolithic transition; *Homo sapiens*; subsistence behaviour

# 47 Introduction

#### 48 The Initial Upper Palaeolithic

49 A key question in human evolution relates to which mechanisms drove the global dispersal 50 of groups of early Homo sapiens out of Africa and the subsequent replacement of local 51 populations of other hominins (Hublin, 2013, 2015; Higham et al., 2014; Fu et al., 2015; 52 Ruebens et al., 2015; Boaretto et al., 2021; Hajdinjak et al., 2021; Lalueza-Fox, 2021). In 53 Europe and western Asia, this dispersal intensified after 50ka. with the emergence of the 54 Initial Upper Palaeolithic (IUP) record. The IUP is defined based on a specific type of blade production that retains elements of Levallois technology but with a volumetric core 55 56 exploitation and Upper Palaeolithic tool types (Kuhn et al., 2009; Kuhn and Zwyns, 2014; 57 Zwyns et al., 2019). A small number of faunal assemblages associated with IUP contexts 58 have been recovered, mainly from caves, with open-air contexts exhibiting poor or no bone 59 preservation [e.g., Bohunician in central Europe; Svoboda and Bar-Yosef (2003); Skrdla 60 (2014); Ruebens et al. (2015)]. At IUP sites with good organic preservation, ornaments and 61 bone tools are also abundant (e.g., Üçağızlı cave in Turkey, Bacho Kiro Cave in Bulgaria, 62 Ksar 'Akil in Lebanon; [Marks (1990); Kuhn et al. (1999); Hublin et al. (2020); Kuhn et al. 63 (2001); Bosch et al. (2015); ;Zwyns et al. (2014); Bosch (2018)]. Overall, our understanding of

64	IUP subsistence practices, carcass exploitation and resource use is still limited, especially
65	for Europe, and requires further investigation and comparison with local Neanderthal
66	subsistence (Kuhn et al., 2009; Bosch et al., 2015; Bosch, 2018).
67	New excavations at Bacho Kiro Cave (Bulgaria) have provided early and substantial
68	evidence of the dispersal of Upper Palaeolithic Homo sapiens into Europe dated around 45
69	ka BP (Fewlass et al., 2020; Hublin et al., 2020). This paper will present in-depth taphonomic
70	and zooarchaeological analyses of the rich faunal assemblages recovered from the Middle
71	and Initial Upper Palaeolithic layers of this cave, providing new and much needed insights
72	into the subsistence strategies and dietary practices of these early groups of IUP Homo
73	sapiens.
74	The site of Bacho Kiro Cave
75	Bacho Kiro Cave is a critical site for discussions relating to the transition from Neanderthal
76	to modern human populations in Europe due to its stratigraphic sequence rich in well-
77	preserved archaeological material (Kozłowski and Ginter, 1982; Tsanova, 2008; Hublin,
78	2015; Ruebens et al., 2015). The cave is at the mouth of a large karstic system located 5km
79	west of the town of Dryanovo, on the northern slope of the Balkan Mountains range (Stara
80	Planina) and about 70km south of the Danube River.
<b>Q</b> 1	
01	Dorothy Garrod (American School of Prehistoric Research) and Rafail Popov (Bulgarian
82	Dorothy Garrod (American School of Prehistoric Research) and Rafail Popov (Bulgarian Academy of Science) conducted one of the first excavations in 1938, though the scope of

84 stratigraphy and context (Garrod et al., 1939; Ginter and Kozlowski, 1982). Subsequent

85 excavations (1971-1975) led by Boleslaw Ginter and Janusz K. Kozlowski provided the most comprehensive record of the site, stratigraphy and archaeology (Kozłowski and Ginter, 86 87 1982). These excavations produced large assemblages of lithics and fauna (Kozłowski and 88 Ginter, 1982), alongside fragmentary human remains that were subsequently lost. The cave 89 is notable for the distinctive lithic assemblages from Layers 11 and 11a consisting of 90 elongated Levallois-like blades, retouched points, end scrapers and splintered pieces 91 (Kozłowski and Ginter, 1982; Tsanova, 2008, 2012) as well as pendants made of animal 92 teeth (Guadelli, 2011). The lithic assemblage from Layers 11 and 11a was originally labelled 93 'Bachokirian,' and interpreted as being transitional between the Middle Palaeolithic (MP) 94 and Upper Palaeolithic (UP; (Tsanova and Bordes, 2003; Tsanova, 2008). The assemblage is 95 now recognized as part of the IUP, representing the earliest occurrence of Late Pleistocene Homo sapiens in Europe (Kuhn and Zwyns, 2014; Fewlass et al., 2020; Hublin et al., 2020). 96 97 Kozłowski and Ginter (1982) described the faunal remains from these excavations in a 98 series of detailed chapters within the final site report. While these provided detailed information about the palaeoenvironmental context and change throughout sequence, 99 100 taphonomic data is limited and it has hindered our understanding of site formation and 101 the role and importance of carnivores and humans in site formation.



103 Figure 1: a) Interior of Bacho Kiro Cave highlighting the location and proximity of the Main Sector 104 and Niche 1 (modified from Fewlass et al., 2020: Supplementary Fig. 1); note the dark color of Layer I 105 within Niche 1. The 1970s excavation is located beneath the concrete floor; b) Site plan and 106 excavation grid at Bacho Kiro Cave (modified from Hublin et al., 2020: Extended Data Fig. 1). Fauna 107 from the squares colored dark red have been analyzed fully while the light red squares indicate that 108 excavation and faunal analysis is ongoing; c) Stratigraphic section from CC8-BB8 (orange line on site 109 plan) illustrating position of Lavers I, J and K in Niche 1 (numbers represent old laver assignments by 110 Kozlowski and Ginter, 1982; letters represent layer assignments from new excavations as detailed in 111 Hublin et al., 2020); d) Frontal view of stratigraphic section from Niche 1 sector showing layer 112 subdivisions; note the distinctive dark color and composition of Layer I (modified from Hublin et al., 113 2020: Extended Data Fig. 1).

114 New excavations were initiated in 2015 led by the National Archaeological Institute with

115 Museum-Bulgarian Academy of Science in Sofia and the Max Planck Institute for

116 Evolutionary Anthropology. Fieldwork focused on two sectors that contained well-

117 preserved sequences: the Main Sector (ca. 3m<sup>2</sup> excavated) and the previously unexcavated

118 Niche 1 (ca. 8m<sup>2</sup> excavated; Figure 1). The recovered archaeological material illustrates that

Layer I from the Main Sector (and its equivalent in Niche 1, N1-I) is consistent with Layer 11

120 and Layer J (and its equivalent in Niche 1, N1-J) is consistent with Layer 11a from Ginter and

121 Kozlowski's excavations (Kozłowski and Ginter, 1982). This is supported by an extensive set

122 of new radiocarbon samples that were dated with exceptional precision (Fewlass et al.,

123 2020). The IUP at Bacho Kiro Cave starts within Layer J (ca. 46,000 years ago), and

124 intensifies within Layer I which is dated between 45,040 and 43,280 cal BP (95.4%

125 probability; <sup>14</sup>C dates recalibrated using IntCal20; Reimer et al. (2020)). The presence of

several directly dated *Homo sapiens* bone fragments in Layer N1-I confirms the modern

127 human association with the IUP record (Hublin et al., 2020). In Niche 1 these IUP layers are

128 underlain by one layer of Middle Palaeolithic (Layer K). The vast majority of archaeological

129 material from these new excavations come from the Niche 1 area where the find density is

also higher (see Figure 1-2). Densities are much lower in Layer K (Table 1), but the lithic
assemblage, consisting mostly of Levallois flakes, is distinct from the overlying Initial Upper
Palaeolithic in terms of technology, typology and raw material usage (Hublin et al., 2020).
Lithic material from Layer K is produced, mainly, on coarser grained igneous rocks, while
the IUP from Layers I and J is manufactured on fine grained imported flint and is often
fragmented, reduced and reused.

136 Table 1: Fauna from Layers I, J and K in Niche 1 and Main Sector.

Layer	Archaeological Unit	Lithic	Bone	nbuckets	Volume (m <sup>3</sup> )	Litres	bone/l	lithic/l
I	IUP	1,701	12,685	100	0.9	900	14.1	1.89
J	IUP	38	1,294	179	1.6	1,611	0.8	0.02
К	MP	81	714	159	1.4	1,431	0.5	0.06

Abbreviations: Lithic = number of lithics >20 mm, Bone = number of bones >20 mm, nbuckets = number of buckets of excavated sediment (a bucket is 9 liters), bone/l = number of bones per liter of excavated sediment, lithic/l = number of lithics per excavated liter of sediment.

137 Importantly, these new excavations have produced a large, well-contextualized faunal

assemblage of individually piece-plotted faunal remains from throughout the stratigraphic

139 sequence (total number of specimens = 18713). Most of these remains (number of

specimens = 16402) were recovered from layers associated with the IUP (Layers I and J) and

141 MP (Layer K; see Table 1-2) and several contact zones. During excavation, due to relatively

142 high water content in the clay portions of the sediment it was often difficult to assign bone

143 material to a specific layer at the interface between Layers I and J or J and K, so these bones

are assigned into layer contacts I/J or J/K (for a detailed breakdown see Supplementary

145 Online Material [SOM] Table S1). . All sediment was collected by 9 litre buckets and wet-

screened on site through 6 and 1.2mm meshes to form two fractions (Hublin et al., 2020).

147 From both fractions all lithic and faunal remains were collected and will form part of a later148 study.

149 Figure 2 visualises the distribution of all piece plotted faunal specimens >20mm (Figure 2a) 150 and the number of bones per litre of excavated sediment (Figure 2b) from Layers I-K within 151 both Niche 1 (squares A to DD) and the Main Sector (squares G-E). This figure illustrates 152 both the large quantity of faunal remains from Niche 1, compared to the Main Sector, and 153 also the high density of remains within Layer I (see Table 1). Indeed, bone per litre of 154 excavated sediment is 17.5 times greater in Layer I compared to Layer J and 28.2 times greater than in Layer K. Micromorphological analyses of Layers I and J show, at times, crude 155 156 bedding of sands and silts, suggesting temporal hiatuses with exposed surfaces being 157 affected by low energy sheet wash (Hublin et al., 2020). While these gaps have been 158 identified in, at least, the top of Layer J and in Layer J, further micromorphological research 159 is needed for the lower deposits of Layer K. Independently, however, sedimentation rates 160 do not seem to be significantly high and the accumulation of these layers most probably 161 relates to several visits to the site, hence to the normal time-average nature of 162 archaeological deposits. Thus, previous analyses have illustrated the link between the IUP 163 deposits (Layers I and J) in the Main Sector and Niche 1 both in terms of sedimentology and 164 chronology (Fewlass et al., 2020; Hublin et al., 2020), so the fauna from these layers in both 165 sectors are combined and analysed together along with Layer K from Niche 1.



166

Figure 2: a) Spatial distribution of piece plotted faunal specimens from Niche 1 and Main Sector subdivided by excavation layer (NSP = number of specimens); b) Number of bone specimens/liter of excavated sediment subdivided by layer. Squares are 1 x 1 meter , and the corresponding excavation numbers for each square can be obtained by joining the y-axis letter and the x-axis number.

# 172 Materials and methods

173 For this study, 7431 faunal remains from the 2015-2018 excavations at Bacho Kiro Cave 174 were investigated (curated at History Museum in Dryanovo). This includes all of the fauna 175 from the excavation squares indicated in dark red on Figure 1 alongside a sample of 176 material from row 8 (light red excavation squares on Figure 1, for which excavation and 177 analyses are ongoing), covering both the Niche 1 and Main sector and the IUP and MP 178 layers. This includes all piece plotted material (bone fragments >20 mm [n = 6,808; 91.6] and morphologically identifiable remains <20 mm [n = 79; 1.1]) and a small portion of the 179 180 piece plotted fauna that fell below the recording cut-off of 20mm (<20mm; n = 544; 7.3).

Sector	Layer	NSP	Analysed	%
	I	133	87	1
Main Sector	I/J	126	108	1
	J	137	98	1
	T	12,558	5,544	75
	I/J	1,392	193	3
Niche 1	J	1,157	678	9
	J/K	185	117	2
	К	714	606	8
Total		16,402	7,431	100

Table 2: Detailed breakdown of total piece plotted faunal material (NSP) excavated between 2015-2018 by sector and layer.

Abbreviations: : NSP = number of specimens.

183 The first section of this paper presents a new zooarchaeological and taphonomic analysis 184 of faunal material recovered from Layers I, J and K (n = 7013; for data on the contact zones 185 I/J and J/K see SOM Table S1). A specially designed database was constructed using the 186 freely available E4 software (https://www.oldstoneage.com/). Faunal material was recorded 187 using a text based zonal system based on previous methodologies (Smith, 2010, 2013, 188 2015) ), where a zone was only recorded if >50% was present. This allowed for the 189 comprehensive quantification and calculation of the number of identifiable specimens 190 (NISP), minimum number of elements (MNE), minimum number of individuals (MNI) and 191 associated indices such as minimum anatomical units (MAU). NISP was calculated as the 192 number of specimens identified to species and element (Grayson, 1984; Lyman, 1994), 193 though if species determination was unclear fragments were recorded to the family level 194 (e.g. Ursidae sp.). MNE was calculated assessing which zone had the most representation of

195 >50% present and this was further combined with side and fusion data for each specific 196 element (Lyman, 1994; Lyman, 2008; Smith, 2010). The MNI was calculated for each specific 197 element (including left and right) and the final MNI value for each taxon chosen by selecting 198 the highest value. MAU values were normalized by dividing MNE values by the frequency of 199 this element within the skeleton. These values were then normed into %MAU by dividing 200 each MAU by the greatest MAU value in the assemblage [Lewis R. Binford (1981);L. R. 201 Binford (1981); ;Lyman (1994); Lyman (2008); Rendu et al. (2019)].In order to further 202 understand specific site formation processes at Bacho Kiro Cave, zooarchaeological data, 203 such as species and body part identification, were combined with a wide variety of 204 recorded taphonomic attributes.

205 Behrensmeyer's (1978) scheme was used to record the weathering stage of all bones and 206 provides a qualitative scale for understanding the exposure (short/long duration) of faunal 207 material prior to burial. Other biotic and abiotic modification agents recorded included root 208 etching and abrasion (expressed as a percentage of bone surface affected). The schemes 209 range from 0% (no visible modification observed), thorough to 100% (the whole bone 210 surface covered; Smith (2010); Smith (2015)]. Burnt remains were recorded using the 211 specific colour and surface changes as identified by Stiner (1995). Recording the presence, 212 intensity and distribution of these taphonomic agents across the site and throughout the 213 layers at Bacho Kiro Cave provides a detailed framework to contextualize carnivore and 214 human behaviour and site use.

215 All faunal material was studied under magnification (20x) using an oblique light source, 216 which allowed for a detailed analysis and recording of bone surface conditions and 217 modifications. The identification and distinction of human modifications (skinning, cut 218 marks, deliberate marrow fractures) from other non-anthropogenic processes (trampling, 219 carnivores) has generated considerable debate (Bunn, 1981; Gifford-Gonzalez, 1989a, 220 1989b, 1991; Fisher, 1995; Domínguez-Rodrigo, 1999; Galán et al., 2009). More recent 221 approaches have attempted to provide quantitative data through the application of high 222 resolution microscopy and the application of machine learning protocols (Cifuentes-223 Alcobendas and Domínguez-Rodrigo, 2019; Moclán et al., 2019; Pizarro-Monzo and 224 Domínguez-Rodrigo, 2020). Despite much discussion about the criteria and methods for 225 identifying and distinguishing cut marks on fauna (Domínguez-Rodrigo et al., 2017, 2019) 226 the use of low-powered approaches has proven effective for differentiating human from 227 natural bone surface modifications, especially within Middle and Upper Palaeolithic 228 contexts (Blumenschine et al., 1996; Smith, 2015). 229 Specific carnivore modifications recorded included tooth pits, scratches, crenellation and 230 damage from digestion. Human modifications included those related to butchery and 231 carcass processing such as cut marks, skinning marks, deliberate marrow 232 fractures(identification of impact point and/or percussion notch; see (Lyman, 1994; Fisher, 233 1995), alongside other secondary uses of organic material for informal bone tools

234 ('retoucher'), formal bone tools (*lissoirs*, awls etc.) and ornaments. To understand fully the

behaviour of *Homo sapiens* at Bacho Kiro Cave, these new faunal analyses are further
contextualized with data from sedimentology, micromorphology and lithic data.

237 To understand whether human groups occupied the site during specific seasons and 238 focused on specific age classes, and if this varied across species, required the recording of 239 different age and seasonality indicators from various species using both cranial (mainly 240 teeth eruption and wear) and post-cranial bone fusion data (Reitz et al., 1999; Weinstock, 241 2009). Herbivore age was calculated using various methods depending on tooth type. For 242 species with low-crowned teeth such as *Bos/Bison* and cervids the quadratic crown height 243 measure (QCHM) was applied (Steele and Weaver, 2002, 2012, 2012; Steele, 2004, 2004) 244 along with established wear stages (Grant, 1982). For equids, crown height was measured 245 on juveniles and adults and calculated using established equations (Fernandez and 246 Legendre, 2003; Bignon, 2006) and tooth wear stages documented (Levine, 1982). Bear 247 dentition was scored according to the three stage scheme devised by Stiner (1998) and 248 used extensively at numerous Pleistocene sites (Kindler, 2012; Abrams et al., 2014; 249 Romandini et al., 2018). All analyses were undertaken in R v. 4.0.2 (R Core Team, 2020) 250 using RStudio v. 1.4.1103 (RStudio Team, 2021), mainly by using the 'tidyverse' packages v. 251 1.3.1 (Wickham et al., 2019) and with statistics performed using the 'rstatix' package v. 0.7.0 252 (Kassambara, 2020). Figures were produced with the 'ggplot2' package v. 3.3.3 (Wickham, 253 2016) and the 'ggtern' package for ternary graphs (Hamilton and Ferry, 2018) with the 254 exception of the maps that were produced using QGIS v. 3.18.3 (QGIS Development Team, 255 2009) and the manuscript was written in rmarkdown (v. 2.6) (Xie et al., 2018, 2020; Allaire et

- al., 2021). The raw data and RMarkdown scripts to reproduce the article and its analyses
- along with the SOM are available at https://osf.io/62pbr/.

### 258 **Results**

- 259 Species representation and variation
- 260 Species representation
- 261 The species representation of the new collection is similar to that originally identified by
- 262 Kozłowski and Ginter (1982), though the proportions vary (see Figure 3). Importantly, the
- identified macro faunal species are consistent between both the Niche 1 and Main Sector,
- 264 which support the stratigraphic correspondence of layers between these two excavation
- areas (also see discussion and analysis in Hublin et al. (2020)).



266

Figure 3: Percentage of identifiable specimens (%NISP) per taxon by layer; the total percentage of identifiable remains by layer is indicated in the panel title.

269 Within all layers species identification rates for bone fragments is, relatively, high (I = 19.9%

270 ;J = 31.6%; K = 26.1%) especially for sites of this age range in Europe (Morin, 2008, 2012;

271 Morin et al., 2019; Rendu et al., 2019).

272	The most frequently identified species include <i>Bos/Bison</i> (I = %; J = %; K = %), cave bear
273	( <i>Ursus spelaeus</i> ; I = 16.6%; J = 45.4%; K = 20.1% ) and red deer ( <i>Cervus elaphus</i> ; I = 11.9%; J =
274	1.7%; K = 3.2%; see Figure 3), though other carnivore (I = 4.6%; J = 8.8%; K = 7.1%) and
275	herbivore (I = 18.2%; J = 9.6%; K = 27.3%) species are represented. Carnivores include cave
276	lion (Panthera leo spelaea), leopard (Panthera pardus), cave hyaena (Crocuta crocuta spelaea),
277	wolf ( <i>Canis lupus</i> ), red fox ( <i>Vulpes vulpes</i> ), brown bear ( <i>Ursus arctos</i> ) along with large to
278	medium sized herbivore taxa (horse [ <i>Equus ferus</i> ], European ass [ <i>Equus hydruntinus</i> ], giant
279	deer [ <i>Megaloceros giganteus</i> ], ibex [ <i>Capra ibex</i> ], chamois [ <i>Rupicapra rupicapra</i> ]). Megafaunal
280	species including mammoth ( <i>Mammuthus primigenius</i> ; K = 1) and rhino ( <i>Stephanorhinus</i>
281	<i>hemiotechus</i> ; I = 0.2%; J = 0.8%), are represented by very few specimens throughout all
282	layers (see SOM Table S2). Overall, the fauna recovered throughout Layers K-I is
283	characteristic of Marine Isotope Stage 3 (MIS 3) throughout south-east Europe, with a mix
284	of cold and more temperate adapted species that have a broad range of climatic/ecological
285	tolerances [Guérin (1982); Hublin et al. (2020); Made (2018); Figure 3).
286	This variation in species representation is also evident when examining the examining the
287	examining the MNE and MNI values (see SOM Table S3). While these layers include a range
288	of species (see Figure 3) most of these are represented by a low number of elements and
289	individuals (), especially for carnivores (excluding Ursidae; MNI: Layer I = 8; Layer J = 8; Layer
290	K = 6), <i>Leporidae</i> sp. (MNI: Layer I = 1; Layer J = 1), birds ( <i>Aquila chrysaetos</i> ; MNI: Layer I =1,
291	Aves sp. MNI: Layer I =1) and fish (Osteichthyes sp. MNI: Layer I = 1; see SOM Table S3). The
292	exception for carnivores are the Ursidae specimens, which includes Ursus arctos and Ursus

sp., but is dominated by cave bear (*Ursus spelaeus*), and represented by a relatively high
number of elements and individuals (I: MNE =24; MNI = 11; J: MNE = 17; MNI = 10; K: MNE =
4; MNI = 3)

Within Layer I, herbivore species are most frequent and are, generally, represented by
higher numbers of elements and individuals; for example, Bos/Bison, which includes *Bos primigenius*, *Bison priscus* and *Bos/Bison* sp.(MNE = 25; MNI = 12), *Cervus elaphus* which
includes both *Cervus elaphus* and *Cervidae* sp. (MNE =21; MNI = 9) and Equidae sp. (MNE

300 =10; MNI = 7), which includes *Equus ferus*, *Equus hydruntinus* and *Equidae* sp...

# 301 Species variation

302 To investigate further whether there is a significant change in species representation 303 between layers, we assessed the NISP values for identifiable species from Layers K-I with a 304 chi-square test. In order to observe changes in the representation, the most common 305 species were grouped into broader categories of: Bos/Bison (Bos primigenius, Bison priscus 306 and Bos/Bison sp.), Ursidae (Ursus spelaeus, Ursus arctos and Ursidae sp.) and Cervus elaphus 307 (*Cervus elaphus* and Cervidae sp.). The remaining identifiable species were grouped into 308 broader categories of either herbivore or carnivore, irrespective of body size. The null 309 hypothesis states that the variables of layer and taxon are independent of each other.

310 Table 3: Number of identified specimens (NISP) by layer and maje	or taxon
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Taxon	NISP I	AR I	NISP J	AR J	NISP K
Bos/Bison	289	6	23	-4.3	40
carnivore	50	-3	21	0.6	11
Cervidae	285	6	18	-2.2	22

Taxon	NISP I	AR I	NISP J	AR J	NISP K
herbivore	199	3	23	-4.6	42
Ursidae	268	-12	154	7.6	39
chi-square		167		66.9	

Abbreviations: AR = adjusted residuals and composite chi-square values. Significant values in bold.

311 The change in the proportion of these NISP values was tested through the calculation of 312 composite chi-square values and adjusted residuals (Table 3). These residuals refer to the 313 layer to the left of the residuals column, respectively, and should be read as standard 314 normal deviates (Grayson and Delpech, 2003; VanPool and Leonard, 2011). Absolute values 315 over 1.96 indicate a significant change between layers (these are highlighted in bold in 316 Table 3). Table 3 illustrates changes in the relative abundance of species within Layers K-I. 317 This is driven by a significant decrease in herbivore species between K and J ( $\chi^2$  = 66.9, p = 318 <.001). Likewise the abundance of all species within Layer I differs significantly from those 319 within Layer J ( $\chi^2$  = 167, p = <.001). Within Layer I this results from a significant increase in 320 all herbivore species relative to carnivore (and especially Ursidae remains) compared to the 321 underlying Layer J. Thus, taxon is dependent on layer: there is an increase in proportion of 322 herbivore and decrease in carnivore taxa within Layer I compared to the underlying layers 323 (see Figure 3).

### 324 Bone fragmentation

Bone fragmentation, as expressed by the mean bone length, which was measured across
the longest axis of each bone specimen, is similar within Layers I (41.5 ± 20.8mm), J (43.3 ±
23.6mm) and K (43.4 ± 25.3mm). Overall, the distribution of bone fragment lengths appears

- 328 similar across layers, with a large proportion of specimens <100mm, and few outliers with
- 329 larger dimensions. This can be seen in Figure 4 where the mean for each layer is







Figure 4: Figure 4. a) Violin plot of the length of piece plotted bone fragments in main layers from Bacho Kiro Cave; b) Boxplot of the length of piece plotted bone fragments for major taxa from main layers (BB = Bos/Bison, Ce = Cervus elaphus, Us = Ursus spelaeus). Black line indicates median and diamonds indicates mean; box represents the interquartile range; box base is 25th percentile while box top represents the 75th percentile with potential outliers plotted. Y-axis on both figures is at the same scale.

338 A t-test illustrates no significant difference between the mean bone lengths between layers

339 (Layer I versus Layer J: t = -1.7, df =628, p = 0.3; Layer I versus K: t = -1.6, df =557.8, p = 0.3;

340 Layer J versus Layer K: t = -0.1, df =1009, p = 1; Figure 4a.).

341 Similarly, a t-test of mean bone length for the three major species (Ursus spelaeus, Bos/Bison

- 342 sp. and Cervus elaphus) from Layer I (sample sizes in Layers J and K were too small)
- 343 illustrates no significant difference in the overall fragment length distributions (Bos/Bison

344 versus Cervus elaphus: t = 1.1, df =254.6, p = 0.5; Bos/Bison versus Ursus spelaeus: t = 2.2, df

345 =168.7, p = 0.1; *Cervus elaphus* versus *Ursus spelaeus*: t = 1.2, df =201.6, p = 0.5). Therefore,

bone fragmentation does not appear to explain the observed pattern in species

347 representation within Layers K-I (see SOM Tables S2-S3).

Taken together, these statistics illustrate variation between the Middle Palaeolithic Layer K at the base of the sequence and the overlying IUP Layers I and J in terms of changes in the relative proportions of carnivore and herbivore taxa. Therefore, it is important to test whether such changes in species representation are related to differences in depositional history within Layers K-I as a result of either natural, carnivore or human action or a combination of all of these.

354 Species and bone element survival

To understand specific deposit formation processes and the taphonomic history of the 355 356 Bacho Kiro Cave fauna, especially for Layers I, J and K, requires a detailed assessment of 357 skeletal element representation for the three major species. We merged again the 358 identifiable remains from these species into general categories of Ursidae, Cervidae and 359 *Bos/Bison*. Similarly, identifiable element were merged into more general body portions 360 (cranial: antler, horncore, cranium, mandible, teeth; axial: vertebrae, pelvis; forelimb: 361 humerus, radius, ulna; hindlimb: femur, tibia; foot: carpals, metacarpal, tarsals, metatarsal, 362 phalanges) to provide a broader overview of patterns of representation (modified from 363 Stiner, 1991a, 1991b).



364

Figure 5: Percentage of identifiable specimens (%NISP) for combined body part portions across three
major taxon from Layer I; cranial: antler, horncore, cranium, mandible, teeth; axial: vertebrae, pelvis;
forelimb: humerus, radius, ulna; hindlimb: femur, tibia; foot: carpals, metacarpal, tarsals, metatarsal,
phalanges. Modified from Stiner (1991a, 1991b). BB = *Bos/Bison*; C = Cervidae; U = Ursidae.

369 Only Layer I contain sufficient numbers of specimens identifiable to taxon and element

portion to discuss patterns of body part representation (Figure 5) . For Layer I, data

371 illustrate differences in the representation of different body parts with both Bos/Bison and

372 cervids showing higher proportions of limbs (*Bos/Bison* forelimb = % and hindlimb = %;

373 Cervidae forelimb = % and hindlimb = %), while the ursid remains have a higher percentage

of cranial elements (%) compared to limb bones (forelimb = %, hindlimb = %). We ran

375 separate chi-square tests to see whether such differences between taxa and body portion

376 were statistically significant. There is no significant difference between the element

representation of *Bos/Bison* and cervids within Layer I ( $\chi^2$  [df = 4, n = 528] = 8.5, p = 0.1). In contrast, comparing *Bos/Bison* and cervids with ursids illustrates significant difference between the element representation within Layer I (*Bos/Bison* vs. Ursidae:  $\chi^2$  [df = 4, n = 455] = 79.8, p = <.001; Cervidae vs. Ursidae:  $\chi^2$  [df = 4, n = 463] = 62.7, p = <.001). Such variation in element representation could represent different site formation histories, perhaps with the *Bos/Bison* and cervid remains being transported into the cave while the ursid remains indicate that the bears died in the cave itself.

384 This pattern is confirmed when looking at the minimum anatomical units (MAU) for these taxa from Layer I (see SOM Table S6). The skeletal profiles for Bos/Bison show an under-385 386 representation of cranial and axial parts (NISP = 29; MAU rib =5.4), with a similar pattern also identified for cervids (NISP = 23; MAU rib =2.1). Skeletal profiles from these species 387 388 highlight a higher proportion of bone elements from forelimb (*Bos/Bison* NISP = 89; MAU = 389 22) and hindlimb (NISP = 87; MAU = 18.5). While ursids have high values for some long 390 bone elements such as femur and radius, it is notable that their skeletal profile is 391 dominated by cranial (especially teeth) and also foot elements (cranial NISP = 77; MAU 392 cranial =29; foot NISP = 35; MAU foot =5.3).

393 Further, plotting relative bone density values (Kreutzer, 1992; Lyman, 1994; Lam et al.,

1998, 1999, 2003; Lam and Pearson, 2005) for the most abundant herbivore species within

395 Layers K-I (Bos/Bison, cervids and equids) does not illustrate a specific predominance of

396 skeletal remains, though long bone remains appear common (see Figure 6).



397

398 Figure 6: Plots of the number of identifiable specimens (NISP) against relative bone density for three 399 major herbivore species from Bacho Kiro Cave Layers I-K (a = Bos/Bison; b = Cervidae, c = Equidae) 400 Note that Layer I is absent because no elements were present to correlate with bone density. Bone 401 density values for Bos/Bison are based on volume density (VD) measures from Kreutzer (1992), and 402 Equidae and Cervidae from BMD1 mean from Lam et al. (1999). Abbreviations on plots relate to specific scan zones on elements: AT = atlas; CA = calcaneus; CE = cervical vertebra; FE = femur; HU = 403 404 humerus; IS = Ischium; LU = lumbar vertebra; MC = metacarpal; MR = metatarsal; RA = radius; TH = 405 thoracic vertebra; TI = Tibia; UL = ulna.

406 Figure 6 illustrates element NISP plotted against relative bone density for *Bos/Bison*, cervids

407 and equids. In Layer I there is no significant relationship between relative bone density and

- 408 preservation. In Layers J and K there are some positive associations with cervids and
- 409 equids, respectively, suggesting selective preservation of denser skeletal portions, but
- 410 smaller samples sizes warrant caution in this interpretation. Therefore, in Layer I it appears

- 411 that there has been neither significant selective destruction of weaker skeletal portions nor
- 412 an over representation of the densest elements. Taken together with skeletal profile and
- 413 MAU data this suggests that there was a biased transport of skeletal elements from
- 414 herbivore species into the cave during the accumulation of Layer I with this transport not
- 415 including cranial, axial and, to a lesser extent, foot elements of those species.
- 416 Bone surface visibility and weathering
- 417 Overall, bones from Layers K-I show low proportions of both sub-aerial weathering (stages
- 418 0-2; Behrensmeyer (1978)] and abrasion (0-50%), which translates into high bone surface
- 419 visibility (>90%; Figure 7 and SOM Tables S7-S9 for detailed data breakdown).



420

Figure 7: Bone surface preservation and readability. a) Percentage of specimens displaying low weathering (stage 0–2) or high weathering (3–5) based on Behrensmeyer (1978); b) Percentage of specimens exhibiting low (0–50%) and high surface abrasion (50–100%); c) Percentage of specimens with low (0–50%) and high (50–100%) surface readability.

- 425 The extraordinary bone preservation at Bacho Kiro Cave has been recognized in the high
- 426 collagen yields extracted for radiocarbon dating and ZooMS.
- 427 *Carnivore and human bone surface modifications*
- 428 The excellent preservation of the bone surfaces provides ample opportunity to identify and
- 429 classify bone surface modifications from both carnivore and human action (see Figure 8;
- 430 SOM Table S10).



431

Figure 8: Percentage of specimens (%NSP) with carnivore or human modifications within Layers I-K
from Bacho Kiro Cave; this excludes burnt specimens (see SOM Tables S10-S15 for detailed
breakdown of bone surface modifications including burnt remains).

- 435 Overall, Figure 8 illustrates a change in the proportion of bone surface modifications
- 436 between the MP Layer K (carnivore modification = 11.4%; human modification = 7.4%) and
- 437 the IUP Layers (J carnivore modification = 7.9%; J human modification = 7.9%; I carnivore
- 438 modification = 1.3%; I human modification = 12.6%), showing a clear temporal trend of a
- 439 decrease in carnivore modification and an increase in human modification. We tested the
- 440 change in this proportion between layers by calculating the composite chi-square values
- 441 and adjusted residuals (see Table 4). The null hypothesis states that modification types are
- 442 independent of layers.
- 443 Table 4: Number of specimens (NSP) by layer with carnivore or human modifications.

Modification	NSP I	AR I	NSP J	AR J	NSP K
carnivore	76	-12	61	-2	69
human	709	12	61	2	45
chi-square		131		2	

Modification	NSP I	AR I	NSP J	AR J	NSP K

Abbreviations: AR = adjusted residuals and composite chi-square values. Significant values in bold.

444	There is no significant difference in %NSP of bones with carnivore and those with human
445	modifications between Layers K and J ( $\chi^2$ = 2.2, p = 0.1) and thus the null hypothesis cannot
446	be rejected (see Table 4). In contrast there is a strong relationship in the proportion of
447	different modifications between Layers J and I ( $\chi^2$ = 130.7, p = <.001; see Table 4). The data
448	for Layers I and J indicate that modification type is dependent upon layer. The main driving
449	factor for this pattern appears to be the large increase in human modifications on bones of
450	Layer I, which is consistent with geoarchaeological and micromorphological data that
451	illustrates increased anthropogenic input in the formation of this deposit (Hublin et al.,
452	2020) and also with the increase in density of lithic material (see Table 1). We also ran chi-
453	square tests to assess whether different modification types (carnivore, human) illustrate
454	significant differences between body size class and across the different layers. All test
455	results were not significant (at 0.05 level). Overall, the large increase in human
456	modifications within Layer I is statistically significant, but there is no relation to how these
457	modifications are distributed across various species body size classes or between layers.
458	Carnivore bone surface modifications
459	Carnivore modifications are recorded in very small quantities, compared to human
460	modifications, and distributed across a variety of taxa including common species such as
461	<i>Bos/Bison</i> and cave bear.

Layer	NSP	%gast	%scratch	%scallop	%tp
I	5,631	0.8	0.1	0.2	0.5
J	776	7.1	0.3	0.6	0.8
К	606	11.1		0.7	0.5

Table 5: Percentage total number of specimens (%NSP) with different carnivore modifications in Layers I-K.

Abbreviations: %gast = percentage of bones with gastric etching; %scratch = percentage of bones with tooth scratch; %scallop = percentage of bones with tooth scalloping; %tp = percentage of bones with tooth pit.

Table 5 illustrates that Layers J and K have the highest proportion of bones with recorded 464 465 carnivore modifications, and the most common modification recorded is digested and acid 466 etched bone (Layer K = 11.1%; Layer J = 7.1%). The higher proportions of carnivore 467 modifications in these layers combined with evidence for coprolites in the 468 micromorphology thin sections (Hublin et al., 2020), and a lower incidence of human 469 modifications, suggests a more substantial role for carnivores in bone accumulation and 470 modification (Figure 9 and SOM Tables S8-S9). The type and frequency of modifications, 471 especially gastric etched bone, suggests activities of cave hyaena though other small 472 carnivore taxa cannot be ruled out. However, the low incidence of carnivore modifications 473 within Layer I, and especially the dramatic reduction in digested bone, suggests a more 474 minimal role for carnivores in the formation of this faunal record. The predominance of human action in the formation of Layer I and upper Layer J is illustrated, further, by the low 475 476 incidence of carnivore and human modifications on the same specimen (Layer I = 9; Layer J 477 =3; Layer K = 3). Bacho Kiro Cave offered a safe location for carnivore species to transport 478 and consume carcasses during periods when the site was unoccupied by humans.

- 479 However, such opportunities appear to have been more infrequent during the IUP
- 480 compared to the MP.



Figure 9: Examples of carnivore bone surface modifications; a) *Ursus spelaeus* scapula (BB7-1384, I/J) with extensive gnawing and crenellation around glenoid and scapula spine; b) Unknown mammal bone fragment (BB8-1934, I/J) with extensive surface smoothing through carnivore digestion; c) Unknown mammal bone (BB7-1977, Layer K) with extensive surface damage caused by carnivore digestion; d) *Ursus spelaeus* femur (AA7-1214, Layer I) with carnivore gnawing and crenelation

- 487 Human bone surface modifications
- 488 The change in proportions of human modifications within the MP-IUP layers at Bacho Kiro
- 489 Cave is statistically significant. Table 6 shows the numbers and proportions of different
- 490 types of bone surface modifications by humans across the three layers. Layer I contains the

491	highest quantity of modifications for each category and the highest proportion of total
492	modifications (see SOM Table S12). Cut marks make up the largest quantity of
493	modifications in most layers, comprising of between 2-8% of bone fragments with the
494	highest proportion within Layer I. Within Layers J and K the frequency of bones with cut
495	and scrape marks is lower compared to Layer I, while there is a higher proportion of bones
496	that exhibit deliberate fractures related to marrow exploitation. Combined with higher
497	levels of carnivore presence (Figure 8) it seems that human groups were using the cave
498	more intermittently and over shorter periods of time.

Table 6: Number of specimens (NSP) and percentage of specimens with different human modifications in Layers I-K.

Layer	NSP	%cm	%scrape	%marrow	%burn
I	5,631	8	2	4	0.7
J	776	3	1	4	0.4
К	606	2	1	5	0.5

Abbreviations: %cm = percentage of bones with cut marks; %scrape = percentage of bones with scraping marks; %marrow = percentage of bones showing marrow extraction (includes impact points and percussion notches); %burn = percentage of bones showing traces of burning.

Layer I is again distinct in terms of the quantity and variation of different modifications but also in the increase in proportion of modifications across both carnivore and herbivore taxa, across all body size classes, but especially an increased focus on smaller carnivores and herbivores (see Figure 10 and 11; SOM Table S13). There also appears to be variation in the distribution of different modification types across body size classes for both herbivores and carnivores; for example, higher proportions of marrow fractured bones in

507 large compared to small herbivore taxa with medium sized animals having a value between

- 508 the two. Additionally, within Layer I the proportion of human bone surface modifications
- 509 increases across all carnivore body size classes (including wolf, wolverine, cave hyaena,
- 510 cave bear).







f 20 mm



h









i

512 Figure 10: Examples of human bone surface modifications; a) Rupicapra rupicapra radius (A7-773, 513 Layer I) with disarticulation marks (white arrows) overlain by carnivore tooth pit (black arrow); b) Bos 514 primigenius proximal epiphysis of second phalanx (CC7-2120, Layer I) with disarticulation marks; c) Ursus spelaeus ulna fragment (BB7-1190, Layer I) with filleting and cut marks overlain by retouching 515 516 damage; d) Ursus spelaeus phalanx (BB7-458, Layer I) with skinning and disarticulation marks; e) 517 Mammal long bone fragment (BB8-283, Layer I) with two separate episodes of use as a retoucher; f) 518 Ursus spelaues phalanx (AA7-2043, Laver I) with skinning and disarticulation marks; g) Carnivore rib 519 fragment (CC8-1564, Layer I) with cut and disarticulation marks; h) Crocuta crocuta spelaea phalanx 520 (BB7-1062, Layer I) with disarticulation marks; i) Aquila chrysaetos talon (BB7-721, Layer I) with cut 521 mark suggesting disarticulation/removal of talon (compare with figures in Romandini et al. (2014) 522 and Radovčić et al. (2015)); j) Ursus spelaeus phalanx (BB7-588, Layer I) with cut marks suggesting 523 claw removal.

524 When comparing the distribution of human modifications across the major species for

525 Layer I the emphasis on the limb bone elements for *Bos/Bison* and cervids is evident with

526 high proportions of all three types of modification (scrape, cut and marrow fractures;

527 Figure 12), supporting the selective transport of limb bone elements to the site and

528 subsequent processing. *Ursidae* remains show a similar level of processing of limb bones

529 but also increased modifications on cranium and foot portions, indicative of skinning and

530 first stages of fur removal (Münzel and Conard, 2004; Kindler, 2012; Romandini et al., 2014).

531 This could represent the direct procurement of such taxa as raw material for bone tools

and personal ornaments (see Hublin et al. (2020), Fig. 3) but also potentially for fur (see

533 Figure 11). Further modifications on small-medium sized carnivores (for example Gulo gulo,

534 *Canis lupus, Crocuta spelaea*; modified from Morin (2012) are more limited but again

535 distributed across cranium, limbs and foot elements, which suggests a more sporadic

targeting of such species for fur. Nevertheless, Layer I illustrates clearly an increased and

537 more systematic focus on carnivore species, relative to herbivores, which is distinct from

538 the underlying Layers.





540 Figure 11: Bone surface modifications across carnivore (carn) and herbivore (herb) grouped by body 541 size class; carnivores: small: wolf (Canis lupus), fox (Vulpes vulpes), dhole (Cuon alpinus); medium: 542 hyaena (Crocuta crocuta spelaea); large: cave lion (Panthera leo spelaea), leopard (Panthera pardus), 543 bear (Ursus spelaeus, Ursus arctos); herbivores: small: roe deer (Capreolus capreolus), goat (Caprinae 544 sp.), fallow deer (Dama dama), ibex (Capra ibex), pig (Sus scrofa), ungulate small, ungulate small/med; 545 medium: reindeer (Rangifer tarandus), wild ass (Equus hydruntinus), horse (Equus ferus), red deer 546 (Cervus elaphus), Cervidae sp., ungulate med/large; large: mammoth (Mammuthus primigenius), rhino 547 (Stephanorhinus hemeiotechus), giant deer (Megaloceros giganteus), Bos/Bison (Bison priscus, Bos 548 primigenius), ungulate large. Size classes are modified from Morin (2012). Burning data are not 549 included.

550 An interesting feature of the faunal assemblage from Bacho Kiro Cave is the low proportion

- of bone remains exhibiting evidence for being burnt (total remains from all layers=1.5%;
- see Table 6; SOM Tables S14-S15). The majority of burnt remains were identified from
- 553 Layer I (0.7%) and this contrasts within comparatively high figures of burned lithics (Layer I=
- 13.3%; Layer J= 0%; Layer K= 2.6%). In particular, this low quantity of burnt faunal remains
- appears at odds with the micromorphological data, which suggests that the composition of
- 556 Layer I, and especially the dark colour, is a direct result of burnt material, with common
- 557 charcoal fragments (Hublin et al., 2020). Further analyses of the smaller screened fraction
- is ongoing and will assess the destruction, fragmentation and overall intensity of burning
- 559 within the MP-UP sequence, especially from the IUP layers.



# 560

Figure 12: Percentage of specimens with human bone surface modifications across major taxa from Layer I at Bacho Kiro Cave separated by body portion; cranial: antler, horncore, cranium, mandible, teeth; axial: vertebrae, pelvis; forelimb: humerus, radius, ulna; hindlimb: femur, tibia; foot: carpals, metacarpal, tarsals, metatarsal, phalanges. Modified from Stiner, 1991a; 1991b. BB = *Bos/Bison*; C = Cervidae; U = Ursidae.

566 Alongside human butchery and processing modifications there is, potentially, direct

567 evidence for hunting in the form of possible projectile impact marks (PIMs) from both

568 Layers I and K (Fig. Figure 13). These two specimens, both large ungulates, exhibit damage

- 569 consistent with projectile impact including notch formation with bevelling on the rib margin
- 570 (BB8-1061) and a bending fracture on another rib (BB7-1870; Smith et al. (2020); O'Driscoll
- and Thompson (2014); lovita et al. (2014); Rots and Plisson (2014); Smith (2003); Gaudzinski-

- 572 Windheuser et al. (2018)]. Further study of these modifications is required, as well as
- 573 correlation with ongoing lithic usewear studies, to be able to fully interpret these marks.



# 574

575 Figure 13: Potential projectile impact marks (PIMs) on ungulate rib fragments; a) BB8-1061 (N1-I) 576 exhibits a notch on the rib margin and bevelling (see expanded photo); b) BB7-1870 (N1-K) exhibits a 577 bending fracture and impact point illustrated by white arrow.

- 578 Finally, the faunal assemblage from Layers I-K illustrates the use of a range of animal
- 579 carcasses as raw material both for bone tools (*n* = 92; this includes bone retouchers) and
- 580 personal ornaments (*n* = 29). These were recovered across the site from all the squares
- 581 excavated in both the Niche 1 and Main Sector. Informal bone tool types, such as
- retouchers (*n* = 48), are found throughout Layers K-I. Contrary, formal objects (*n* = 19; 0.3%)
- are only identified within the IUP occupations of Layers I and J and include awls and *lissoirs*

- 584 (smoothers). Animal teeth pendants and pendant fragments (*n* = 27) were likewise
- identified only within the IUP Layers and are produced mainly on cave bear teeth, along
- 586 with wolf and a few herbivore taxa (Hublin et al., 2020). Ongoing work will characterize and
- 587 contextualize the nature and manufacture of these objects against the broader
- 588 background of the MP-UP transition in Europe (Martisius et al., *in preparation*; NEWCOMER
- and WATSON (1984); Newcomer (1974); Bosch et al. (2015); Kuhn et al. (2009); Soressi et al.
- 590 (2013); Gaudzinski (1999)).
- 591 Mortality profiles, site use and seasonality
- 592 Bone fusion
- 593 Overall, the faunal assemblage from Layers K-I produced 65 unfused bone elements
- representing a small proportion of the total (0.9%) and a limited number of these were
- assigned securely to both taxa and element (n = 12; Table 7).

Layer	Species	Element	n		FFD	LFD	SFFD	SLFD
I	Bos primigenius	Metatarsal-Distal		1	24	36		
I	Bos primigenius	Phalanx 2-Distal		1	18	18	Autumn	Autumn
I	Bos primigenius	Phalanx 2-Proximal		1	18	24	Autumn	Spring
I	Capra caucasica	Vertebra-Thoracic-Centrum		1	48	60		
I	Cervidae sp.	Metatarsal-Proximal		1	0	0	Spring	Spring
I	Cervidae sp.	Phalanx 2-Proximal		1	11	17	Spring	Autumn
I	Cervidae sp.	Radius-Proximal		1	5	8	Autumn	Winter
I	Cervus elaphus	Axis-Centrum		1	35	42	Spring	Autumn
I	Cervus elaphus	Humerus-Distal		1	12	20	Spring	Autumn

Table 7: Bone elements from different species at Bacho Kiro Cave with first fusion date (FFD) and last
 fusion date (LFD) in months and season of FFD and LFD (SFFD, SLFD)

Layer	Species	Element	n		FFD	LFD	SFFD	SLFD
I	Equus ferus	Phalanx 2-Proximal		1	9	12	Winter	Spring
I/J	Cervidae sp.	Humerus-Proximal		1	42	42		
I/J	Ursus spelaeus	Phalanx 2-Distal		1	24	36		

Fusion data based on Reitz et al. (1999) and Weinstock (2009).

598 The unfused proximal metatarsal from a cervid, which is normally fully fused at birth, 599 suggests that this was a foetal individual. At least four of the elements identified have a 600 first fusion date (FFD) around 3 years (36 months) suggesting these individuals were, at 601 least dentally, prime adult and suggesting this individual died during the spring season. 602 Furthermore, additional elements (n = 4) of individuals less than 12 month old suggest a 603 season of death during spring/summer and winter/autumn, assuming an early May 604 birthing season. Overall, the available post-cranial fusion data suggests a focus on prime-605 aged animals, at least for herbivore species, and the use of the cave by IUP groups during 606 all seasons.

# 607 Dental remains

Dental remains have been identified for a variety of species though ursid remains are most common throughout all layers. Ursid teeth were grouped to combine teeth from cave bear, brown bear and Ursidae sp. providing a larger sample for analysis. Bears have an unusual dental development and eruption alongside a different season of birth (winter, January) compared to other carnivores (hyaena and canids) and ungulates (generally spring time late May; Discamps and Costamagno (2015); Stiner (1990)]. Much of the information on ageing bear remains from teeth comes from modern brown bear (Stiner, 1990; Stiner, 615 1994, 1998). All bears are born during hibernation and are toothless, developing the full 616 deciduous dentition by the third month with the M1 usually by the fifth month. Bears 617 generally have all permanent dentition erupted by the end of the first year with the 618 eruption of the permanent canines starting during the second year and completion by the 619 end of the third year of life. Knowing the specific timing and eruption of deciduous and 620 permanent dentition allows for the development of a tooth eruption wear scheme that 621 includes nine stages, grouped into three age categories (Juvenile [I-III], Prime [IV-VII], Old 622 [VIII-IX]; Kindler (2012); Stiner (1994); Stiner (1998)]. While the scheme does not provide an 623 estimate for the age at death it provides the ability for inter and intra-site comparisons at 624 an ordinal scale (Figure 14; Stiner (1998): p.311).



Figure 14: Ternary plot with percentage of Ursidae teeth in the juvenile, prime and old categories within Layers I-K from Bacho Kiro Cave. Wear stages defined by Stiner (1994, 1998) and Kindler [(2012);]. Tooth position si represented by different symbols and layers represented by different colors. J = juvenile dominant mortality, NNVA = normal non-violent attrition, LS = living structure, P = prime dominant mortality, O = old dominant mortality.

- 631 Ursid deciduous dentition recovered from Layers I and J are all unworn or in very early
- 632 wear, suggesting these individuals died during winter or early spring time possibly towards
- 633 the end of hibernation period (March/April). Further, the presence of at least two
- 634 individuals with permanent M1 not yet erupted suggests individuals under five months of
- 635 age that died, similarly, during late winter-early spring. In total 74 teeth could be assigned
- to the wear stages developed by Stiner (1994). Despite low sample sizes for some teeth

Ursid mortality profiles for Layers K-I contain a mix of all three age classes (juvenile, prime
and old individuals) with perhaps slightly elevated proportions of juvenile and old animals
(Figure 14). Overall, these patterns are close to the natural non-violent attrition (NNVA)
profile, which Stiner (1998) attributes to natural hibernation death, which also correlates
well with the tooth eruption data and skeletal part representation patterns observed,
especially within Layers I and J.

643 The seasonal nature of bear occupation at caves, including at Bacho Kiro Cave, suggests 644 that there were extended periods of time where both humans and bears could safely 645 occupy the site. Indeed, Stiner (1998) notes that any disturbance at a denning location can 646 deter potential hibernating bears. While mortality data suggests bear remains at Bacho 647 Kiro Cave accumulated largely as a result of natural attrition, active exploitation of 648 hibernating bear individuals by humans cannot be completely excluded (Kindler, 2012; 649 Romandini et al., 2018). The high proportion of skinning and butchery modifications on 650 these remains suggests access to such remains soon after the individual died in order to 651 exploit skins and other carcass resources, which has been documented at other sites in 652 Europe (Münzel and Conard, 2004; Kindler, 2012; Abrams et al., 2014; Romandini et al., 653 2018), and also to exploit abundant dental remains for pendants (Hublin et al., 2020). 654 Further seasonality data was obtained from additional carnivore taxa including red fox 655 (Vulpes vulpes) and cave hyaena (Crocuta crocuta spelea). As Layer I (and the contact I/J) is 656 accumulated largely as a result of human activity these remains likely represent the 657 deliberate accumulation by human groups. In Layer I, at least three adult cave hyaenas are

658 represented alongside a single deciduous third premolar (Stage I of hyaena wear scheme; 659 (Stiner, 1994): p325). Previous work has documented that modern spotted hyaenas 660 reproduce aseasonally, though in modern groups this tends to peak during the summer 661 (June-August; Stiner (1994); Kruuk (1972)]. Undoubtedly Pleistocene hyaena populations in more northern latitudes, compared to their modern day distribution, had a more restricted 662 663 breeding season (Stiner, 1994). Therefore, an approximate season of death is spring-664 summer time, based on modern data. Within Layer J there are no juvenile cave hyaena (all the teeth are permanent) though the crowns are unworn or in the early stages of wear 665 666 perhaps suggesting the teeth have only just erupted (ca.9-12 months of age) again suggesting a spring-summer season of death. Red fox dentition from Layers I and J is 667 668 limited (I = 3; J = 1) but contains erupted yet unworn premolars (P2) and molars (M1) in the 669 early stages of wear (Stiner, 1994). Red foxes normally breed between March-April with the 670 permanent premolars and molars erupting around 4 months (Stiner, 1994). The deciduous 671 dentition is generally replaced by permanent teeth when the individual is ca. 6 months old, 672 supporting a human occupation during the spring-summer at Bacho Kiro Cave.

Herbivore age and seasonality data is more limited due to an overall lack of cranial and
dental fragments, presumably resulting from differential transport decisions by human
groups. For *Bos/Bison*, crown height could be measured on seven teeth from Layers K-I and
ages range between 3-10 years indicating prime age animals (juvenile: 0-3 years; prime: 312 years; old: 12-20 years; based on Discamps and Costamagno (2015)). There were no
cervid remains suitable to measure crown height so age and seasonality cannot be

679 adequately assessed. Most of the teeth recorded in terms of wear and eruption indicate 680 prime aged individuals though in Layer J there are at least three juvenile individuals as 681 expressed by unworn or early wear dP2 and dP3. This indicate these individuals were 682 potentially no older than 6 months old suggesting they died between spring and autumn. 683 Finally, deciduous and permanent equid teeth were assessed in terms of eruption, tooth 684 wear and crown heights were measured, where possible. Individuals assigned to age 685 classes based on the revised schemes of Discamps and Costamagno [(2015); juvenile: 0-2 686 years; prime: 2-15 years; old: 15-25 years). Within Layer I three permanent teeth were 687 measured (ages 14-21 years) and assigned to prime and old age classes with at least one 688 juvenile deciduous premolar (dP4) in early wear suggesting a very young individual up to 1 689 month old (Levine, 1982) that died during spring. Layer J produced a similarly low number 690 of specimens (n = 3) with preserved crown heights again producing prime-old age 691 individuals (ages 7-25 years). A single deciduous incisor suggests at least one juvenile 692 individual from Layer J and the heavy wear suggests the animal died between spring and 693 autumn (Levine, 1982). Finally, Layer K preserved seven specimens with enough tooth 694 crown to measure and allowed all teeth to be assigned to prime-old age individuals (7-17 695 years) (see SOM).

696 Overall ageing and seasonality data illustrates that the IUP record at Bacho Kiro Cave 697 accumulated year round based on carnivore and herbivore bone fusion, dental eruption 698 and wear and tooth crown height. Most information comes from the extensive bear 699 remains that suggest a season of death during or soon after hibernation and most likely

represent natural attrition. Data from herbivore taxa is more limited. Juvenile remains from
cervids and equids, along with some *Capra sp.* remains, suggest death during the springautumn seasons and quite soon after birth. The herbivore taxa illustrate mainly prime-old
age individuals with occasional juvenile specimens though the numbers are insufficient to
investigate more thoroughly the mortality profiles and hunting practices.

705 Overall ageing and seasonality data illustrates that there was no preferential season for 706 accumulation during the IUP faunal record at Bacho Kiro Cave. Most information comes 707 from the extensive bear remains that suggest a season of death during or soon after 708 hibernation and most likely represent natural attrition. Data from herbivore taxa are more 709 limited with mainly prime-old age individuals with occasional juvenile specimens though 710 the numbers are insufficient to investigate more thoroughly the mortality profiles and 711 hunting practices. Juvenile remains from cervids and equids, along with some Capra sp. 712 remains, suggest death during the spring-autumn seasons and quite soon after birth. 713 Seasonality data indicate that faunal material accumulated at Bacho Kiro Cave as a result of 714 repeated use of the site by both human and carnivore groups throughout Layers K-I. The 715 intensity of site use by humans within Layer I was substantially greater than earlier layers, 716 either because more people were present, stayed longer, or both.

#### 717 **Discussion**

718 Site use, diet and carnivore exploitation

This study represents the first in depth taphonomic and zooarchaeological analysis of

fauna from Bacho Kiro Cave, characterizing the subsistence behaviour of humans during

721 the Initial Upper Palaeolithic. The faunal composition within Layers K-I illustrates climatic 722 shifts at a local and regional scale to a greater extent than previously suggested (Kozłowski 723 and Ginter, 1982; Spassov et al., 2007) and a diversity of habitats surrounding the site. The 724 identification of woolly mammoth (*Mammuthus primigenius*), reindeer (*Rangifer tarandus*) 725 and wolverine (*Gulo gulo*) from Layers I and J indicate a substantially colder climate than in 726 present day, which is also consistent with the, currently available, microfaunal data (Hublin 727 et al., 2020). Importantly, these species could have been more environmentally tolerant 728 compared to modern day populations. Species representation correlates well with high 729 resolution oxygen stable isotope data (Pederzani et al., 2021) suggesting mean annual air 730 temperatures 10-15°C below modern day (Layer ]: mean annual temperature  $-1.1 \pm 3.3$ °C; 731 Layer I: mean annual temperature -3.4 ± 2.5°C). Hence, palaeoclimate reconstructions for 732 Layer J suggest a continental climate similar to present day Russia or central Asia, while the 733 later IUP occupation in Layer I occurred during a climatic phase with a smaller difference in 734 summer-winter temperatures that is closer to modern-day northern Scandinavia. Despite 735 the considerably colder climate and environment around Bacho Kiro Cave, seasonality 736 indicators illustrate human occupation within Layer I throughout all seasons of the year. 737 Therefore, early groups of IUP Homo sapiens appear to have occupied south-eastern 738 Europe during colder climates than previously considered and were hunting a range of 739 herbivore taxa from a variety of local environments (see supplementary information in 740 Hublin et al., (2020)). Overall, such data have broader implications for our understanding of 741 the environmental and climatic conditions during the spread of Late Pleistocene Homo 742 sapiens (Müller et al., 2011; Hublin, 2013; Staubwasser et al., 2018).

Micromorphological and sedimentological analysis indicate increased anthropogenic input
towards the top of Layer J with human activities intensified within Layer I. This resulted in
the distinct dark colour of Layer I, coming from organic matter, including charcoal and, to a
lesser extent, burnt bone but also knapped chert, bone splinters, plant remains and some
coprolites (Hublin et al., 2020). Results from this study characterise the faunal assemblage
from Layer I as an accumulation primarily resulting from human action.

749 The richness of Layer I is exemplified by the high volume of excavated bone material from 750 Layer I (14.1/litre of sediment) compared to the underlying layers (Layer J = 0.8/litre of 751 sediment; Layer K = 0.5/litre of sediment). This is further emphasised by the excellent 752 identification rate (19.9%), which is high especially for Pleistocene localities (Morin et al., 753 2017a, 2017b; Rendu et al., 2019). This is also the case for Layers J and K and the contact 754 between these layers (I/J and J/K). Faunal data from Bacho Kiro Cave illustrates that the diet 755 of the IUP groups within Layer I remained relatively consistent compared to the underlying 756 Middle Palaeolithic of Layer K with a focus on large-medium sized herbivores (especially 757 Bos/Bison, cervids and equids). However, within Layer I there appears to be a more 758 deliberate focus on carnivore species, especially cave bear, representing a specific 759 subsistence behaviour that is distinct from the underlying MP at Bacho Kiro Cave. Detailed 760 analysis reveals an increase in carnivore species alongside a diversification in other 761 herbivore species during the IUP occupation in Layer I and appearing to begin within Layer 762 J. The variation in identification and body portion for major species in Layer I is related to 763 differences in transport decisions (e.g., transport of herbivore limb elements), site

formation histories (cave bear, natural accumulation), butchery and processing behaviour
and the use and modification of bone for tools and personal ornaments by IUP groups at
Bacho Kiro Cave.

767 Bone surface modifications from Layers K-I shows an increase in the proportion of human 768 modifications in Layer I and a corresponding decline in carnivore modifications compared 769 with the underlying horizons. Throughout Layer K the intensity of anthropogenic input is 770 significantly lower in terms of frequency and intensity. Indeed, various proxies (carnivore 771 modified bones, digested elements) suggest that carnivore taxa had a more important role 772 in bone accumulation within this layer. This should in no way be seen to diminish the 773 capacity and hunting capabilities of Neanderthals (Stiner, 1994; Smith, 2010, 2015; 774 Discamps et al., 2011; Starkovich, 2017; Marin et al., 2020) but fits with other indications of 775 the low intensity of Neanderthal occupation signatures at some cave sites and the 776 frequency of large carnivore modifications within these assemblages (Rendu et al., 2019). 777 This could be related to more mobile lifeways resulting in shorter duration of site 778 occupation compared to the IUP occupation in Layer I. The distribution of human 779 modifications within Layer I illustrates a large increase across a range of herbivore and 780 carnivore species and includes unusual species such as raptors (golden eagle [Aquila 781 chrysaetos]) and Leporidae (Peresani et al., 2011; Morin and Laroulandie, 2012; Romandini 782 et al., 2014). Taken together, this suggests IUP subsistence at Bacho Kiro Cave focused on a 783 range of large to medium-sized herbivores along with the more opportunistic, perhaps 784 occasional hunting, of smaller and larger carnivores including cave bear. At Bacho Kiro

785 Cave the exploitation of carnivore taxa, especially cave bears, appears to be related to the 786 use of these species for fur as well as raw material for bone tools and personal ornaments. 787 At a broader scale, whether this increased focus on carnivores, and small numbers of other 788 lower ranked resources (leporids, birds and fish), represents the beginnings of dietary 789 diversification related to population or dietary pressures requires additional analyses and 790 comparisons to later Upper Palaeolithic sites and faunal assemblages (Morin, 2008, 2012; 791 Stiner, 2009; Starkovich, 2012; Morin et al., 2019). However, this is beyond the scope of this 792 paper which aims to characterise subsistence strategies across the IUP archaeological 793 record.

# 794 IUP subsistence behaviour: A spatial and temporal review

795 The spread, intensity and duration of IUP occupations remains a source of debate (Ginter 796 et al., 2000; Kuhn et al., 2009; Müller et al., 2011; Hublin, 2013, 2015; Kuhn and Zwyns, 797 2014; Ruebens et al., 2015; Hublin et al., 2020) especially since genetic evidence suggests 798 limited genetic transfer from these initial groups to later Upper Palaeolithic and even 799 modern day populations (Hublin et al., 2020; Hajdinjak et al., 2021; Lalueza-Fox, 2021). 800 Further the scarcity of IUP sites with well-preserved faunal remains has limited our 801 understanding of the environmental and climatic tolerances of these early Homo sapiens 802 groups, their subsistence behaviour and how this compares to local Neanderthal populations. This is especially problematic for the European record (Figure 15) and 803 804 therefore Bacho Kiro Cave provides the first well-contextualized, comparative data point of 805 IUP subsistence behaviour in Europe. Nevertheless, in the regions surrounding south-

- 806 eastern Europe several extensive and well published sites offer the potential for
- 807 comparison with new data from Bacho Kiro Cave to begin the process of categorizing and
- 808 describing IUP subsistence behaviour.



809

810 Figure 15: Map showing location of Bacho Kiro Cave and other key Initial Upper Paleolithic (IUP) 811 sites; white dots: sites with good bone preservation; black triangles: sites with poor bone 812 preservation; black dots: sites with no bone preservation.

- 813 Figure 15 illustrates some of the major IUP sites, highlighting the problem of poor bone
- 814 preservation. In Bulgaria the cave sites of Temnata and Kozarnika, which are situated
- 815 relatively close to Bacho Kiro Cave, have produced layers containing IUP technology and
- fauna (Ginter et al., 2000; Guadelli and Delpech, 2000; Guadelli et al., 2005; Sirakov et al.,

817 2010; Tsanova et al., 2021). At Temnata I Layers 4 and VI illustrate a similar range of species 818 including carnivores (cave hyaena [Crocuta crocuta spelaea], bear [Ursus spelaeus], fox 819 [*Vulpes vulpes*]) alongside a similar range of herbivore taxa, indicative of various 820 environmental types including open (horse [Equus caballus cf. germanicus], bison [Bison 821 priscus], rhino [Coelodonta antiquitatis]), more closed (aurochs [Bos primigenius], cervids 822 [*Cervus elaphus*]) and mountainous (ibex [*Capra ibex*], chamois [*Rupicapra rupicapra*]) 823 settings (Guadelli and Delpech, 2000). Faunal representation suggests a similar mix of 824 environments, characteristic of MIS 3, though the presence of the cold-adapted moose 825 (Alces alces) within Layer VI in Temnata suggests human occupation, initially, during colder 826 phases as in Bacho Kiro Cave Layer I and J. Bone surface modification data illustrate the 827 use of the cave by human and carnivore groups. The early IUP (Temnata-II Layer VI) is 828 characterized by high carnivore, especially hyaena, (n = 84; 6.8%) input compared to human 829 (n = 34; 3.1%) suggesting a less intensive use of the site and, potentially, repeated periods 830 of human absence. In contrast the later IUP, exemplified by Layer 4 from Temnata-I, has a 831 higher proportion of human (n = 184; 12%) compared to carnivore (n = 6; 0.4%) 832 modifications suggesting a more frequent and perhaps intensive use of the site by human 833 groups. At Kozarnika, similar species representation has been noted (Guadelli, pers comm; 834 Guadelli et al. (2005)) though further publication of taphonomic and lithic data is necessary 835 for a more detailed comparison. Overall, these Bulgarian cave sites containing IUP layers 836 illustrate similar species representation and high proportion of human modifications 837 across a range of herbivore and carnivore taxa.

ka cal BP	n	NISP	%h	%с	%sm	burn	%cm	%hm	bt	orn	refe
ca. 45-43	5,537	1,091	71	29.1	1.00	0.7	1.4	13	yes	yes	thic
ca.46	760	239	27	73.2	0.40	0.4	7.9	8	yes	yes	uns
48-40	1,530	81	4	0.8	0.00		1.7	51			Gin 202
>45,000	3,683	1,823	50	1.2	0.60	37.4	0.2	11		yes	Dec
undated	272	170	62	1.1	0.02	1.3	0.0	16		yes	BOS
	3,822	1,264	95	3.4	2.00				yes	yes	
ca 45-38	1,813	654	95	2.1	2.60				yes	yes	Kuł
cu. 45 56	3,581	1,139	97	2.4	1.10				yes	yes	201
	1,114	360	94	2.8	3.00				no	no	

838 Table 8: Initial Upper Palaeolithic sites with published faunal data

of identified specimens; %h = percentage of herbivore taxa; %c = percentage of carnivore taxa; %sm = percentage of small taxa; %burn = percentage of burnt faunal i hm = percentage of human modified remains; bt = presence of bone tools; orn = presence of ornaments. Kozarnika Layer VI not included as data are currently unpub

839 Üçağızlı cave (Turkey) preserves a deep sequence spanning most of the Upper Palaeolithic 840 and contains extensive IUP layers (F-I and including sub-layers; Kuhn et al. (2009); Kuhn et 841 al. (1999)] with recent redating suggesting the beginning of the IUP ca. 45,000-43,000 years 842 ago (Kuhn et al., 2009; Douka, 2013). The IUP Layers Fa, Fb, Fc and H1-H3 have abundant 843 ash and charcoal remains and a high anthropogenic input suggesting a more intense or 844 continuous use of the site (Goldberg, 2003). Interestingly, the earliest IUP occupations at 845 Üçağızlı (Layers H, H1-3 and upper I) are represented by thin, sharply defined lenses within 846 these layers suggesting relatively brief events of accumulation (Goldberg, 2003; Kuhn et al., 847 2009). Overall, the pattern of occupation at Üçağızlı cave during the IUP with more sporadic 848 site use at the beginning of the IUP occupation followed by a more intensive use is similar 849 to that identified at Bacho Kiro Cave in terms of the transition from Layer J into Layer I. IUP

850 subsistence at Üçağızlı is dominated by medium-large ungulates including fallow deer 851 (Dama mesopotamica), bezoar goat (Capra aegagrus), and roe deer (Capreolus capreolus) with 852 wild boar (Sus scrofa), red deer (Cervus elaphus), and aurochs (Bos primigenius) present 853 though less abundant. Small game forms a small proportion of the diet in the IUP layers, 854 but is more diversified compared to the Middle Palaeolithic, though the importance of 855 smaller taxa increases significantly in the later Upper Palaeolithic at the site (Kuhn et al., 856 2009). Again carnivores form a small but consistent portion of the faunal assemblage with 857 human modifications on numerous species including bear and other large carnivores (see 858 Table 8).

859 The recent redating of Ksâr 'Akil (Lebanon) has produced an age of ca. 45,000 years ago 860 and is associated with IUP lithics and human remains (Bosch et al., 2015; but also see 861 Douka et al., 2015). Detailed zooarchaeological analysis of fauna from Layers XXII and XXV 862 has provided detailed information on the site formation history and shifts in human 863 subsistence behaviour at the site (Bosch, 2018). The burnt bone recovered from the IUP 864 layers illustrates a low proportion of burnt materials in the early IUP Layer XXV (n = 3; 1.3%) 865 with a substantial increase within Layer XXII (n = 1289; 37.4%). This is a similar to both 866 Bacho Kiro Cave and Üçağızlı, suggesting more intensive use of the cave during the 867 formation of the later IUP in Layer XXII. Fallow deer (Dama mesopotamica) are the dominant 868 species throughout the IUP layers, though there is a shift in species diversity. Bosch (2018) 869 demonstrates a decrease in aurochs and wild boar (Sus scrofa), which is replaced by 870 caprines (Capra ibex, Capra aegagrus) and roe deer (Capreolus capreolus). Evidence for

marine mollusc consumption occurs initially in Layer XXII though is rarely recorded in the
IUP layers with a similarly low exploitation of smaller game, though this again expands in
the later Upper Palaeolithic. Further, these layers contain various carnivore taxa, though
the absence of associated modifications from the IUP layers (<1%) and the predominance</li>
of human butchery modifications (11.8%) suggests that Layers XXII and XXV accumulated as
a result of human action.

877 Overall, this comparative review has highlighted some interesting similarities in IUP 878 subsistence strategies. Comparing new faunal data from Bacho Kiro Cave with other IUP 879 sites suggests that early phases of occupation were characterized by, less intensive or 880 shorter term occupations (for example Layer J at Bacho Kiro, Layers H-I at Üçağızlı, Layers 881 XXV at Ksâr 'Akil). Once established, occupation and site use appears more intensive and 882 perhaps more continuous as exemplified by the large charcoal and ash deposits at sites 883 such as Bacho Kiro Cave and Üçağızlı and the extensive evidence for burnt material in Ksâr 884 'Akil Layer XXII. This is also illustrated by the increase in density of both lithic and faunal 885 material within later IUP occupations. . Across all sites, IUP subsistence appears to be 886 focused mainly on large-medium sized herbivores with a limited exploitation of small 887 game. The presence of humanly modified carnivore remains appears to be a consistent 888 feature of these faunal assemblages suggesting, perhaps, a more specific focus on these 889 individuals for, presumably, skins and furs but at Bacho Kiro Cave possibly also for dietary 890 resources and raw material/ornaments. Despite the environment and climatic differences 891 observed between these various IUP sites, the observed similarities in terms of human

occupation and subsistence behaviour are striking, though further work focused on
refining the chronology of the emergence and spread of the IUP is required. Overall, this
comparative analysis highlights the importance of faunal remains in understanding
similarities in subsistence practice (including diet and carnivore exploitation) across the
IUP.

#### 897 **Conclusion**

898 Bacho Kiro Cave represents a key locality for understanding the subsistence behaviour 899 associated with the expansion of Late Pleistocene Homo sapiens into Europe. We identified 900 a change in site use and occupation intensity across the Middle to Upper Palaeolithic 901 transition. IUP Layer I is marked by a significant increase in find density and human 902 modifications on the faunal remains. Together with seasonality data indicating a use of the 903 cave in all seasons, this indicates more frequent and/or more long-term use of the site by 904 these early groups of Homo sapiens. Whether this represents continuous occupation 905 remains unclear, especially as micromorphological data (e.g., clay lenses) has identified 906 potential short periods of site abandonment (Hublin et al., 2020). Furthermore, the 907 presence of wolverine and reindeer suggests, especially within Layer I, that conditions were 908 considerably colder than had been previously considered (Kozłowski and Ginter, 1982; 909 Spassov et al., 2007) and that IUP groups inhabited Europe during varied climatic 910 conditions (Hublin, 2013, 2015; Staubwasser et al., 2018; Zwyns et al., 2019). 911 Across the IUP and the MP layers at Bacho Kiro Cave the dietary focus is similar, centred on 912 the exploitation of a range of large to medium herbivore taxa representing a diverse set of

913	habitats around the cave site. The large faunal dataset from Layer I allowed for the
914	identification of the selective transport of large herbivore body parts, especially limb bones,
915	into the site. This contrasts with the abundant cave bear remains, including cranial
916	portions, indicating the bears died in the cave itself. Furthermore, a distinct aspect of the
917	IUP at Bacho Kiro Cave is an increase in humanly modified carnivore remains, including
918	both small (wolf, fox) and larger taxa (cave hyaena, cave bear). This relates to procurement
919	of such taxa as raw material for personal ornaments (e.g., cave bear teeth pendants) but
920	also potentially for skins and fur. This pattern of exploitation is distinct from the
921	Neanderthal archaeological record at Bacho Kiro Cave.
922	At a broader scale, a distinct set of similarities was identified with other IUP sites with
923	faunal preservation across Europe and western Asia. Interestingly, the earliest IUP
924	occupations seem to have been shorter and less intense, as represented by lower
925	proportions of ash and burnt bone, as well as lower proportions of human modifications.
926	During subsequent IUP occupations site use was more intensive and, potentially, for a
927	longer duration to the exclusion of other large carnivores. At all these sites small game
928	exploitation by IUP Homo sapiens was limited. The consistent exploitation of carnivore taxa,
929	of a variety of body size classes, for both skins and potentially other resources occurs at all
930	these sites and could be viewed as something distinct for IUP Homo sapiens.
931	Future work should focus on further contextualising the distinct pattern of intense IUP site
932	use and carnivore exploitation identified here. Firstly, within the IUP itself, with additional
933	data coming from sites for which data publication is forthcoming or excavation still

934 ongoing. This would allow for the further assessment of the role of these subsistence 935 strategies in the spread of Homo sapiens groups into Europe and further afield. Secondly, 936 comparison with later Upper Palaeolithic (e.g., Proto-Aurignacian and Early Aurignacian) 937 subsistence strategies would help to understand the specific nature of IUP subsistence and 938 adaptation compared to later groups of incoming *Homo sapiens*. Thirdly, more in-depth 939 comparisons with local MP sites are needed to fully understand the differences between 940 Neanderthal and early *Homo sapiens* subsistence and their role, if any, in population 941 replacements. Overall, with this paper we hope to have created a new data-driven 942 characterisation of IUP subsistence which can now form the basis for a range of 943 comparisons at various temporal and geographic scales.

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