

Neanderthal selective hunting of reindeer? The case study of Abri du Maras (south-eastern France)

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Keywords

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50 Neanderthal; Subsistence; Seasonality; Monospecific faunal assemblages; Reindeer predation; Mass procurement

Abstract

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56 Monospecific exploitation of reindeer by Neanderthals is common behaviour in the Upper Pleistocene of Western
57 Europe. However, reindeer-dominated assemblages have largely been reported from regions of northern Germany and
58 south-western France, with few examples noted in south-eastern France, where faunal assemblages are most of the time
59 dominated by a variety of other large ungulates such as red deer, horse and diverse bovids. Here, we present multi-
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strand (bio- and eco-) archaeological datasets from the site of Abri du Maras (level 4.1), situated at the mouth of the Ardèche and Rhône rivers, a new example of a reindeer-dominated Neanderthal site in south-eastern France. Dated to the beginning of the MIS 3, the zooarchaeological assemblage is dominated by reindeer (88% of the NISP, representing 16 individuals), but also includes horse, bison, megaceros, red deer, ibex and lagomorphs. The combination of zooarchaeological, cementochronological and tooth microwear analyses evidence a single-species dominated spectrum, with catastrophic mortality and repeated autumnal deaths. This integrated approach provides an extensive picture of human subsistence behaviour, pointing to short-term hunting episodes of reindeer herds in an exceptional context of a quasi-exclusive Neanderthal accumulation. The high number of individuals and selective butchery may correspond with a cooperative and planned mass hunting strategy. The multidisciplinary approach undertaken here also incorporating paleontological, charcoal, ecological, and isotopic analyses places the archaeological and zooarchaeological data within a broader regional palaeoenvironmental framework, providing valuable landscape-contextual information. The zooarchaeological data suggest a subsistence behaviour different from other Neanderthal reindeer-dominated assemblages often connected with specialised butchery or hunting sites.

Introduction

The hunting abilities of Neanderthals are now well documented, not least due to the many debates at the end of the 20th century concerning the recognition of human versus carnivore faunal accumulations and the question of hunting versus scavenging in Middle Palaeolithic occupations (e.g. Binford 1981, 1988; Chase 1986; Stiner 1994; Marean 1998; Patou-Mathis 1997). More recently, other important advances have been made in archaeological research and associated fields, which not only demonstrate the proficiency of Neanderthal (and their predecessors) hunting, and have also revealed further similarities, and a far closer relationship, to modern humans than previously thought. For example, recent advances in genomic research have now demonstrated direct interaction between modern humans and Neanderthals through interbreeding (Green et al. 2010; Fu et al. 2015). The decreasing gap in the perceived biological distance between modern humans and Neanderthals is mirrored by archaeological research, as the behavioural juxtapositioning of ‘Humans vs. Neanderthals’ is increasingly called into question. In the field of subsistence and game exploitation, new evidence of hunting weapons discovered at Schöningen (Thieme 1997; Schoch et al., 2015), combined with many archaeozoological studies (e.g. Gaudzinski-Windheuser 1996; Patou-Mathis 2000), have highlighted specialized Neanderthal predation of medium and large-sized ungulates, and archaeozoological and isotopic studies have evidenced targeted interception hunting (e.g. Gaudzinski and Roebroeks 2000; Britton et al. 2011; Julien et al. 2015; Kuitens et al. 2015; Rivals et al. 2015).

Single-taxa assemblages are significant as the tactic of specialized and mass hunting involves planning and collaborative behaviours. This is particularly the case when assemblages are the result of focused temporally constrained hunting activities, where resources are seasonally restricted (e.g. due to their migratory behaviour) or where the condition of prey-species is highly seasonally varied (for example, in reindeer). Often species targeted are gregarious, and would have been intercepted by humans at places attracting the aggregation of many individuals, for example, at water sources, or more seasonally at calving grounds, during the rut, or along migratory corridors. Monospecific assemblages that are rapidly accumulated such as single mortality events are also significant in that they suggest mass food procurement, and through this imply the planning of carcasses processing and the storage and transport of meat and marrow for deferred consumption (David and Enloe 1993; Costamagno 2006; Gaudzinski-Windheuser and Kindler 2012; Rendu et al. 2012). In this sense, monospecific assemblages, imply advanced planning and cooperative hunting behaviours, and an in-depth knowledge of prey and landscape.

1 Monospecific faunal assemblages appear from stages 9 to 7 with pre-Neanderthals and become more common from the
2 beginning of the Last Glacial period to the end of the Middle Palaeolithic (Gaudzinski 1996; Patou-Mathis 2000;
3 Gaudzinski-Windheuser 2006; Gaudzinski-Windheuser and Kindler 2012), without any specific increase during the
4 Upper Palaeolithic (Grayson and Delpech 2002, 2003; Kitagawa et al. 2012). Indeed, many pre-Neanderthal and
5 Neanderthal sites in Europe and in the Middle East highlight specialized hunting for a wide variety of middle-sized or
6 large-sized ungulates: reindeer at Salzgitter-Lebenstedt, Les Pradelles and Jonzac (Gaudzinski and Roebroeks 2000;
7 Costamagno et al. 2006; Airvaux 2004; Niven et al. 2012); camel at Umm El Tlel (Boëda et al. 2001); aurochs and/or
8 bison at La Borde, Mauran, Wallertheim and Il'skaja I (Jaubert et al. 1990; Farizy et al. 1994; Gaudzinski 1995;
9 Hoffecker, Baryshnikov and Potapova 1991); red deer at Saint-Marcel and Le Lazaret (Daujeard 2007, 2008; Valensi et
10 al. 2013); horse at Orgnac 3, Zwolen, Kabazi II and Starosele (Gautier 1989; Patou-Mathis 1999; Burke 2000, 2006;
11 Moncel et al. 2012); or small bovids, ibex or chamois at Scladina (Patou-Mathis 1998), Baume des Peyrards (Daujeard
12 2008), Zafarraya (Caparros et al. 2012) and in the numerous Middle Palaeolithic sites of the Pyrenean, Alpine,
13 Cantabrian and Caucasus mountains (e.g. Patou-Mathis 2000; Yravedra and Cobo-Sanchez 2015).

14 Monospecific assemblages at Neanderthal sites often share common characteristics. For example: accumulation via
15 regular short events; the predominance of remains of a single species (and many individuals) associated with lithic
16 artefacts and cutmarks; catastrophic mortality profiles; and selective transport of carcass portions from the kill site to
17 the base camp (Gaudzinski-Windheuser 2006; Costamagno et al. 2006; Gaudzinski-Windheuser and Kindler 2012;
18 Rendu et al. 2012). In light of cross-site similarities, ungulate mass procurement hypothesis is often confirmed or
19 refuted through a similar compilation of multiple zooarchaeological lines of evidence, e.g. threshold number of prey
20 bones, mortality caused by humans, single depositional episode and single mortality event (Lubinski 2013).

21 However, the assessment of monospecific (and other) faunal assemblages, and their interpretation, is blighted by the
22 problem of equifinality in accumulations resulting from combined carnivore and anthropogenic action (Rogers 2000;
23 Lyman 2004). Despite huge progress in the recognition of the various agents of accumulation over the last decades
24 (mainly thanks to archaeological and experimental data on bone surface modifications; age and skeletal profiles or
25 faunal spectra: Cruz-Urbe 1991; Blumenshine et al. 1996; Blumenshine and Selvaggio 1998; Pickering 2002; Guadelli
26 2008; etc.), exclusively human accumulations still represent the best contexts to study human behaviours.

27 Unfortunately, such sites remain rare in the Middle Palaeolithic, but are vital for confidently inferring past behaviours.
28 Here, we present new zooarchaeological, archaeological, paleontological and isotopic data from the Middle Palaeolithic
29 site of Abri du Maras, Ardèche, in Southeast France. The site was first excavated by R. Gilles and J. Combier during the
30 second half of the 20th Century and research was resumed at the site in 2010 by one of the authors (M.-H. Moncel). Abri
31 du Maras is now the focus of a major multi-disciplinary archaeological investigation. This vast rock shelter is situated
32 along the right bank of the Middle Rhône Valley, at the confluence with the Ardèche River and features several well-
33 preserved levels of occupation dated to the first half of the Last Glacial period (MIS 4-3) (Moncel and Michel 2000;
34 Richard et al. 2015). Abri du Maras comprises an extensive assemblage of anthropogenically-modified animal bones
35 associated with Middle Palaeolithic lithic artefacts, with very few carnivore remains and little evidence of carnivore
36 activity. Due to the excellent spatial preservation of level 4.1, which is dominated by reindeer, and the likelihood that
37 Neanderthals were practically the sole accumulators, this phase of the site is ideal for furthering our understanding of
38 Middle Palaeolithic monospecific and mass faunal assemblages, and therefore, for elucidating Neanderthal landscape
39 use, hunting practices, and social behaviours.

40 **Abri du Maras**

Geographical setting

1 The site of Abri du Maras (170 m a.s.l.) is situated on the right bank of the Middle Rhône Valley, in a small dry valley
2 of the Ardèche River, at the outer edge of the gorges (Fig. 1). It is perched 70 m above the river, and is all that remains
3 of a huge, former south-east facing rock shelter. This rock shelter is the relict of successive phases of tectonic activity,
4 dissolution and erosion processes that contributed to exposing and altering a pre-Quaternary karst network. The
5 presence of large limestone slabs throughout the sequence evidences the vaster expanse of the shelter at the time of
6 occupation and also to its final collapse soon after the last occupation (Debard 1988; Moncel et al. 2010, 2015).
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Figure 1.

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15 The Rhône Valley comprises notable archaeological and topographical features: a vast corridor linking the North of
16 Europe to the Mediterranean zone, and a key position between two mountainous regions – the Massif Central to the
17 west and the Alpine foothills to the east. Many East-West tributaries on the right bank of the Rhône River connect the
18 Rhône Valley to the plateaus of the Massif Central. In this region, previous studies of Neanderthal subsistence
19 suggested a probable seasonal model, based on the presence of sites with different occupation types. Evidence of
20 settlement in caves and rock shelters clustered around the Ardèche gorges results from the seasonal activities of larger
21 groups, focusing on monospecific prey, while the occasional bivouac occupations of other sites are more likely to
22 represent opportunistic faunal exploitation alternating, for example, with carnivore visits (Daujeard 2008; Daujeard and
23 Moncel 2010; Moncel and Daujeard 2012; Daujeard et al. 2012).
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Stratigraphy and dating

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33 The first archaeological investigations at Abri du Maras revealed a stratigraphic sequence of about 3 m including eight
34 levels with Middle Palaeolithic deposits. This site was renowned in the past for its Middle Palaeolithic (MP) deposit
35 with a Levallois laminar debitage (level 1) (Gilles 1950; Combiér 1967; Debard 1988; Moncel et al. 1994). The new
36 excavation only concerns the middle and lower parts of the sequence, from previously assigned levels 4 to 8. The
37 stratigraphic unit 5 (levels 8-6 of earlier excavations) is at present the oldest currently known unit and lies abruptly on
38 the erosional contact of the limestone substratum at the back of the shelter. The overlying unit 4 (this study, has been
39 extensively exposed across the rock shelter and consists of a silt and sandy-silty sedimentary accumulation (0.5 to 1 m
40 thick). The coarse fraction results from frost shattering the walls of the rock shelter. The fine fraction can be assigned to
41 loess-like deposits of aeolian origin (Antoine 2002), on the basis of sedimentological data (Figs. S1a-b). The
42 mineralogy (Nowak 2013; Puaud et al. 2015) indicates that the deposit appears to have mostly originated from the wind
43 erosion of the fluvio-glacial terraces of the Middle Rhône valley during the cold and dry conditions of MIS 3.
44 Micromorphological features (Fig. S1c) show that the entire unit 4 appears to have been affected by moderate
45 pedological evolution, mostly expressed by earthworm bioturbation and the biogenic redistribution of calcium
46 carbonate (Brochier 1976; Jaillard et al. 1991; Canti 1998; Kooistra and Pulleman 2010).
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50 Unit 4 contains in its upper part two archaeological levels, 4.2 and 4.1 (Fig. 2). The excavation showed that these two
51 levels (previously 5 and 4) correspond respectively to two well-preserved human occupation phases marked by
52 abundant artefacts with scant traces of combustion and occasional diffuse ash lenses. Unit 4 is currently excavated over
53 an area of more than 50 m², in the front of the remaining shelter (Moncel et al. 2014). Finally, only scattered and rare
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artefacts have been encountered in the overlying units (3, 2, and 1), which contrast with unit 4 by their coarse texture and the abundance of large blocks.

Figure 2.

U/Th dating applied to bones from the top of unit 5/bottom of unit 4 yielded ages of 72 ± 3 ka, 87 ± 5 ky, 89 ± 4 ky, and 91 ± 4 ky (Moncel et al. 1994; Moncel and Michel 2000). New preliminary ESR-U/Th dating of ungulate teeth confirmed the chronology of unit 5 (90 ± 9 ky) but gave more recent ages for unit 4, attributed to MIS 3. Level 4.1 (upper part of unit 4) thus dates to between 40 ± 3 ky and 46 ± 3 ky ($n=2$) (also MIS 3), while samples from level 4.2 provided ages ranging from 42 ± 3 ky to 55 ± 2 ky ($n=3$) (MIS 3) (Richard et al. 2015).

Archaeology and environment

The close association of archaeological materials with coarse fraction issued from the pedogenic alteration of the limestone cliff together with collapsed limestone slabs in the two occupation levels (levels 4.1 and 4.2) of unit 4 enables us to establish strict synchrony between human presence and climatic conditions characterized by seasonal moisture and mild temperatures. In contrast, the fine silt texture typical of aeolian dust, the weak effect of pedogenesis and the lack of coarse limestone fraction in the sterile level deposited between levels 4.1 and 4.2 indicate that the site was not occupied when the climate was colder and drier. Microfauna, charcoal and pollen are very rare at the site due to poor preservation. Previous faunal studies highlighted the presence of temperate species such as red deer, roe deer and wild boar in unit 5, whereas cold and open environment species such as reindeer, horse and bison are more common in unit 4 and in the overlying units. The varied faunal spectrum previously obtained for the unit 4 is composed, in order of abundance, of *Rangifer tarandus*, *Equus ferus* cf. *germanicus*, *Cervus elaphus*, *Bison priscus*, *Capra ibex*, *Equus hydruntinus* and *Megaloceros giganteus*. All along the sequence, faunal remains are mainly related to anthropogenic activities and carnivore marks are scarce (Moncel et al. 1994; Daujeard 2008; Daujeard and Moncel 2010; Moncel et al. 2015).

In this paper, we focus on level 4.1, the uppermost occupation unit 4, due to the lack of carnivore action, remarkable spatial preservation with short object displacements, technological behaviour based on similar strategies suggesting occupations close in time and the presence of ash lenses. Level 4.1 has been exposed over a surface of 34 m². The excavation revealed a dense accumulation of archaeological remains reaching a total thickness of 20 cm. However, the clayey-sandy silt sedimentary matrix of level 4.1 is homogenous throughout and does not display any significant change in colour, structure or texture, in close association with the occurrence of the archaeological remains. Based on the lack of field evidence, it was presumed that archaeological level 4.1 did not present well-preserved living floors. However, the meticulous excavation of this level revealed the scattered occurrence of fire traces, mostly represented by poorly preserved mm-sized charcoal fragments which are finely incorporated in the matrix. Burnt flint and burnt bone also provide evidence of the use of fire and are dispersed over the archaeological level. In addition, occasional cm-sized lenses formed of dark-brown to brownish-grey silty clay, consisting of densely packed biogenic aggregates with high quantities of fine charcoal, ash micro-aggregates, burnt bones and polymer films occur throughout level 4.1. Based on their field facies and the abundance of combustion residues, the lenses have been assumed to be relicts of fire-related activities. They are all located at a same deepness, suggesting a main phase of occupation. An important number of faunal and lithic refits have been identified in level 4.1 (Fig. 3). In the case of the faunal assemblage, the total number of refits is 65 ($n=44$ on fresh and 21 on dry bones) connecting 148 items. The longest refit is formed by eight elements

($n=1$) but the majority have only two elements ($n=51$). In addition, 22 faunal anatomical connections, grouping 68 bones, were also identified. There are also 10 lithic refits comprising a total of 20 pieces (mainly flakes and all formed by two elements). The raw materials involved are flint ($n=7$) and quartz ($n=3$). The connection lines are mainly related to knapping sequences ($n=6$) although some are the result of fractures (during knapping $n=2$ and post-depositional $n=2$). The fact that faunal and lithic connections lines are short (mean of 1.5 m) and some of the connected items are small (≤ 1.5 mm), corroborates the low level of disturbance of the archaeological assemblage from level 4.1.

Figure 3.

The lithic material in level 4.1 totals 1 844 items. The density is 135 pieces/m² and 54/m³. Lithic analysis, undertaken by several of the authors, revealed that the technical strategies applied mainly to flint and secondarily to other stones (quartz, quartzite and granite) indicate the fragmentation of reduction processes into local and semi-local perimeters around the site (Moncel et al. 2014). The main core technology is Levallois, generally on cortical flint cores on flakes. Flint flakes, blades and points are the main components of the series and the technological aims of the debitage. The largest flint flakes, Levallois blades (cortical or not) and Levallois points were produced elsewhere, to the north and south of the site (up to 20-30 km), according to the geological study, and then brought to the shelter. Flake-tools are very rare (3%), and never modified the shape of the pieces. Levallois products were never retouched. We may mention one Quina scraper made on a thick and large flint flake. Evidence of impact fractures suggests that some points, brought to or prepared on the site, could have been used as projectile tips (Hardy et al. 2013). The lithics attest to the management of local and semi-local stones in a perimeter of 30 km around the site (possibly more due to some unidentified flint) and an anticipation of domestic needs. Imported artefacts and artefacts made on the site were used for the same range of activities and materials (butchery, plant and woodworking). Neanderthals exploited a wide range of resources including large mammals, fish, ducks, raptors, rabbits, mushrooms, plants, and wood. Twisted fibres on stone tools provide possible evidence of making string or cordage (Hardy et al. 2013).

Material and Methods

The faunal material included in this study comes exclusively from archaeological find level 4.1 from Abri du Maras. The analysis of the faunal assemblage features a range of scientific approaches and methodologies including taphonomic and zooarchaeological analysis in order to explore the species present, age-at-death (where possible), and infer anthropogenic modifications and other taphonomic features; cementochronology to infer season-of-death; stable isotope and dental microwear analysis to explore the niche feeding behaviours of the exploited species, and palaeoenvironmental proxies (faunal and charcoal) in order to gain better insight into the MIS 3 ecosystem surrounding Abri du Maras.

Taphonomy and zooarchaeology

The taphonomic and zooarchaeological studies concern all the faunal remains from level 4.1 since the 2006 excavations. We report the total number of skeletal remains (NR), the number of taxonomically and anatomically identified specimens (NISPt and NISPa), the minimum number of elements (MNE) and the minimum number of individuals (MNI) (Binford 1984; Lyman 1994). In level 4.1, small and large mammals represent 11,123 remains including indeterminate remains (Table 1). The number of coordinated remains is 2,919 and 1,347 remains have been

1 identified to the anatomical level and 1,170 to the species level. Fish remains account for 167 bone elements, birds are
2 represented by two remains and we recorded five micromammal anatomical elements. Systematic sieving was
3 undertaken during the excavations and the scarcity of microfauna is mainly due to poor bone preservation (see below).

4 **Table 1.**

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7 In order to discuss the meat procurement strategy (hunting or scavenging), selective carcass transport to the site and
8 differential bone preservation, we used the percentage of Minimal Animal Unit (MAU, Binford 1984), the Food Utility
9 Index (FUI) (Metcalf and Jones 1998; Lyman 1994), the volume of the marrow cavity (Binford 1978, in Jones and
10 Metcalfe 1988) and the bone bulk density (Lyman 1984; Lam et al. 1999). Carcasses were divided in seven main
11 anatomical parts: head (skull, mandibles, isolated teeth excepted); axial elements (vertebrae, ribs, sternum); forequarters
12 (scapula, humerus, radio-ulna); forefoot (carpal, metacarpal); hindquarters (pelvis, sacrum, femur, tibia, patella);
13 hindfoot (tarsal, metatarsal); indeterminate foot (phalanges, sesamoids, metapodials) (after Wilson 1989, modified).
14 Seasonality and ontogenic age-at-death of prey specimens is based on dental eruption and replacement patterns (for
15 deciduous teeth concerning the season of death) and then on tooth-wear (wear stages for reindeer: cf. Bouchud, 1966
16 and Miller, 1974; for red deer and by analogy megaceros: Riglet 1977; for bison: Brugal and David 1993 and for horses:
17 Guadelli 1998; Forsten and Moigne 1998 or Bignon 2003). Five main age groups were established: juveniles (with
18 deciduous teeth), young adults (with erupted P4 and M3), prime-age adults (with moderately worn P4 and M3), old
19 adults (with heavily worn P4 and M3) and senile (almost no enamel remains on P4 and M3) (Grant 1982; Klein and
20 Cruz-Urbe 1984; Forsten and Moigne 1998). For reindeer, these five age classes represent nearly the same lifetime
21 with juveniles ranging from 0 to 2.5 years old; young adults: 2.5 to 5; prime-age adults: 5 to 7.5; old adults: 7.5 to 10
22 and senile: up to 10 years old. In order to use ternary diagrams established by Stiner (1990), the three age categories
23 were corrected – juveniles (< 2.5), adults (2.5 to 10) and old individuals (> 10) – according to their relative lifespans.
24 For larger ungulates, such as bison and horse, the adult category begins later, with the loss of the D4 and the eruption of
25 the P4 and M3, at about 40-50 months old.

26 For comparative purposes for large mammal representation, richness and diversity indexes were calculated (Simpson
27 1949; Magurran 1988; Grayson and Delpech 2002; Valensi et al. 2013): 1) The taxonomic richness: $R = S - 1 /$
28 $\ln MNI$ (with S = number of species and MNI = total minimum number of individuals); 2) the Simpson index:
29 $D = \sum ni[ni - 1] / N[N - 1]$ (with ni = the number of specimens for each species and N = the total number of specimens);
30 3) The Shannon diversity: $H = -\sum [(MNI_{sp} / MNI_{tot}) \log_2 (MNI_{sp} / MNI_{tot})]$ (with MNI_{sp} = minimum number of
31 individuals for each taxon and MNI_{tot} = total minimum number of individuals) or $H = -\sum [(NISP_{sp} /$
32 $NISP_{tot}) \log_2 (NISP_{sp} / NISP_{tot})]$ (with $NISP_{sp}$ = number of identified specimens for each taxon and $NISP_{tot}$ = total
33 number of identified specimens) and 4) The Equitability index or Evenness is obtained by the Shannon index/Ln (n
34 taxa).

35 For the taphonomic analysis, the dimensions (length, breadth and thickness) and modification data were recorded for all
36 the coordinated and identified specimens. Indeterminate fragments less than 25 mm were only used for counts,
37 fragmentation studies (type and size classes) and carbonization analyses. The identification of the type of breakage
38 (green, dry or recent bone fractures) was made based on the fracture colour, shape, feature and angle and associated
39 marks (Villa and Mahieu 1991). The recorded percussion marks are (Blumenschine and Selvaggio 1988; Capaldo and
40 Blumenschine 1994; Blasco et al. 2013): medullary or cortical percussion notches (negative flake scars); impact flakes
41 (positive flake scars); percussion pits; adhering flakes; peeling and micro-notches (Vettese 2014). The shaft fragments
42 were differentiated by size and circumference classes (cf. Villa and Mahieu 1991). For indeterminate fragments, two
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1 main size categories were established, adapted to the ungulates present in our sample: (1) medium-sized ungulates with
2 a weight between 50 and 300 kg (red deer, reindeer and ibex) and (2) large-sized ungulates with a weight between 300
3 and 1000 kg (large bovids, horse and megaceros).

4 All bone surfaces were visually assessed, with some studied further using a stereomicroscope (Leica S8 APO,
5 magnification 10-80x) in order to distinguish surface modifications, and photographed. Type and location of
6 modifications were recorded, including those made by rodents, carnivores or hominins as well as climatic and edaphic
7 modifications (including cracking, desquamation, polish, concretion, root marking, chemical corrosion and oxides
8 coloration). The identification of these main taphonomical modifications was based on the criteria defined by
9 Behrensmeyer (1978), Binford (1981), Lyman (1994) and Fisher (1995). The illegible remains were not included in the
10 percentages. Trampling marks were distinguished from butchering marks using the works of Binford (1981), Shipman
11 and Rose (1983, 1984), Behrensmeyer et al. (1986), Olsen and Shipman (1988), Blasco et al. (2008) and Dominguez-
12 Rodrigo et al. (2009). The location and morphology of the latter may indicate the related butchering activity, including
13 evisceration; skinning; dismemberment; disarticulation; periosteum removal; cutting tendons and defleshing (Binford
14 1981; Nilssen 2000; Pobiner et al. 2008; Costamagno and David 2009). Following Binford (1981), Haynes (1983) and
15 Campmas and Beauval (2008), carnivore marks were classified as follow: pits, punctures, scores, notches or corrosion
16 by gastric acids. Damage due to burning was recorded using the different colour stages described by Stiner et al. (1995)
17 (Table S1). In addition, burnt elements were categorized according to their length and intrinsic characteristics:
18 spongy, compact or dental portions.
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27 *Isotopic studies: Methods and material*

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30 As part of a broader multi-isotope study incorporating faunal bones and teeth from multiple archaeological find levels at
31 Abri du Maras, a small number of bones ($n=9$) from three different taxa (*Equus*, *Megaloceros*, *Rangifer*) were selected
32 from level 4.1 for collagen extraction, and carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope analysis. The stable isotope
33 analysis of bone collagen is not only useful in archaeological studies to infer human palaeodiet, but can also provide
34 information about the broader environment, and also about niche partitioning and feeding behaviours of different
35 herbivore taxa, even within purely-C3 plant communities (e.g. Bocherens 2003; Feranec 2007). For example, the
36 consumption of lichens, which exhibit higher $\delta^{13}\text{C}$ values than other terrestrial C3 plants (Ben-David et al. 2011;
37 Drucker et al. 2001, 2012), or feeding in forested environments, which typically have more negative $\delta^{13}\text{C}$ values due to
38 the 'canopy effect' (Cerling et al. 2004; Noe-Nygaard et al. 2005). Although they are on the same trophic level, absolute
39 $\delta^{15}\text{N}$ values of herbivore tissues depend on a number of factors, and in particular on the varying ^{15}N levels of the plants
40 they consume (and ultimately the soils) at the base of the food chain. For a recent review of the factors influencing
41 nitrogen isotope ratios in plants, including plant physiology, see Szpak (2014). Therefore, given that local variation in
42 soil and plant $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope composition is reflected in local herbivores, the stable isotope analysis of animal
43 bone collagen can be used to investigate resource partitioning and underlying isotopic variations in ancient ecosystems
44 (Britton et al. 2012). Moreover, the absolute $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ determined in herbivore bone collagen at archaeological
45 sites can also be utilised to infer broad palaeoclimatic conditions (e.g. Richards and Hedges 2003; Stevens and Hedges
46 2004; Stevens et al. 2008). This is due to the relationship between 'baseline' ecosystem $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of soils
47 and plants, and changing diachronic environmental factors such as aridity/moisture and temperature (e.g. Heaton et al.
48 1986; Schwarcz et al. 1999; van Klinken et al. 2000). In this way, overall dataset values and trends (between the
49 different herbivore species) can shed light on the palaeoenvironmental and palaeoecological conditions at Abri du
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1 Herbivore bone ($\approx 1\text{-}2\text{g}$) was sampled for collagen extraction using rotary stainless steel cutting implements and cleaned
2 using air abrasion. Collagen was extracted using the Longin method (1971), with modifications based on the
3 recommendations of Collins and Galley (1998), and with the addition of an ultrafiltration step (Brown, et al., 1988), as
4 described in Britton et al. (2012). Collagen samples were analysed (in duplicate) for stable carbon ($\delta^{13}\text{C}$) and nitrogen
5 ($\delta^{15}\text{N}$) isotope ratios at the Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology
6 (MPI-EVA, Leipzig, Germany), on a Delta XP mass spectrometer coupled to a Flash EA 2112 elemental analyser.
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9 *Dental microwear analysis: Methods and material*

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12 Microwear features of dental enamel were examined using a stereomicroscope on high-resolution epoxy casts of teeth
13 following the protocol developed by Solounias and Semprebon (2002). After cleaning, the occlusal surface of the teeth
14 was moulded using high-resolution silicone (vinylpolysiloxane) and casts were created using clear epoxy resin. Casts
15 were observed under incident light with a Zeiss Stemi 2000C stereomicroscope at $35\times$ magnification, using the
16 refractive properties of the transparent cast to reveal microfeatures on the enamel. We used the classification of features
17 defined by Solounias and Semprebon (2002) and Semprebon et al. (2004) and quantified all categories of microwear
18 features (pits and scratches) on the paracone of the upper molars or the protoconid of the lower molars in a standard
19 square area of 0.16 mm^2 using an ocular reticule. Two areas were analysed on each tooth and the results were averaged.
20 We report the average numbers of pits and scratches, as well as a dietary indicator (%0-17, following Semprebon and
21 Rivals 2007). Finally, following Rivals et al. (2015), two measurements of variability of scratch density, namely the
22 standard deviation (SD) and the coefficient of variation (CV) are used to estimate the duration of the “mortality event”
23 of the reindeer from Abri du Maras level 4.1.
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31 *Cementochronology: Methods and material*

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35 Multiple teeth from nine deer including one megaceros and eight reindeer from level 4.1 were selected as these
36 appeared to the naked eye to have intact outer dental cementum. The methodology employed here for dental cementum
37 growth mark analysis (cementochronology) of the cervid teeth follows the protocol described in Pike-Tay (1995), which
38 built upon the methodological contributions of Pike-Tay (1991), Lieberman et al. (1990), and Burke (1993), including:
39 1) the preparation and use of radial “dry” thin sections (ca. 30μ) taken at the mesial-distal midline of the tooth; and 2)
40 the use of polarized transmitted light (common mag. = $40\times$, $100\times$, $250\times$) 3) for taking measurements of consecutive
41 growth zone widths at 2 or 3 cementum transects per tooth in the areas of acellular cementum near the tooth cervix
42 (root/enamel junction) where, on cervid and bovid teeth the apposition of growth increments is most regular.
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49 **Results and data interpretation**

50 *Bone preservation*

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52 The identification index, defined as the number of anatomical identified remains compared to the total number of
53 remains, is around 12%, which is low and mainly due to the high fragmentation of the fauna (Table 1; Fig. S2). Indeed,
54 the faunal assemblage is characterized by an important quantity of bone fragments, which are mainly unidentified bone
55 splinters and by a few isolated teeth (Table 1). Almost three-quarters of the recorded bone remains have one or several
56 green bone fractures (Table S2). Fracture profiles are mainly curved/V-shaped along with oblique angles and smooth
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edges (Fig. 4). Post-depositional fragmentation due to sediment compaction or secondary frost action damaged more than one third of the recorded remains. Only five complete or almost complete long bones were recorded. They are all metapodials: one horse metacarpal (III), three reindeer metacarpals and one reindeer metatarsal. Shaft bone fragments are far more numerous than epiphyseal fragments (Fig. S3). The vast majority (89%) have been reduced to a C1 circumference and have a L1/L2 length (Fig. S4).

Figure 4.

To evaluate the impact of bone preservation on the assemblage, we correlated bone density indexes with the %MAU for reindeer remains, which is the predominant species. The significantly positive correlation obtained between %MAU and bone density (with Spearman's $r_s=0.65$, $df=29$ and $t=4.67$: $p<0.001$) indicates strong differential destruction within the faunal assemblage. However, bone preservation is variable, depending on the excavated surface areas of the rock shelter. Some display an excellent degree of preservation and others show a high bone destruction index. In general, the bone destruction index, calculated as the number of isolated teeth compared to the total number of anatomically identified remains, is around 17%, which is moderate, but this rate may also be due to a strategy of abandonment of the heads at the kill site (see below) (Table 1). The representation of the various long bone portions confirms the impact of differential bone destruction on the sample (Fig. S3). Indeed, the best represented extremities are those with greater bone density, i.e. metapodials, radius-ulna and distal humerus (see Lam et al. 1999). The good preservation of some articular portions can be explained by the almost complete lack of carnivorous action. Only 10 bone elements bear carnivore marks, which represents less than 1% of the coordinated and legible remains. These are long bone articular portions of horse and reindeer and a few indeterminate remains. Besides that, there are also a very few remains (NR=7; <1%) with random striations on their surface which can be associated with trampling.

Remains with illegible surfaces are numerous, representing one third of the coordinated remains (Table 1). They have been excluded from the cut-mark or bone retoucher analyses in order to avoid biasing the calculation of the rates. This illegibility is mainly due to root etching which is present on almost 90% of the coordinated bone remains, with more than 50% being invasive on two-thirds of the surfaces (Table S3). Evidence of weathering is scant and concretions and polishing are practically inexistent. Black and orange colorations (oxides) are omnipresent but limited over bone surfaces (mostly stage 1).

Palaeoenvironments: the faunal, isotopic and charcoal evidence

Among small and large mammal remains, 98.7% of the NISP are ungulates and 1.3% are lagomorphs. There are no carnivore remains. They include, in order of abundance (Table 2): reindeer (*Rangifer tarandus*), horse (*Equus ferus* cf. *germanicus*), megaceros (*Megaloceros giganteus*), bison (*Bison priscus*), red deer (*Cervus elaphus*), ibex (*Capra ibex*) and lagomorphs (*Oryctolagus cuniculus* and *Lepus* sp.). This diversity confirms previous studies of level 4, highlighting open landscapes and a cold and arid climate (Comber 1967; Moncel et al. 1994; Daujeard 2008; Daujeard and Moncel 2010; Moncel et al. 2015). With 1 170 bone and teeth remains, reindeer is by far the most abundant species in level 4.1, representing 88% of the NISP and 55% of the MNI. The total MNI of the reindeer is estimated at 16 individuals. Horse is the second species, with 75 specimens and four individuals. The richness (2.08) and diversity indexes (Shannon indexes for MNI=1.5 and NISP=0.44; Simpson index=0.81 and $1/D=1.23$) and Evenness index for NISP=0.21) are low, highlighting limited diversity regarding the type of species.

Table 2.

1 Cervids are the most abundant taxa in level 4.1 with reindeer, red deer and giant deer. Reindeer (*R. tarandus*) were
2 affected by body size variation during the Pleistocene (Bouchud 1966; Delpech 1975; Weinstock 2001; Kuntz 2011),
3 but the bone remains from Abri du Maras level 4.1 are mostly badly preserved and very fragmented and are therefore
4 not suitable elements for a morphometric analysis. Antler preservation also prevents such analysis. Furthermore, the
5 much better preserved teeth seem to be a too stable indicator for this purpose. Red deer remains are also scarce and do
6 not allow for an appropriate discussion of *C. elaphus* status and its biochronological implications. Giant deer (*M.*
7 *giganteus*) displays typical dental morphology with a thick cingulum, wide and high entostyle, and strong styles and
8 stylids on both upper and lower molars. Upper premolars are also characterized by a thick, sometimes crenulated
9 cingulum. These elements are consistent with morphologies observed on other Upper Pleistocene specimens (Prat 1968;
10 Lister 1994; Vislobokova 2012).

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12 Only a few elements from horses from level 4.1 are suitable for paleontological and metric analysis. Nevertheless, they
13 all belong to the chrono sub-species *E. ferus* cf. *germanicus*, present throughout unit 4. Another equid species is present
14 in level 4.2, *Equus hydruntinus*, which is only represented by an upper molar with a very similar morphology to that of
15 the sub-species *E. hydruntinus davidi*. As it is very poorly represented in the sequence, the absence of this most
16 thermophilic species in level 4.1 does not appear significant. From a biochronological point of view, the *E. germanicus*
17 and *E. hydruntinus davidi* association is consistent with the chronological attribution of unit 4 to MIS 3 (Guadelli 1987;
18 Boulbes 2009). More precisely, the dimensions of the only complete horse metacarpal present in the level 4.1 are close
19 to those of other series from Tournal cave (B/D levels), Pair-non-Pair or Combe-Grenal, contemporaneous of the
20 beginning of the MIS 3. The few dental elements of large bovids enable us to identify the large steppic bison *B. priscus*.
21 A number of fish bones, mostly vertebrae, scales and fragments, have been retrieved from the excavation of the squares
22 H6, I6 and J6 (Table S4). Their preservation varies from bad to very good, but fragmentation is high. Out of a total
23 number of 167 fish remains, 46 could be identified to at least the family level. Two families are present: cyprinids
24 (NISP = 34) and percids (NISP = 12). Among the cyprinids, the chub (*Squalius cephalus*) has been identified on the
25 basis of a pharyngeal bone and several vertebrae. Percids are only represented by typical ctenoid scales belonging to the
26 European perch (*Perca fluviatilis*). Both species are currently common inhabitants of the Ardèche River. Chub size has
27 been estimated through direct comparisons with modern specimens from the reference collection. Estimated body
28 weights range between 550 and 850 g. In the absence of any fish predator at the site, as well as signs of chewing or
29 digestion, the presence of these fish remains in level 4.1 may result from anthropogenic activity. Nevertheless, more
30 information about dating and taphonomic analyses are required to support this assumption.

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32 The micromammals can be assigned to *Rodentia*, and are represented by a lower right M2 which has been assigned to
33 *Microtus* ex gr. *arvalis-agrestis* (MNI = 1). The presence of such species may indicate a rather open environment,
34 although it is impossible to estimate the degree of humidity due to the small number of collected anatomical elements.
35 Some bone surfaces seem to be altered, but no digestion marks were observed and it is therefore not possible to
36 confidently explain the origin of these elements at the site.

37
38 Isotopic results from the animal bone collagen extracted and analysed from Abri du Maras level 4.1, are presented in
39 Table 3 ($n = 9$; %C, %N and C:N also presented) and shown in Figure 5.

40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 **Table 3 and Figure 5.**

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58 Apart from a single sample (s-eva-30226), the atomic C:N ratios of the analysed samples range between 3.1 and 3.5,
59 and are therefore within the expected range for well-preserved bone (after van Klinken 1999), a range confirmed by
60 recent experimental data (Dobberstein et al. 2009). The majority of samples have %C and %N resembling that of

1 modern collagen (van Klinken 1999), and although a minority of samples have <11%N, C:N ratios all lie within the
2 acceptable range. The collagen preservation displayed in level 4.1 is unusual for material of this age, although collagen
3 has been successfully extracted from other archaeological sites of similar or even older ages in Northern Europe (e.g.
4 Britton et al. 2012, Jones et al. 2001, Richards et al. 2008, Kuitens et al. 2015).

5 As shown in Table 3 and Figure 5, despite the small number of samples, inter-species differences in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$
6 are apparent, albeit with a greater range in $\delta^{15}\text{N}$ values. *Equus* values exhibit both the lowest mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$
7 values, indicative of grazing, with *Rangifer* $\delta^{13}\text{C}$ values slightly elevated, which is commonly attributed to the
8 consumption of lichens. However, the most elevated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are exhibited in the two *Megaloceros*
9 samples. This is unusual, as previous isotopes studies of pre-LGM *Megaloceros* bone collagen from south-west France
10 indicated them occupying a similar niche to red deer (*Cervus elaphus*) (Immel et al. 2015), with lower $\delta^{13}\text{C}$ (relative to
11 reindeer) associated with leaf feeding in forested environments (Bocherens, 2003, Drucker, et al., 2008). These values
12 are therefore likely reflecting the contemporary environmental and ecological suite of this part of France (i.e. a lack of
13 extensive woodland cover), and also serve to confirm variability in *Megaloceros* dietary niche, which is consistent with
14 the suggestion that this species was a mixed/opportunistic feeder (Chritz et al. 2009). Elevated $\delta^{13}\text{C}$ values were also
15 determined in Irish *Megaloceros* dental enamel in a previous study, were related to the consumption of plants such as
16 forb species or sedges, which typically exhibit more positive $\delta^{13}\text{C}$ values (Chritz et al. 2009: 142). The higher $\delta^{15}\text{N}$
17 values seen in *Megaloceros* at Abri du Maras could also be consistent with this. The elevated $\delta^{13}\text{C}$ could also be
18 consistent with the consumption of mosses or lichens, as with reindeer. However, the rumen microbiology of modern
19 (and presumably archaeological) reindeer/caribou, unlike other extant deer species, is adapted for lichen-consumption
20 (Sundset et al. 2008), and it is not known if this would have been the case for *Megaloceros*. Overall, a range of ca. 3 ‰
21 is observed in $\delta^{15}\text{N}$ values across the dataset (from 2.2 ‰ to 5.5 ‰), and there are clear inter-species differences, which
22 probably reflect these different niche feeding behaviours.
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33 Tooth microwear data for the reindeer (Table 4) were obtained from eight specimens out of the 14 moulded specimens
34 from level 4.1. Six specimens were excluded for taphonomic reasons (weathering or root alterations). The average
35 number of scratches and pits, as well as the %0-17, indicate a diet that can be classified as grass-dominated mixed
36 feeding. Compared to other samples of fossil reindeer (Table 4), the population from Abri du Maras is similar to that of
37 Portel-Ouest (Ariège, France) (Fig. 6). The average number of pits, as well as other variables like the percentage of
38 large pits or scratch width, are very similar, suggesting the same dietary traits at both sites. This resemblance is
39 probably related to a similar environmental context in Southern France during the Late Pleistocene. The horse is only
40 represented by two teeth, but even with a very small sample size, the microwear pattern indicates pure grazing (Fig. 7).
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47 **Table 4 and Figures 6 and 7.**

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50 The charcoal study was based on the analysis of only 17 charcoal fragments handpicked during the excavation among a
51 great quantity of very small-undetermined fragments. The remains from Abri du Maras are probably related to the use
52 of fuel. Three different taxa, comprising *Betula* (birch) (13 fragments), *Pinus sylvestris* type (scots pine type) (2
53 fragments) and cf. Fabaceae (1 fragment) and 1 undetermined fragment. *Betula* is the most abundant, however due to
54 the low number of fragments, the taxa should be considered to be equally represented. These results are similar to those
55 from the other layers from Abri du Maras, where *Pinus sylvestris* type is the most recurrent taxon throughout the
56 sequence (unpublished report; Moncel et al. 2015). However, level 4.1. is the only level with *Betula*. *Pinus sylvestris*
57 includes the three mountain types *Pinus sylvestris*, *Pinus uncinata* and *Pinus nigra* ssp. *salzmanni*, which cannot be
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1 distinguished due to their similar wood anatomy (Schweingruber 1990). These taxa correspond to heliophilous trees
2 growing under dry and cold conditions. *Betula* can also grow under cold conditions but needs higher soil humidity rates.
3 Both taxa are colonizer species and could form part of open forests or forest grooves. *Betula* has also been described in
4 other sites from, for example, Northern Iberia where it is related to increased precipitation and a more humid
5 environment (Uzquiano 2008). The results from the charcoal analyses back up the characterization of mosaic
6 environments during MIS 3 with open landscapes but also arboreal cover. Other European anthracological records show
7 similar patterns with a dominance of conifer forests and *Betula* as the main arboreal cover. These species would
8 probably coexist, as also observed in other MIS 3 records from Northern Iberia and Central France (Théry-Parisot and
9 Meignen 2000; Théry-Parisot and Texier 2006; Uzquiano 2008; Uzquiano et al. 2008; Uzquiano et al. 2012).

13 *Neanderthal hunting: animal population and seasonality*

16 The 16 reindeer individuals are composed of seven juveniles, two young adults, two prime age adults, three old adults
17 and two senile individuals (Table 2). No foetal remains were discovered, probably because of the differential bone
18 preservation of the sample. This age distribution shows a majority of young individuals. Once plotted on a ternary
19 diagram and after correction as mentioned above in the Methods section, the reindeer population falls into an L-shaped
20 zone (Living structure or catastrophic mortality profiles) (Fig. 8). As noted above, unfortunately, the bad preservation of
21 the reindeer bones and antlers precludes any morphometric and thus sex ratio analyses.

27 **Figure 8.**

30 Taking into account the period of birth for reindeer (May-June) and the period of death for young individuals, four
31 juveniles died during the fair season (possibly from spring to summer) and five others during the autumn (from
32 September to December). Two juveniles are about 3-5 months old, two are 12-15, one is 17-20 and two are 22-27
33 months old. Two sub-adults (category young adult) died at the age of 27 to 30 months.

36 Regarding cementochronology, out of the nine studied samples in level 4.1, only four gave positive results (Table S5).
37 They correspond to four reindeer teeth and indicate periods of death during the autumn. These results confirm those
38 based on the periods of tooth eruption, i.e., a majority of animals died during the late summer and autumn. This period
39 corresponds to the present-day great migrations (end of summer and then end of autumn) and rut (October) periods for
40 reindeer (after Miller, 1971), a time of the year when all age classes and both sexes herd together.

44 Age determination was possible in a small number of individuals of other taxa (Table 2), although ages were mixed and
45 there were insufficient numbers for any clear trends to emerge. The horse series yielded one deciduous foal incisor (0-3
46 months old) indicates a period of death during the summer (births in early May).

49 The variability of scratch microwear density is used as a proxy for the duration of occupation at archaeological sites. In
50 the case of level 4.1 of Abri du Maras, it corresponds to low variability both in terms of CV and SD (Table 4). Such
51 values fall within the area of seasonal events (or shorter), i.e., area [A] on Figure 6. Values are similar to the signal
52 observed for the reindeer from Salzgitter Lebenstedt (Germany), where animals (MNI = 86) were hunted during a
53 seasonal event in the fall (Gaudzinski and Roebroeks 2000; Rivals et al. 2015). The pattern is significantly different to
54 that reported for longer-term occupations (longer than a season), as at Kent's Cavern (UK) or level G of the Caune de
55 l'Arago (France).

61 *Carcass transport and processing*

1 For reindeer, for the survival rates for each anatomical element, upper and lower long bones largely dominate the
2 distribution (Fig. 9). Among them, we observe a strong and positive correlation between the volume of the marrow
3 cavity and %MAU of long bone elements (with Spearman's $r_s=0.72$, $df=9$ and $t=5.56$: $p<0.001$). The good
4 representation of tibias, which have the highest marrow content, must be moderated, as it is easier to determine them.
5 Taking into account the seven main carcass portions (%MAU), the skeletal profile underlines the scarcity of the head
6 and of the limb extremities, the near absence of the vertebral column and the predominance of forequarters and
7 hindquarters (Fig. S5). No correlation exists between FUI indexes and %MAU for all types of reindeer elements (with
8 Spearman's $r_s=-0.04$, $df=13$ and $t=-0.19$: $p>0.8$). However, before interpreting these data in terms of human strategies,
9 we have to consider the positive correlation between MAU rates and density indices (see above). This indicates some
10 preservation bias of the bone assemblage. Nevertheless, the deficiency of isolated teeth and cervid antlers confirms the
11 rarity of heads (Figs. 9 and S5). Similarly, the scarcity of basipodials and phalanges cannot be explained by a problem
12 of determination or density and thus highlights a real absence. Finally, it is difficult to specifically determine ribs and
13 vertebrae, but all parts of these elements, even the densest ones, are rare, in the same way as the indeterminate elements
14 belonging to the middle-sized ungulate category. Thus, here too, we can consider the rarity of the trunk as a reality.
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23 **Figure 9.**

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26 For the other animals, the number of remains is not sufficient to calculate the MAU, but based on the NISP we can
27 make some comments. For the horse, we observe the same rarity of the trunk (with only one rib fragment) and
28 inversely, the important presence of heads. Two isolated bison teeth and six hindquarter elements are represented: four
29 tibias, one femur and one metatarsal. The megaceros comprises 20 elements, made up of one mandible, one maxillary,
30 one lumbar vertebra, one radius, one hamate, one femur, five tibias and nine metatarsals. Red deer is only represented
31 by six long bone remains: one humerus, one radius, one tibia and one metatarsal. Caprines are represented by four
32 isolated teeth and one femur shaft fragment. As for lagomorphs, rabbit remains comprise one isolated tooth and one
33 metacarpal and the hare one scapula, one humerus and one tibia. Indeterminate lagomorphs regroup two isolated teeth,
34 one scapula, one humerus, one radius, one phalange, one femur, one tibia and two indeterminate elements.
35 21.8% of the legible remains bear cut marks, scraping marks and incisions made by sharp lithic tools. All the main
36 ungulate species have been processed (Table 5). Slightly less than a third of the reindeer and horse elements bear cut
37 marks. Some bison, red deer and megaceros portions also show butchery striations. Concerning the *chaîne opératoire* of
38 carcass processing, depending on the taxa, various stages were processed in the shelter: skinning, dismembering and
39 retrieving tendons, periosteum, flesh, marrow and bone grease removal.
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49 **Tables 5 and 6.**

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52 Reindeer include 199 bone elements with cut marks. Most of these are long bone shafts (Table 6). The forelimbs were
53 skinned, as indicated by numerous metacarpal fragments with oblique and parallel incisions of various lengths spread
54 along the anterior and medial faces, and then dismembered (humerus/radius-ulna) and defleshed. This latter step is
55 mostly represented on humerus and radius-ulna by oblique or longitudinal striations spread along the shafts. Tendons
56 were retrieved resulting in transverse marks on the posterior face of some metacarpals. Six fragments of metacarpals
57 bear scraping marks as well as longitudinal long incisions representative of periosteum removal before marrow
58 extraction. One vestigial metapodial displays thirty short and oblique cut marks typical of the skinning process. As for
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1 the hind limbs, metatarsals point to skin, periosteum and tendon removal, femurs and tibias were defleshed and
2 disarticulation was observed, for tibia/femur on three proximal tibias and for tibia-tarsal on two distal tibia portions and
3 one astragalus with short and deep cut marks on its medial surface. Two fragments of cut-marked mandibles indicate
4 the recovery of cheek meat. Finally, seven rib fragments are cut marked, some due to evisceration, but most of them as
5 a result of defleshing.

6 For the horse, cut marks show forelimb dismembering (humerus/radius-ulna) and flesh (cheek) removal on two
7 mandible fragments, two tibias and one femur. Bison remains comprise two tibia shaft fragments with filleting marks
8 and one metatarsal fragment with scraping and skinning marks. Evidence of megaceros skinning is present on a
9 metatarsal bone, defleshing on a tibia shaft and evisceration on a lumbar vertebra. One red deer humerus bears a dozen
10 short and deep cut marks on its lateral epicondyle (distal end), indicating disarticulation.

11 Five of the 10 lagomorph elements highlight the presence of cut marks and/or green bone fracturing. These elements are
12 the distal extremity of a hare humerus, two proximal scapula portions (hare and indeterminate), two femur shaft
13 fragments and a tibia (indeterminate), showing meat removal and the disarticulation process.

14 Marks with diagnostic criteria of intentional anthropogenic breakage are present on 481 remains of taxonomically
15 identified ungulate long bones. These marks are mainly percussion notches or impact flakes. Incipient percussion pits
16 are rare (1) and peelings were not observed, partly due to the poor conservation of the bone surfaces (root etching). We
17 did not identify any adhering flakes. Concerning positive flake scars, only eight '*boutons de manchette*' were observed,
18 mostly in shaft bone fragments (undetermined bones). Long bone shaft parts present the highest rates of percussion
19 marks (99%), distributed over the diaphysis surface with no preferential location (cf. Vettese, 2014). Only six articular
20 portions display percussion marks. Regarding taxa distribution, the megaceros (33%) bears the highest proportion of
21 percussion notches, followed by the horse (29%), red deer and reindeer (25%) and bison (17%). Notches are more
22 abundant on tibias and humeri (37%), femurs (35%) and then metacarpals (22%), metatarsals (20%) and radio-ulnas
23 (18%). Apart from long bone elements, a few horse and reindeer mandibles and three calcanei were fractured for
24 recovering marrow. All the phalanges were complete or almost complete.

25 Burning damage was observed on 20.7% of the faunal remains (Table S6). The majority of these remains are
26 represented by small fragments with a length of less than 25 mm (95.4%). In that size category, compact bones are
27 dominant. Nevertheless, spongy carbonized bone fragments of all sizes represent a quarter of the burnt elements. The
28 rate of carbonized bone fragments reaches 81.4%. Based on experimental and archaeological data (Costamagno et al.
29 2009), those data are commonly interpreted to reflect the use of bone for fuel. The low percentage of burnt spongy
30 bones may be due to their high vulnerability to atmospheric agents (Gerbe 2010). Out of the 19 identified burnt bone
31 elements, it is noteworthy that four are short articular bones (one lunate bone, one hamate bone and two malleoli), one
32 is a vertebral element (axis fragment), one is a mandible fragment and 13 are long bone portions (shaft and articular
33 portions).

34 Lastly, only one small shaft fragment presents retouching marks on its surface. This artefact was burnt (carbonized) and
35 remains indeterminate. The marks are situated on the apical zone and can be associated with sliding striations due to
36 contact with lithic cutting edges. They are short (< 10 mm), dispersed and perpendicular to the long axis (Patou-Mathis
37 and Schwab 2002).

38 Discussion

39 Assessing the origin of a faunal accumulation necessitates the consideration of numerous aspects, such as the
40 archaeological and sedimentological context, as well as taphonomic data. At Abri du Maras, all the data point towards
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1 an almost exclusively human accumulation. Spatial analyses underline the close association between the faunal and
2 lithic remains unearthed in level 4.1, indicating one distinct occupation phase. Furthermore, the numerous faunal refits
3 ($n=65 - 148$ elements) and anatomical connections ($n=22 - 68$ elements) identified in this level, associated with the
4 short distances between connecting elements, attest to its homogeneity and sub-contemporaneity. In addition, the
5 numerous butchery marks ($\approx 20-30\%$ of the NISP), burnt bones and green bone breakage (70% of long bones), as well
6 as the absence of carnivore remains and the scarcity of carnivore impacts on bones ($<1\%$), allow us to identify this
7 faunal accumulation as human. In this exceptional almost exclusively human accumulation context, data from age and
8 skeletal profiles, as well as seasonality, can be used to assess Neanderthal subsistence behaviours, in a well-defined
9 palaeoenvironmental context.
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12 *Palaeolandscapes of MIS 3: a new framework*

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16 The combination of data, such as the faunal spectrum combined with extant herbivore ecological data, isotopes and
17 tooth microwear, enable us to define the palaeoenvironments in level 4.1 at Abri du Maras. The predominance of
18 reindeer in the faunal spectrum, associated with horse and bison suggest open and steppe landscape, while the presence
19 of ibex highlights the rocky landscapes. Additionally, the identification of *Microtus arvalis-agrestis* within the
20 microfauna supports the idea of an open environment. The presence of (what are typically considered) browsers, such as
21 megaceros and red deer, however, could be indicative of the presence of woodland (see Ecker et al., 2013 for
22 references). Nevertheless, the well-known plasticity of the red deer (Straus 1981; Guérin and Patou-Mathis 1996;
23 Discamps and Royer 2016) associated with the unusual isotope values obtained in this study for the megaceros,
24 contribute to highlight that those species were exploiting different ecological niches. Indeed, whereas the isotope data
25 from horses is typical of grazers, the relatively high $\delta^{13}\text{C}$ observed in megaceros specifically, do not suggest feeding in
26 woodland areas, but instead could indicate mixed-feeding in open environments, indicating that this species was also,
27 like the red deer, an opportunistic feeder. The $\delta^{15}\text{N}$ values show clear inter-species differences, consistent with various
28 niche feeding behaviours on plants with varying $\delta^{15}\text{N}$ values. Tooth mesowear and microwear indicate an intermediate
29 position between grass and browse feeders for reindeer and for horse a graze-dominated diet. Data for reindeer and
30 horse are consistent here with those of the carbon stable isotope values, i.e. no clear habitat preference for reindeer
31 (mixed feeder, incorporating lichens or other browse) and contrariwise preference for open landscape grazing for horse.
32 The analysis of red deer bone collagen and tooth wear for megaceros from the site in a future might illuminate the
33 extent of this woodland.
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36 Although broadly a cool, open environment, the pedo-sedimentary facies at the site does suggest occupation during
37 short humid episodes with pronounced pedological development that alternate with drier and cooler phases dominantly
38 marked by accumulation of aeolian dust during the uninhabited periods. This may be indicative of the abandoning of the
39 landscape by Neanderthals during the harshest periods. Finally, charcoal data identify the predominance of birch
40 relatively to scots pine in the level 4.1, indicating sufficient humidity for the development of birch forests. Thus, these
41 data confirm a cool yet moister climate than expected by the faunal spectrum and thus reinforce the characterization of
42 the mosaic environments during the MIS 3 with open lands but also some arboreal cover. Finally, despite the dating
43 margins of error, human occupations of the level 4.1 of Abri du Maras, dated between 40 ± 3 ky and 46 ± 3 ky ($n=2$)
44 (Richard et al. 2015), may correspond to the warm event or Dansgaard-Oeschger event 12 (DO#12) observed in the
45 Villars speleothem records, just preceding the H4 cooling event, contemporaneous of the Neanderthal demise in western
46 Europe (Genty et al. 2010). According to this study, DO#12 was likely warm and humid with fast growth rate and low
47 $\delta^{13}\text{C}$, consequence of intense soil and vegetation activity. This is consistent with the contemporaneous pollen record of
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the Monticchio lake which indicates a high percentage of woody taxa (with *Quercus*, *Betula*, *Ulmus*, *Fagus*), testifying a woody steppe with relatively warm and humid climate (Allen et al. 2000; Genty et al. 2010).

Selective mass reindeer predation at level 4.1 of Abri du Maras?

With 88% of the NISP, reindeer is the most represented taxon in the faunal spectrum. The richness and diversity indexes highlight a spectrum similar to monospecific ones, such as Les Pradelles (Evenness=0.23 in level 9 and 0.36 in level 10; Costamagno et al. 2006), Le Lazaret-UA25 (Richness=1.41 and Shannon=1.5 for MNI) and the Proto-Magdalenian level of Abri Pataud ($H < 1$) (see Valensi et al. 2015) for cervids (among others). Large bovid-dominated faunal assemblages are also numerous, with examples such as Mauran (Farizy et al. 1994; $E=0.05$ and $1/D=1.02$, in Grayson and Delpech 2002 and $E=0.04$ in Rendu et al. 2012), La Borde (Jaubert et al. 1990; $E=0.16$ and $1/D=1.098$, in Grayson and Delpech 2002) in France or Wallertheim in Germany (Gaudzinski 1995). Even dangerous and solitary species such as the rhinoceros were selectively hunted by humans with the famous example of Taubach in Germany (Bratlund 2000). Mass mammoth hunting by driving is postulated for the Saalian site of La Cotte Saint Brelade in Jersey (Scott, in Callow and Cornford 1986). According to the study of Gaudzinski-Windheuser (2006), such anthropogenic mono-specific faunal spectra increased significantly all over Europe from MIS 5 onwards (see also above in the Introduction).

The age distribution of the 16 reindeer individuals from level 4.1 indicates a living structure. Age profiles pointing to catastrophic mortality are representative of natural disasters, mass kills or non-selective hunting episodes (Lyman 1987; Stiner 1990; Discamps and Costamagno 2015). Mass kills or non-selective slaughters within the herds are both plausible. Similar age profiles have been observed for other Middle Palaeolithic cervid accumulations, such as Salzgitter-Lebenstedt (MNI=86), Les Pradelles (Level 9, MNI=33; Level 10, MNI=22), Roc de Marsal (Layer 4, MNI=12/estimated MNI=78), Jonzac (Layer 22, MNI=18) or Pech de l'Azé IV (layer 4, MNI=25) for reindeer (Gaudzinski and Roebroeks 2000; Costamagno et al. 2006; Niven et al. 2012; Niven 2013; Castel et al. 2016), as well as Pech de l'Azé I (Level 4, MNI=19) for red deer (Rendu et al. 2010), considered to be the result of non-selective hunting. Inversely, some bovid-dominated assemblages, such as Wallertheim (Level B1, MNI=52) (Gaudzinski 1995), show repeated, selective and controlled collective hunting episodes, indicating that human strategies are not the same, depending on the hunted species and environments. All these sites display one single dominated species, and the only difference lies in the number of individuals, mainly depending on the excavated surfaces and the number of human occupation episodes.

At Abri du Maras, seasonality indices can be linked to human hunting activities. Indeed, added to the presence of unretouched Levallois points used as projectile tips and large Levallois blades and points brought to the site (Hardy et al., 2013; Moncel et al., 2014), the taphonomic analysis (see above) clearly associates the faunal assemblage with planned hunting activities. The seasonal indices for level 4.1 show that most of the reindeer deaths occurred during the autumn (September to December). Furthermore, tooth microwear data correspond to seasonal events, similar to those observed for reindeer from Salzgitter, which reflect short-term mass death scenarios during the same period around September. The three short-term stopping places of Les Pradelles, Jonzac and Salzgitter show the same period of death for reindeer (Gaudzinski and Roebroeks 2000; Costamagno et al. 2006; Niven et al. 2012), coinciding with the reindeer's fall migrations. Fall migration is a time of the year where herds are not segregated and males (before and during the rut) and females are in particularly good physical condition, optimizing energy return for hunters. Even amongst sedentary ecotypes, Fall is the period where body condition is optimal and fat reserves are highest in *Rangifer*,

following Summer feeding. Unusually, at Pech de l'Azé IV, humans seem to have hunted reindeer during their spring migration.

Concerning the skeletal profiles, long bones largely dominate the accumulation, and among them, the richest elements in marrow, indicating primary carcass processing on the kill site and then selective transport of the carcass elements. The scarcity of the axial skeleton (head and trunk) and of the limb extremities (short articular bones) could indicate their abandonment at the kill site and/or an in situ differential and/or spatial preservation or treatment (grease bone extraction, use of bone as fuel). These data may be related to the significant and positive correlation between bone density and the %MAU, highlighting the rarity of the less dense bone portions on the site (mainly long bone extremities and axial skeleton). Nevertheless, as indicated above, the rarity of isolated teeth and antlers confirms the absence of the heads. Concerning the trunk, all portions are scarce, even the densest ones and also indeterminate elements. Thus, the near-absence of the axial skeleton cannot be entirely explained by the post-depositional destruction of low-density elements and we can instead postulate that these parts were frequently abandoned at the kill site and/or exploited and thus destroyed by Neanderthals once transported to the site. As for the paucity of carpals and tarsals, the presence of metapodials and of other limb portions at the site raises questions as to their in situ disappearance. As these parts are not particularly fragile, this may also result from specific in situ treatment rather than differential preservation. The scarcity of phalanges is more easily explained, suggesting the hypothesis of skin exportation. However, specific spongy bone processing at the site (for fuel or grease extraction), including articular portions as well as vertebral elements, may also be a valid explanation.

At Roc de Marsal, interestingly, the authors (Castel et al. 2016) observe the same scarcity of heads (including antlers), short articular elements, phalanges and the axial skeleton, as a result of the combination of different causes: in situ differential preservation, in situ specific treatment and the abandonment of some carcass elements at the kill site. Concerning spongy bone treatment, the main difference between both sites lies in the lack of fire evidence at Roc de Marsal and conversely in the many fire indices at Abri du Maras: ash lenses and numerous burnt bones. Nevertheless, other types of carcass exploitation behaviours exist in the Middle Palaeolithic reindeer-dominated assemblages. For example, at Jonzac, the skeletal profiles indicate the transport of whole carcasses to the site, whereas at Les Pradelles (Levels 9 and 10), which is considered as a secondary butchery site, Neanderthals may have mostly selected upper long bones and then exported some fleshy portions to another camp. Due to the absence of evidence of fire and the presence of carnivore tooth marks on bones at Les Pradelles, the same hypotheses regarding the scarcity of spongy bone elements at this site cannot be advanced. At Pech de l'Azé IV, the most nutritious body parts were selectively transported to the site. At the open-air site of Salzgitter-Lebenstedt, the data point towards the hunting of high-quality animals and the in situ processing of limb bone elements for flesh and marrow, with possible evidence of food storage, as at Les Pradelles (Gaudzinski and Roebroeks 2000; Costamagno et al. 2006). In general, in all these reindeer-dominated assemblages, except those of Salzgitter and Jonzac, which served as primary butchering locations where reindeer skeletons were mostly retrieved complete, we observe a deficiency of the axial skeleton (heads, vertebrae and ribs), as well as the girdles (pelvis and scapula) and the short articular bones (carpals, tarsals and phalanges). All these parts cannot be equally affected by low-density differential preservation, and thus large carcass portions appear to have been abandoned at the kill site during the early butchery stages (disarticulation) and/or affected by specific anthropogenic treatment at the base camp (grease bone extraction and/or use of bones as fuel). The lack of fire in many of these places, such as Roc de Marsal, Pech de l'Azé IV (layer 4), Les Pradelles, Jonzac or Salzgitter, may point towards a combination of the frequent abandonment of the trunk, short articular bones, heads with antlers, as well as skins, including phalanges and in situ grease extraction of the transported spongy elements. This moderate presence of skulls and minor presence of phalanges, associated with a representation of the limb bones relative to marrow

contents, has already been highlighted for reindeer assemblages from the Middle Palaeolithic (Gaudzinski-Windheuser and Niven 2009).

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2 Finally, at Abri du Maras, the numerous cut marked elements, associated with the almost systematic green bone
3 breakage of limb elements for marrow recovery and the possible use of bones for fuel, indicate intensive *in situ* carcass
4 treatment and consumption. All stages of the butchery process are identified: from evisceration, to skinning,
5 disarticulation, defleshing and the removal of tendons. Nevertheless, due to the lack or the scarcity of certain skeletal
6 parts (vertebrae, ribs and long bone extremities), evisceration and disarticulation are very poorly represented. As for
7 long bone breakage for marrow, 85% of the long bone remains bear green bone fractures. This rate is high, but still
8 moderate compared to other anthropogenic faunal assemblages where the near totality of yellow marrow bones are
9 fractured, including not only long bones, but also phalanges, tarsals and mandibles (i.e. Les Pradelles or Roc de Marsal
10 in south-western France: Costamagno et al. 2006; Castel et al. 2016 or Saint-Marcel or Sainte-Anne I in the Southeast:
11 Daujeard 2007; Daujeard et al. 2012). Here, very few mandibles and calcanei and no phalanges present green bone
12 breakage. Some anatomical connections (limb bone elements) and whole long bones, especially reindeer metacarpals,
13 were found in level 4.1. The same behaviour has also been observed at Jonzac and Salzgitter-Lebenstedt, where, at the
14 latter site, Neanderthals frequently discarded poor long bone elements and some metacarpals were abandoned whole. In
15 all these reindeer-dominated assemblages, evidence of *in situ* meat filleting and marrow exploitation by Neanderthals
16 has been documented, associated with very scarce indices of carnivore action. The rarity of the presence of traces of
17 fire, only recorded in the level 4.1 of Abri du Maras, may indicate different site functions and possibly longer
18 occupation durations.

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20 At Abri du Maras (level 4.1), the clear monospecific spectrum, catastrophic mortality and autumnal deaths point to
21 short-term hunting episodes of migratory mixed herds. At that time of the year, Neanderthal groups focused on
22 preferential prey, predominantly available in the surroundings. However, as underlined by Costamagno et al. (2006), the
23 question of ‘obligate’ versus ‘deliberate’ specialization is very difficult to assess (see below). Likewise, it is very
24 difficult to discern between successive individual hunting episodes and mass kills. Many criteria, such as sedimentation
25 rates, refits and the volume of the excavation must be taken into account for evaluating the presence of a single
26 depositional episode. Unfortunately, these data are difficult to obtain in the literature and thus difficult to compare.
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28 What can be said of Abri du Maras (level 4.1) is that the presence of numerous short distances refits and of ash lenses at
29 a same depth seems to suggest a main phase of human occupation. Like most of the reindeer-dominated assemblages
30 (except for Salzgitter), level 4.1 has a high MNI of reindeer (between 10 and 30) and indicates that hunters regularly
31 discarded carcass portions at the kill site. Added to the predominance of reindeer in the assemblage and catastrophic and
32 seasonal mortality (Costamagno et al. 2006; Rendu et al. 2012; Lubinski 2013), mass procurement is the most likely
33 explanation.

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35 Finally, at Abri du Maras, carcasses were clearly being butchered elsewhere at the kill site and then the limb elements
36 were commonly selected to be transported to the site. The presence of some long bones, still complete or even in
37 anatomical connections, as at the site of Salzgitter-Lebenstedt, further supports the hypothesis that level 4.1 is
38 predominantly the product of mass hunting episodes.

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55 *Neanderthal hunting of reindeer in the Upper Pleistocene of Western Europe: selective and planned behaviour or*
56 *environmental constraints?*
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59 Reindeer-dominated assemblages are a specific type of single species-dominated assemblage, associated with a seasonal
60 hunting model. This is the case at Les Pradelles, Jonzac, Roc de Marsal, Pech de l’Azé IV in south-western France or
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Salzgitter in the north of Europe. Some authors argue that such assemblages result from the opportunistic response of Neanderthals to taxa availability (Niven et al. 2012; Niven 2013). Neanderthals may have hunted reindeer because of their dominance during cold periods and because of the lack of other ungulates in the environment, such as bison or horse. This observation is similar to that of Grayson and Delpech (2003) for the Magdalenian assemblages at Grotte XVI, where the increase in reindeer remains is interpreted as a direct reflection of what was available in the environment during periods of cold summer temperatures. Similarly, on a regional scale, the study of Magniez and Boulbes (2014) at Tournal Cave underlines the important role of environmental changes on the dietary behaviour of human groups during the Upper Pleistocene, from MIS 3 to MIS 2. This point of view is also supported by the data from Discamps (2013), showing important biomass fluctuations between the Quina and post-Quina periods in south-western France. According to that author, the Quina period corresponds to a low ungulate biomass episode marked by growing reindeer populations. Inversely, during the late Middle Palaeolithic, or 'Post-Quina' period, ungulate biomass increases with the highest rates of horse and bison. Nevertheless, more recent palaeoenvironmental reconstruction from large and small mammal communities (Discamps and Royer 2016) tempers those chronological changes in the South-West, underlining the importance of seasonal and geographical differences. Indeed, the latter is illustrated in the South-West for the Quercy region, where a high ungulate biomass environment persists during the Quina episode (Discamps 2013). About seasonality influence, it should be noted that while limited strontium isotope evidence suggests migratory behavior in late Pleistocene European reindeer, this has yet to be demonstrated for bison (Britton et al. 2011, Julien et al. 2012). One other notable factor is that the faunal spectra of the reindeer monospecific assemblages of Jonzac and Pech de l'Azé IV, as well as in all Upper Pleistocene assemblages of this type, whether they are in Western or Northern Europe, always comprise horse, bison and red deer alongside reindeer. Finally, the recent TL ages of Guérin et al. (2016) at Roc de Marsal (average of 49 ky, $n=5$) suggest a longer duration for the Quina Mousterian with reindeer-dominated assemblage in south-western France, extending until MIS 3, very close to the ages obtained for level 4.1 of Abri du Maras. These new TL ages (Guérin et al. 2012, 2016) also confirm the association of some Levallois assemblages with mixed fauna (red deer, roe deer and reindeer) at the beginning of MIS 4 (ca. 65-70 ky) and that of others with reindeer-dominated spectra at certain moments of MIS 3 in south-western France (Rendu et al. 2014). All those data invalidate the strict association of MIS 4 with Quina technological complex and reindeer-dominated spectra in that region, providing a more complex view of palaeoenvironmental evolution during MIS 4 and MIS 3. Thus, taking into account those difficulties in chronological resolution and environmental reconstruction, we may keep in mind the possibility that this monospecific reindeer hunting behaviour may rather reflect a preferential selection of prey, than environmental constraints (see Castel et al. 2016).

In south-eastern France, a different situation emerges with a very low number of reindeer-dominated assemblages for the Upper Pleistocene. Other Middle Palaeolithic and even Early Middle Palaeolithic single species-dominated assemblages with seasonal slaughters have been observed in the south-east. This is the case at Sainte-Anne I, Saint-Marcel, Abri Moula (interglacial levels) and Le Lazaret (UA25), with spectra largely dominated by cervids or at Baume des Peyrards, in the Vaucluse, where the ibex is the main hunted animal (Daujeard and Moncel 2010; Moncel and Daujeard 2012; Daujeard et al. 2012). Nonetheless, only some Late Middle Palaeolithic occupation phases, Baume Néron, Abri Moula and Abri du Maras, all situated along the Rhône Valley, show faunal spectra dominated by reindeer and followed by bison and horse. All these assemblages correspond to the end of MIS 4 or the beginning of MIS 3 (Defleur et al. 1994; Defleur et al. 2001; Richard et al. 2015), with cold and humid environments. At Abri du Maras, we observe different faunal spectra within a same sedimentary unit and chronological time span (Richard et al. 2015). Indeed, level 4.2, which is situated just below level 4.1, provides a more varied faunal spectrum dominated by bison and horse and followed by red deer, reindeer and megaceros. Besides that, preliminary seasonal data for the horse and

1 megaceros from level 4.2 give different periods of human occupations, during the spring and the summer (Daujeard, in
2 Moncel et al. 2014, unpublished report). Thus, the differences existing between these two sub-contemporaneous levels
3 may be explained here by the planned seasonal organization of Neanderthal groups, depending on the presence of some
4 species in the surroundings, at local and short chronological scales, rather than on a real absence of other animal
5 community. Indeed, the reindeer dominated-assemblage in level 4.1 could result from selective hunting by highly
6 mobile human populations, who knew the location of shallow river crossings (natural fords), facilitating the passage of
7 animals across the Ardèche River, and also possibly the timing reindeer migrations along the Rhône Valley. If reindeer
8 were indeed migratory at this time period, and in this region, the hunting of non-migratory ‘local’ animals, in smaller
9 numbers (relative to reindeer) could also be an important buffer against the time-stress activity of interception hunting.
10 Were the reindeer herds targeted non-migratory, and instead exhibited more local ranging behavior, other factors could
11 explain this selection. For example, the aggregations of males and females that occur during the rut in both migratory
12 and sedentary herds, and the prime condition of the animals during Autumn (in terms of body weight and fat
13 percentage). The strontium isotope analysis of reindeer teeth from Level 4.1 of Abri du Maras would serve to illuminate
14 this further, and help determine if reindeer targeted were indeed migratory. However, whether it was to intercept
15 migratory herds, or to take advantage of the Autumn aggregations of prime conditioned reindeer herds (migratory or
16 non-migratory), the intense and seasonally-restricted nature of reindeer exploitation at Abri du Maras infers the
17 selective, seasonal appeal of this area for contemporary groups on their seasonal rounds . At Abri du Maras, this
18 behaviour, highlighting planned and communal mass hunting strategies, seems here to “imply a deliberate selection of
19 particular species from the total resources potentially available for exploitation” (Mellars 1996: 196). Significantly,
20 Abri du Maras confirms the deeper antiquity of the practice in another region of Europe than previously identified
21 (mainly south-western France and Northern Germany).

22 Thus, the faunal analysis of level 4.1 of Abri du Maras provides evidence of a new occurrence of planned, collective
23 and selective Middle Palaeolithic reindeer hunting, considerably further east than other well-known sites in south-
24 western France, such as Les Pradelles, Jonzac, Roc de Marsal or Pech de l’Azé IV. Indeed, south-eastern France
25 displays rare cases of reindeer-dominated assemblages along the Rhône valley. The sites of Abri du Maras, Abri Moula
26 and Baume Néron present faunal spectra representative of cold and humid occupation phases related to the last
27 glaciation, at the end of MIS 4 and beginning of MIS 3. The main difference with the south-western assemblages, is
28 that, with Salzgitter, these assemblages are all associated with a predominantly Levallois production (points and
29 elongated products) with very few or no Quina retouches. At Salzgitter, a Micoquian series including Keilmesser-types
30 is associated moreover with the Levallois débitage (Tode et al. 1953). Thus, it is interesting to note that the model
31 advanced by Delagnes and Rendu (2011) for the South-West, with a Quina system associated with well-planned
32 reindeer exploitation, a discoïd-denticulate system reflecting more opportunistic behaviours related to bison or horse
33 hunting and a Levallois technology related to foraging mobility with no selective hunting, cannot be applied to other
34 regions. Finally, at Abri du Maras, we must underline that part of tool kit production, such as the use of some points
35 used as projectiles, was planned before arriving on the site. This far-sighted lithic behaviour may be related to the
36 planning of reindeer herd slaughtering by Neanderthal groups. However, despite that observation, we do not observe a
37 link as clear as that observed in the South-West between planned monospecific hunting strategies and lithic
38 technologies, adding to the complexity of the scenario.

39 **Conclusion**

1 The integration of multiple analyses undertaken on the faunal assemblages from level 4.1 at Abri du Maras enabled us
2 to define Neanderthal subsistence behaviours at the site within a precise chronological and palaeoenvironmental
3 framework. Pedo-sedimentary facies, charcoal, stable isotope and tooth wear suggest a cool, but moist regional
4 environment, different from what is highlighted by the faunal spectrum alone, i.e. harsher, steppic conditions. The
5 chronological attribution of the level (beginning of the MIS 3 between 40 ± 3 ky and 46 ± 3 ky, probably between the
6 Heinrich events H5 and H4, cf. Richard et al. 2015) is consistent with the D-O #12 event recorded in the Villars
7 speleothems (Genty et al. 2010), characterised by a woody steppe with a relatively warm and humid climate compared
8 to earlier periods. At Abri du Maras, the almost-exclusive anthropogenic accumulation of the fauna in level 4.1
9 represents an exceptional framework to interpret human subsistence strategies. Here, the reindeer-dominated
10 assemblage is representative of planned and collective Neanderthal hunting activities during the Autumn. The clear
11 monospecific spectrum, associated with seasonal evidence and the selective transport of some carcass portions to the
12 site, points to short-term mass hunting episodes of reindeer herds, not well recognized until now in the south-eastern
13 France for that period. It can be speculated that reindeer were either hunted during their seasonal migrations and they
14 were not present in the region all year round (i.e. they were a *seasonally restricted* resource), or, if they were the
15 sedentary ecotype, they were exploited during their Autumn aggregations when both male and females tend to be in
16 prime condition, in terms of body weight and body fat percentage (i.e. they were a *seasonally selected* resource). Future
17 analyses of materials from the site, such as strontium isotope analysis of reindeer tooth enamel, will provide insights
18 into whether or not the herds targeted by Neanderthals at Abri du Maras were migratory, and further illuminate the
19 nature of this assemblage and therefore the main motivations underlying the regular Autumnal activities of the human
20 groups in this region.

21 In addition to the otherwise specialized nature of Neanderthal activities at Abri du Maras, evidence presented here are
22 also suggestive of more diverse subsistence strategies at the site. For example, the evidence for numerous episodes of
23 fire use and the *in situ* consumption of meat, marrow and bone grease. In addition, lithic debitage, woodworking, and
24 possibly manufacturing string or nets (Hardy et al. 2013), point to mainly non-specialized activities, possibly
25 evidencing adaptable and diverse seasonal behaviours. This corroborates the regional mobility model that has been
26 previously proposed for this region of south-eastern France, i.e. a far-sighted circulating model very closely associated
27 with regional micro-topography and available seasonal resources (biotopes and raw material outcrops) (Daujeard and
28 Moncel 2010; Daujeard et al. 2016). Many Middle Palaeolithic assemblages with monospecific fauna indicate
29 secondary butchery processing with evidence of food storage and no or scant use of fire, indicating short-term human
30 occupations. At Abri du Maras, we cannot confidently associate short-term hunting episodes with short-term
31 occupations of the site, and one does not necessarily preclude the other. Further investigations combining faunal, lithic
32 and spatial analyses will permit to have a better idea of the type and duration of the human occupations within the level
33 4.1. Finally, data of the sub-contemporaneous faunal assemblage from level 4.2 will provide precious additional data for
34 understanding fluctuations in Neanderthal subsistence strategies in the same topographical context in a later period, and
35 under a different climatic regime.

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	NTR	NISPa	Coordinated	Isolated teeth	Illegible bone remains
NR	11123	1347	2919	231	902
%	100.0%	12.1%	26.2%	17.1%	33.2%

Table 1. Bone preservation indexes (NTR: number of total bone remains).

Taxa	NISP	%NISP	MNI	%MNI	Age class
<i>Equus ferus cf. germanicus</i>	75	6.4%	4	13.8%	1J, 1YA, 1PA, 1OA
Perissodactyla	75	6.4%	4	13.8%	
<i>Rangifer tarandus</i>	1030	88.0%	16	55.2%	7J, 2YA, 2 PA, 3OA, 2S
<i>Cervus elaphus</i>	6	0.5%	1	3.4%	-
<i>Megaloceros giganteus</i>	20	1.7%	2	6.9%	1OA
Cervidae indet.	11	0.9%			-
<i>Capra ibex</i>	2	0.2%	1	3.4%	-
Caprinae indet.	3	0.3%			-
<i>Bison priscus</i>	8	0.7%	2	6.9%	1J, 1YA
Artiodactyla	1080	92.3%	22	75.9%	
<i>Lepus sp.</i>	3	0.3%	2	6.9%	1J
<i>Oryctolagus cuniculus</i>	2	0.2%	1	3.4%	-
Leporidae indet.	10	0.9%			-
Lagomorpha	15	1.3%	3	10.3%	
Total NISP/MNI	1170	100.0%	29	100.0%	

Table 2. Large and small mammal spectrum for level 4.1. Number of Identified Specimen (NISP), Minimal Number of Individuals (MNI) and age data (J: juvenile, YA: young adult, PA: prime age adult, OA: old adult, S: senile).

s-eva no.	Taxa	Bone	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	%C	%N	C:N
30051	<i>Equus</i>	Metacarpal III	-20.6	4.8	28.0	9.4	3.5
30050	<i>Equus</i>	Mandible	-20.3	3.2	35.0	12.0	3.4
30226	<i>Equus</i>	Mandible	-24.9	1.0	2.4	0.4	6.9

30052	<i>Equus</i>	Mandible	-20.0	2.2	31.4	11.1	3.3
30053	<i>Megaloceros</i>	Mandible	-19.3	5.5	28.3	10.2	3.2
30054	<i>Megaloceros</i>	Maxilla	-19.4	5.4	27.8	9.9	3.3
30056	<i>Rangifer</i>	Mandible	-19.8	4.7	26.9	9.5	3.3
30057	<i>Rangifer</i>	Mandible	-20.0	5.3	36.1	13.2	3.2
30055	<i>Rangifer</i>	Mandible	-19.9	4.2	32.0	11.6	3.2

Table 3. Stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios of faunal bone collagen extracted from level 4.1, including %C, %N and C:N.

Locality	N	NP	NS	SD	CV	%LP	SWS	%XS	%0-17
Abri du Maras	8	20.06	18.25	2.299	0.126	0.0	1.13	37.5	25.0
Salzgitter Lebenstedt (1)	82	29.12	10.87	1.827	0.170	47.6	0.94	4.9	97.6
Kent's Cavern (2)	12	15.50	15.63	4.012	0.257	25.0	1.33	50.0	75.0
Portel-Ouest F (1)	30	23.23	25.35	3.097	0.122	3.3	1.13	60.0	0.0
Caune de l'Arago G (1)	11	14.15	17.41	4.380	0.281	12.0	0.88	35.0	52.9

Table 4. Tooth microwear summary for the reindeer (*R. tarandus*) from level 4.1 of Abri du Maras and other Middle and Late Pleistocene localities (data from (1) Rivals et al. 2015 and (2) Rivals and Lister, 2016). Abbreviations: N = Number of specimens; NP = average number of pits; NS = average number of scratches; SD = standard deviation on NS; CV = coefficient of variation on NS; %LP = percentage of individuals with large pits; SWS = scratch width score; %XS = percentage of individuals with cross scratches; %0-17 = percentage of individuals with less than 17 scratches i.e. within the browsing range.

Taxa	NRcut	NRI	%NRcut
<i>Equus ferus</i> cf. <i>germanicus</i>	8	26	30.8%
<i>Bison priscus</i>	3	4	-
<i>Cervus elaphus</i>	1	2	-
<i>Megaloceros giganteus</i>	3	14	21.4%
<i>Rangifer tarandus</i>	199	719	27.7%
Lagomorphs	5	10	50.0%

IND coord	230	1288	17.9%
Total	449	2063	21.8%

Table 5. Number (NRcut) and rates (%NRcut) of cut marked remains by taxa (NRI: Number of legible remains).

	NRcut	NISPI	%NRcut
Mandible	2	17	11.8
Ribs	7	36	19.4
Humerus	15	45	33.3
Radius-Ulna	25	115	21.7
Metacarpal	20	53	37.7
Femur	13	26	50.0
Tibia	55	152	36.2
Astragalus	1	2	-
Metatarsal	45	155	29.0
Metapodials	12	54	22.2
Vestigial metapodials & phalanges	2	4	-
Indeterminate shafts	2	-	-

Table 6. Number (NRcut) and rates (%NRcut) of cut marked elements for reindeer (NISPI: Number of legible identified specimen).

Figure captions

Figure 1. Location of the Abri du Maras. Site situation on the edges of the Rhône valley in the context of the south-eastern Middle Palaeolithic (Map adapted from Tessier, in Daujeard et al., 2011).

Figure 2. GIS projections of the faunal and lithic items on the stratigraphic profile: band 6 in unit 4 (Figure by R. Gallotti and Simon Puaud).

Figure 3. Two refitted tibia fragments of a large cervid: *Cervus* or *Megaloceros* (level 4.1, J6-85 and J6-85/1) (Photos by D. Vettese and M.G. Chacon).

Figure 4. Photo of a reindeer metacarpal fragment. This fragment presents green bone fractures and a whole distal portion (level 4.1, J6-39) (Photo by C. Daujeard).

Figure 5. Stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios of faunal bone collagen extracted from level 4.1 (Graph by K. Britton).

Figure 6. Microwear data (Graph by F. Rivals). Boundary lines with the error probability (heat map) based on SD and CV values of microwear data used for the classification of samples into short events (region A), long-term events (region B), or two separated short events (region C). Black dots indicate modern reindeer populations used to build the model. White stars indicate archaeological samples: Abri du Maras (level 4.1), Salzgitter Lebenstedt (SL), Portel-Ouest level F (PO-F), Kent's Cavern (KC), and Caune de l'Arago level G (CA-G).

Figure 7. Bivariate plot of the average densities of pits and scratches in reindeer and horse (Graph by F. Rivals). Bars correspond to the standard deviation (± 2 SD) for the fossil samples. Grey areas correspond to the Gaussian confidence ellipses ($p = 0.95$) on the centroid for extant leaf browsers (B) and grazers (G) from Solounias and Semprebon (2002).

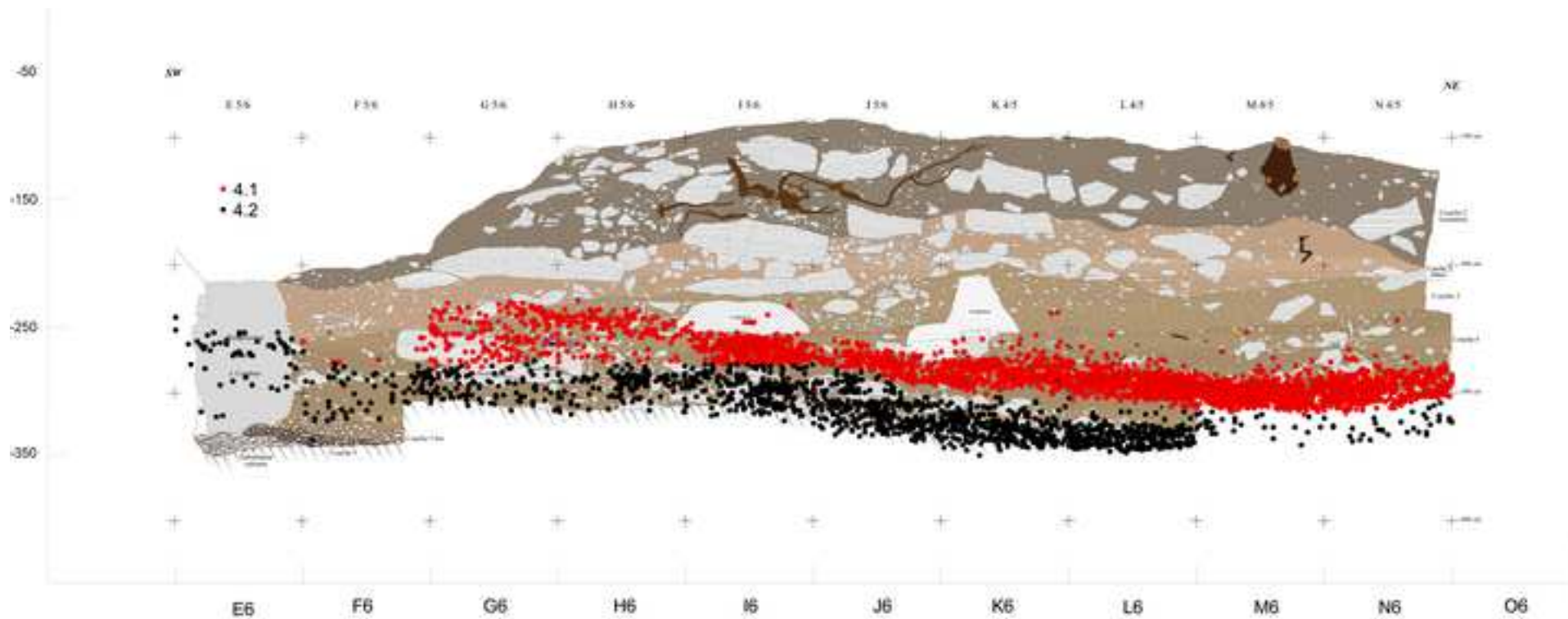
Figure 8. Ternary diagram for reindeer age classes (modified from Stiner, 1990) (Graph by C. Daujeard).

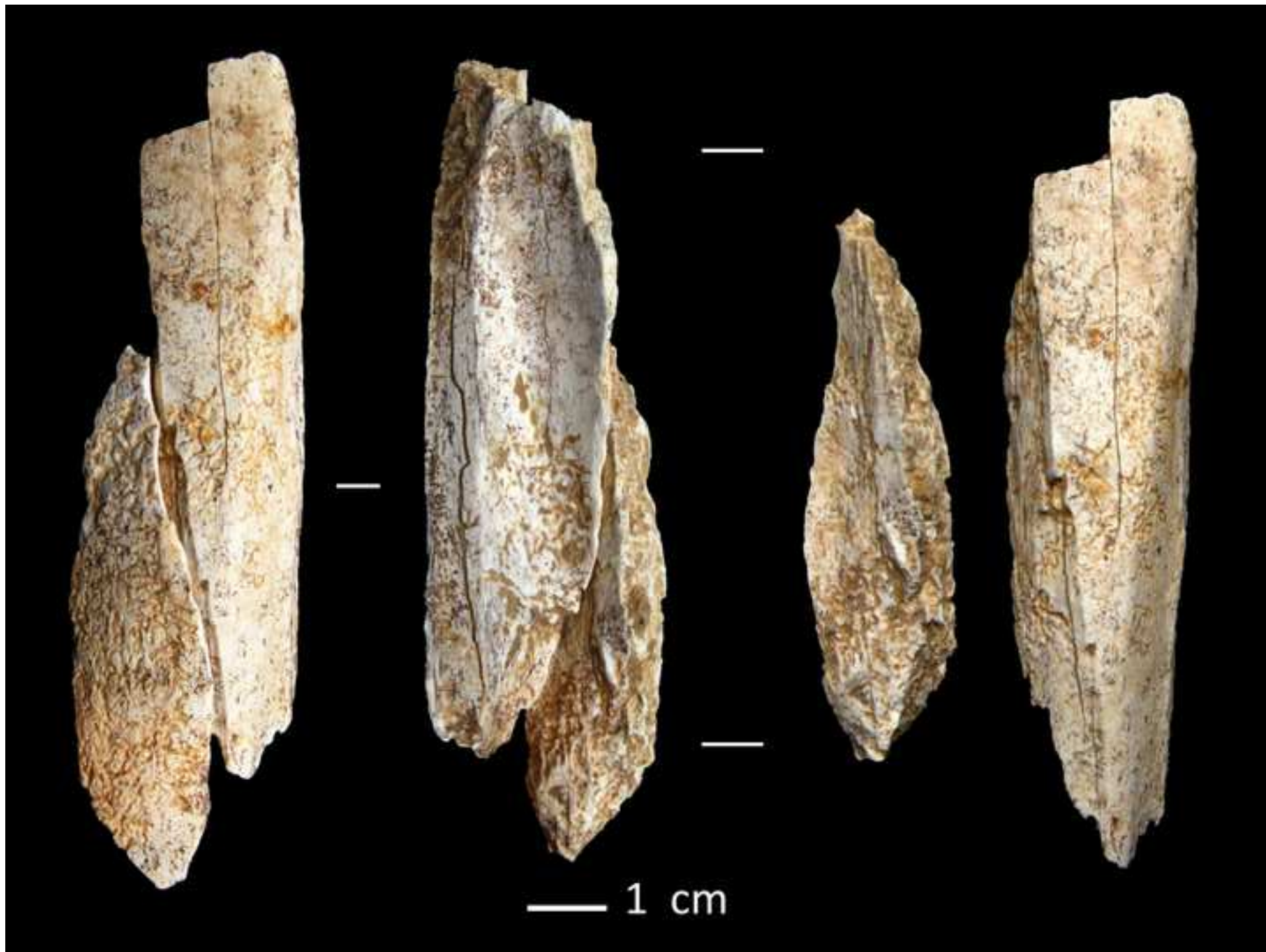
Figure 9. Distribution of the skeletal elements for reindeer by anatomical parts (Graph by C. Daujeard). Survival rates calculation corresponds to $\text{MAU} \times 100 / \text{NMI}_{\text{max}}$.



Figure 2

[Click here to download Figure_2.tif](#)







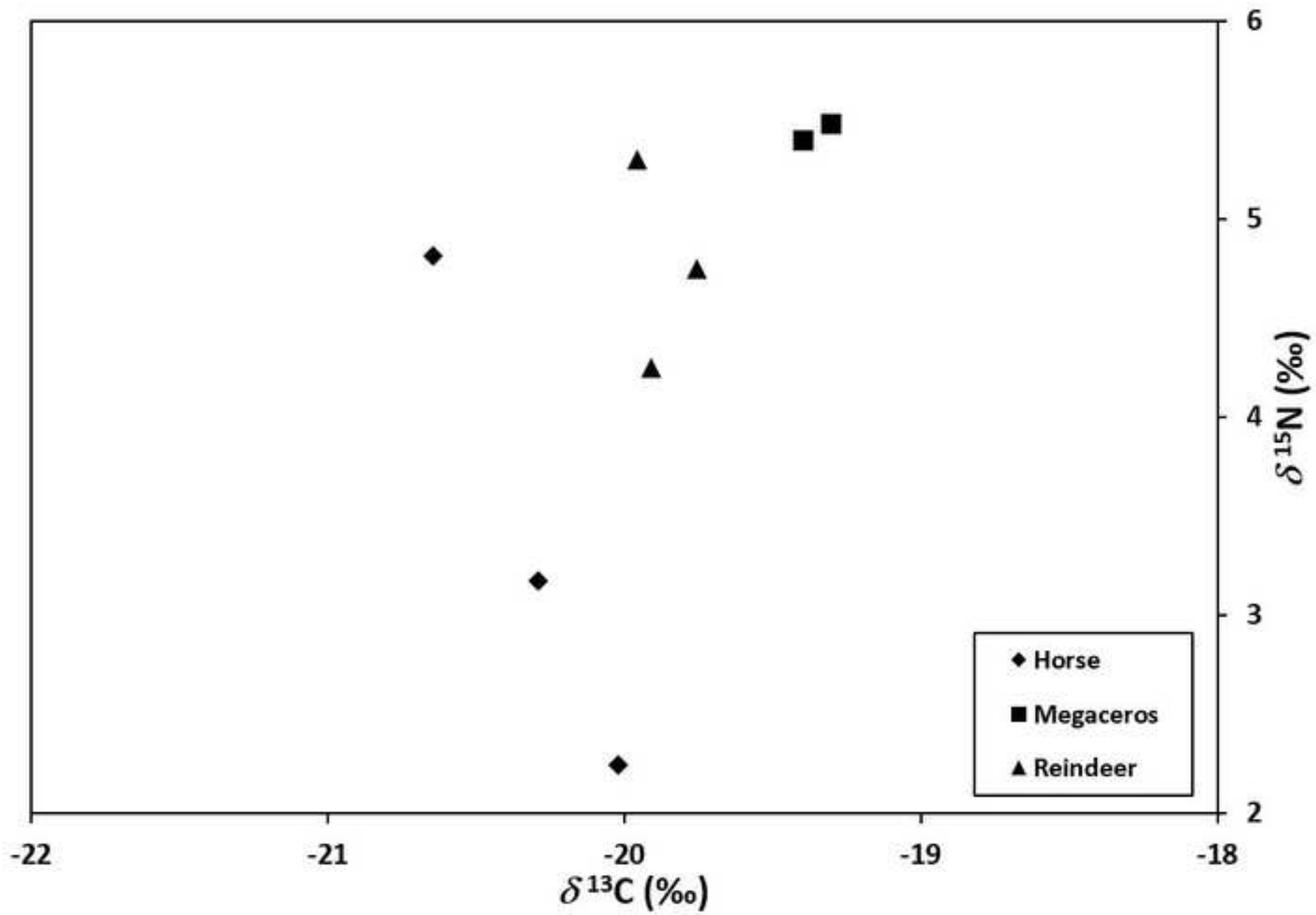
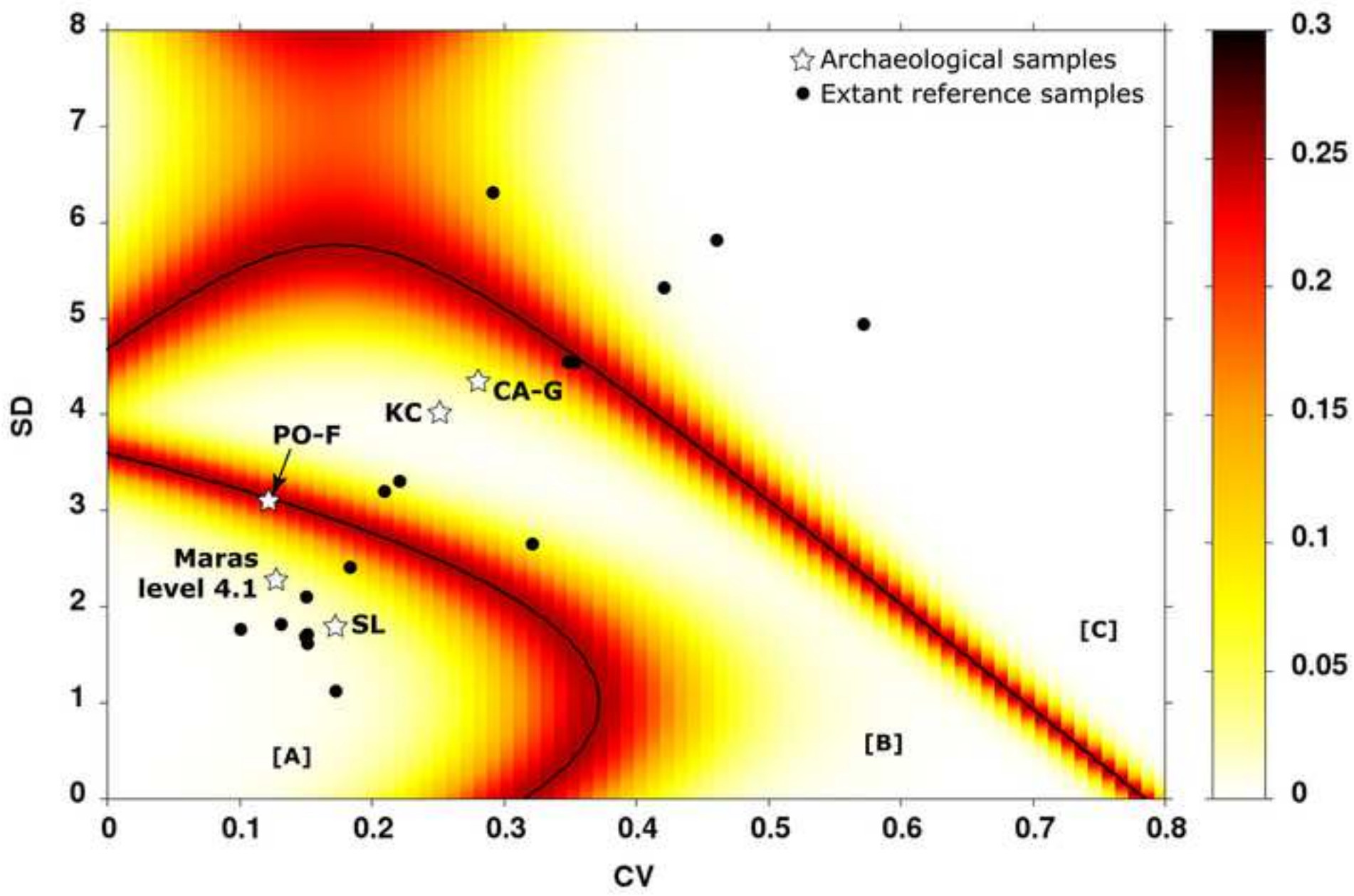


Figure 6



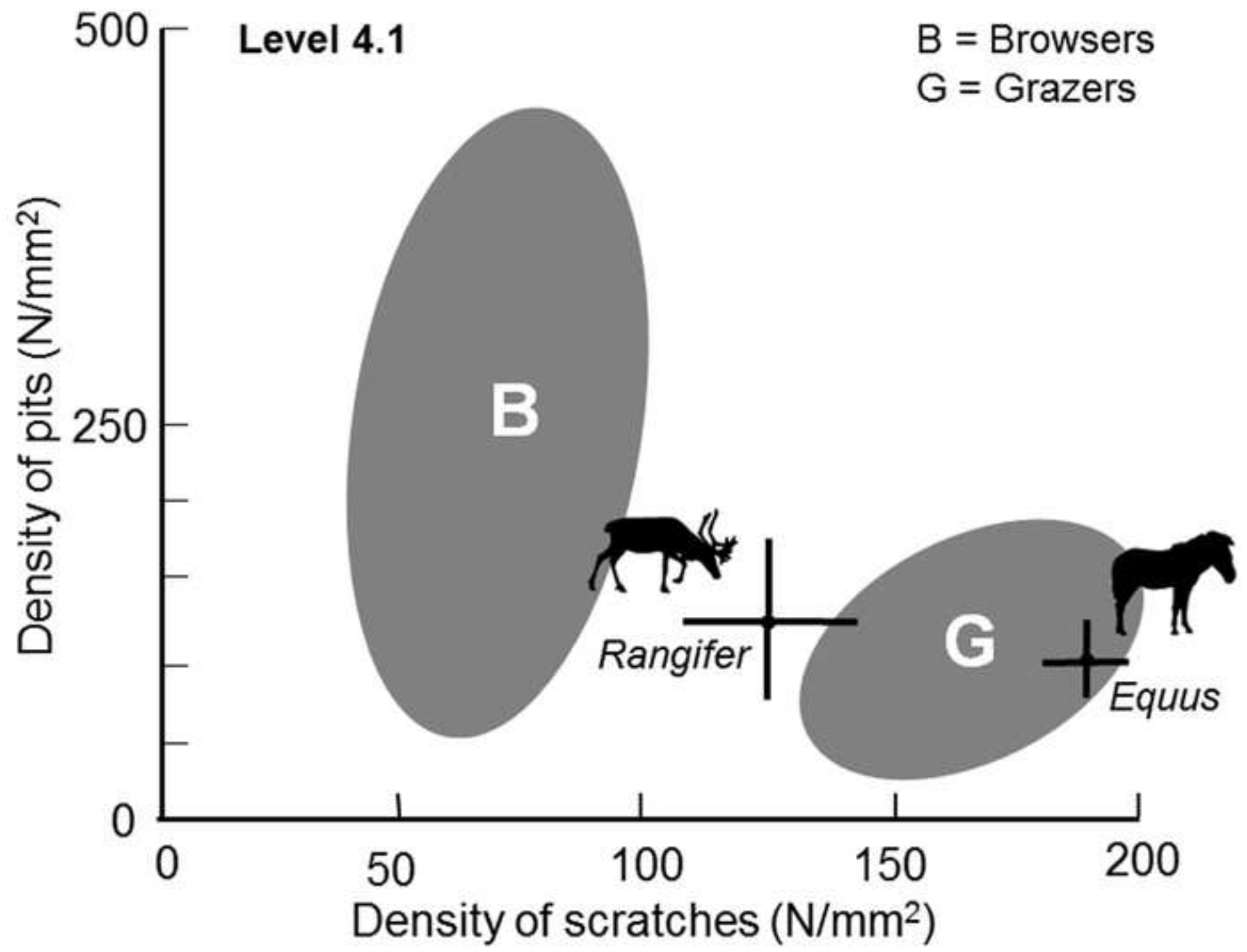


Figure 8.

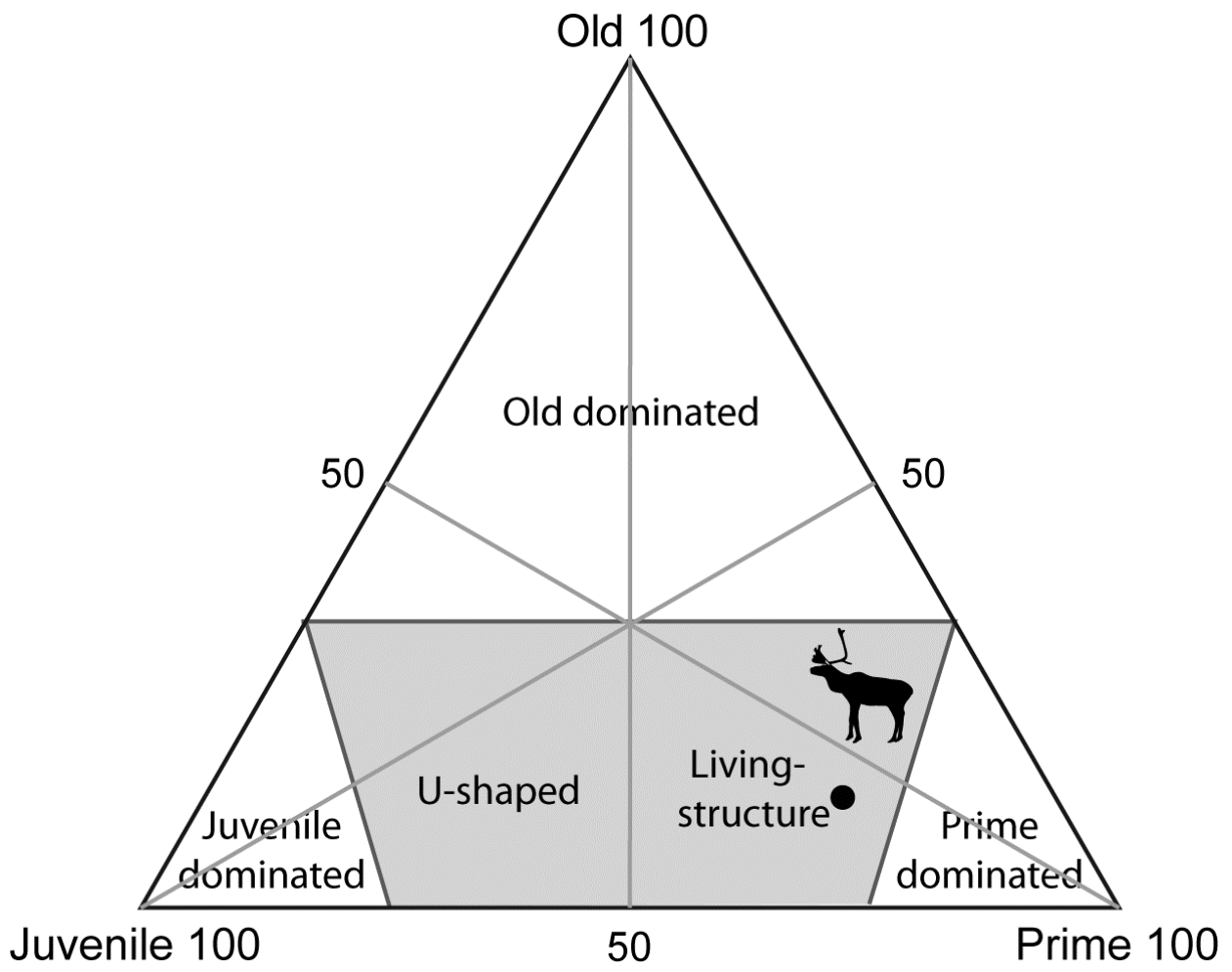
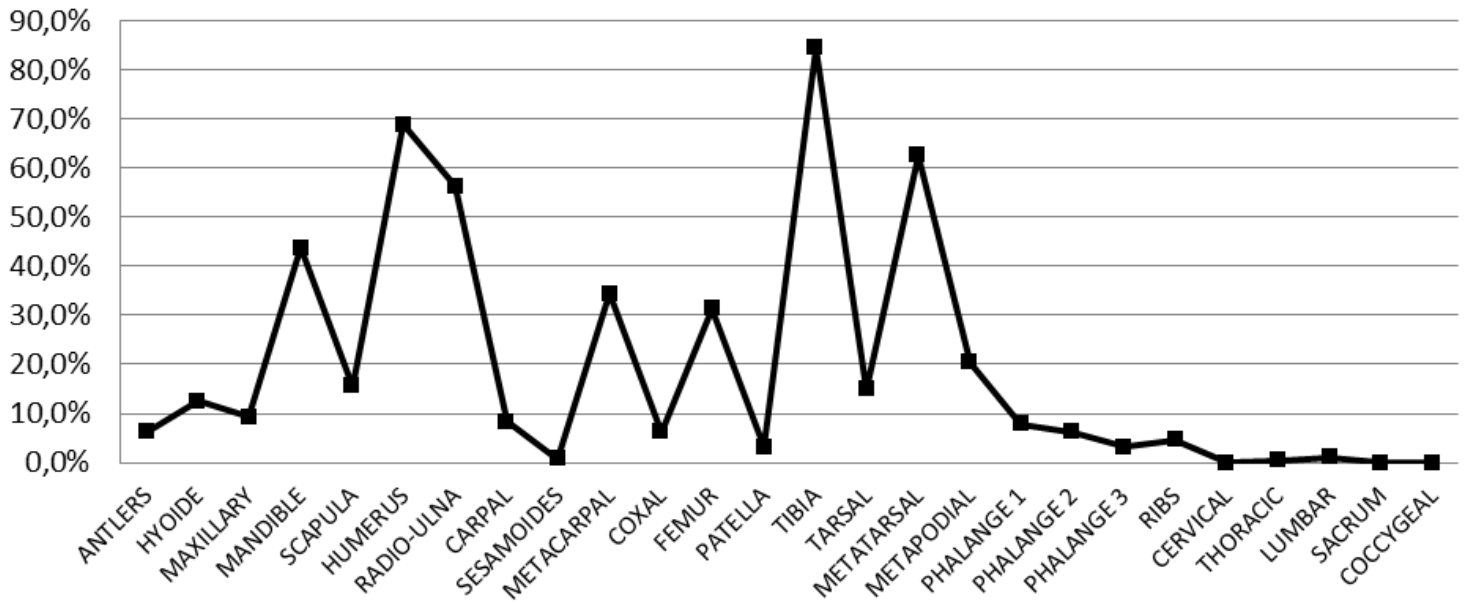


Figure 9.

Survival rates



Supplementary information.

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SI Tables

Table S1. Burning damage categories based on colour (adapted from Stiner et al., 1995).

Burnt stages	Descriptions	Colour
0	Not burnt	Light cream
1	Slightly burnt (localized and < half carbonized)	Brown
2	Slightly burnt (> half carbonized)	Brown/Black
3	Fully carbonized	Black
4	Localized < half calcined	Black/Grey-White
5	> Half calcined	Grey-White
6	Fully calcined	White
7	Highly calcined	White/Turquoise

Table S2. Number and percentage of recorded bone remains (NR=2718) with green, dry, frozen or indeterminate bone breakage.

	Green		Dry		Gelifracts		Indeterminate	
	NR	%	NR	%	NR	%	NR	%
2718	2003	73.69%	950	34.95%	58	2.13	483	17.77%

Table S3. Climatic and edaphic alterations observed for coordinated bone remains (NR=2718).

fissuration	0	1	2	3
NR	2027	675	144	11
%	70.9	23.6	5.0	0.4
desquamation	0	1	2	3
NR	1024	601	620	612
%	35.8	21.0	21.7	21.4
polish	0	1	2	3
NR	2639	168	45	5
%	92.4	5.9	1.6	0.2
concretions	0	1	2	3

NR	2632	188	34	3
%	92.1	6.6	1.2	0.1
corrosion	0	1	2	3
NR	248	1228	718	663
%	8.7	43.0	25.1	23.2
root etchings	0	1	2	3
NR	291	1082	780	704
%	10.2	37.9	27.3	24.6
black colorations	0	1	2	3
NR	984	1401	432	40
%	34.4	49.0	15.1	1.4
red/orange colorations	0	1	2	3
NR	534	489	30	0
%	50.7	46.4	2.8	0.0

Table S4. Fish remains from level 4.1.

m ²	Family	Species	Element	NISP	MNI	Estimated weight (g)
H-6	Cyprinidae	unidentified	vertebrae + rib	5	1	750
I-6	Cyprinidae	<i>Squalius cephalus</i>	vertebrae + pharyngeal bone	12	1	700
I-6	Cyprinidae	unidentified	vertebrae + rib + parasphenoid	16	2	550-850
J-6	Cyprinidae	unidentified	vertebra	1	1	600
I-6	Percidae	<i>Perca fluviatilis</i>	scales	12		
Unidentified fish			fragments	121		

Table S5. Cementochronology results (all lower teeth unless indicated; rt.: right; lft.: left).

Specimen #, context, description	Tooth (Side)	Species	# Annuli, Zone state of completion	Magnification	Estimated season of death
(1) L6 142 et 28	M1 rt.	Rangifer	4+ annuli, last 4 annuli visible; earlier ones too mineralized to count F= nearly complete zone	100x	autumn
(2) M6 338	P4 lft.	Rangifer	4-5 annuli visible F= complete zone	100x with lambda plate	autumn/late autumn
(3) J6 67	P2 lft.	Rangifer	2 or 3 annuli visible F = in growth zone, but too mineralized to assess season	100x	too mineralized, no determination
(4) M6 235	M3 rt. (upper)	Rangifer	too mineralized, no determination		too mineralized, no determination
(5) H7 84	M3 rt. (upper)	Megaloceros	too mineralized, no determination		too mineralized, no determination
(6) N6 178	P2 lft.	Rangifer	6+ annuli F = edge too degraded to assess seasonality	40x	too mineralized, no determination

(7) M6 671	P4-M1 rt.	Rangifer	3 annuli visible F= in growth zone 3/4 complete only final 2 annuli visible F= in growth zone 3/4 complete	100x	autumn
(8) H6 126	M1 lft.	Rangifer	No cementum, not analyzed		
(9) M6 520	M2 lft.	Rangifer	ca. 5 annuli F= nearly complete growth zone	100x	autumn/late autumn

Table S6. Characteristics of burnt elements.

	c1	c2	c3	c4	c5	c6	c7	total	%	NR	%
spongiosa 0-25 mm		75	309	80	42	14	1	521	22.6%	1890	27.6%
compacta 0-25 mm	11	318	1008	214	83	30	14	1678	72.8%	6503	25.8%
spongiosa 26-50		1	4	6	4			15	0.7%	320	4.7%
compacta 26-50	4	8	12	11	1	1		37	1.6%	1129	3.3%
comp-spong > 50	1	4	1					6	0.3%	1050	0.6%
isolated teeth		6	21	8	9	3	2	49	2.1%	231	21.2%
total	16	412	1355	319	139	48	17	2306	100.0%	11123	20.7%
at least carbonized (c3 to c7)								1878	81.5%		
at least calcined (c4 to c7)								523	22.7%		
burnt elements < 25 mm								2199	95.4%		
spongy elements (c3 to c7)								460	24.5%		

SI Figures

Figure S1. Summarized data concerning the aeolian silt sediments in layer 4. a). Calcimetry: measuring the average calcium carbonate content (CaCO_3). b). Grain-size: sediment texture is silty to sandy-silty. c). Microphotographs of micromorphological features of sediment in layer 4: bottom; sandy silt with some coarse sand. Porosity is well-developed, calcium carbonate impregnated the sediment around the pores. Voids and coatings are related to root development. Middle; limestone fragment from the frost-shattering of the shelter wall. Perforations are due to the activity of endolithic lichens. Top; Calcitic biospheroid produced by earthworms (*Lumbricidae*).

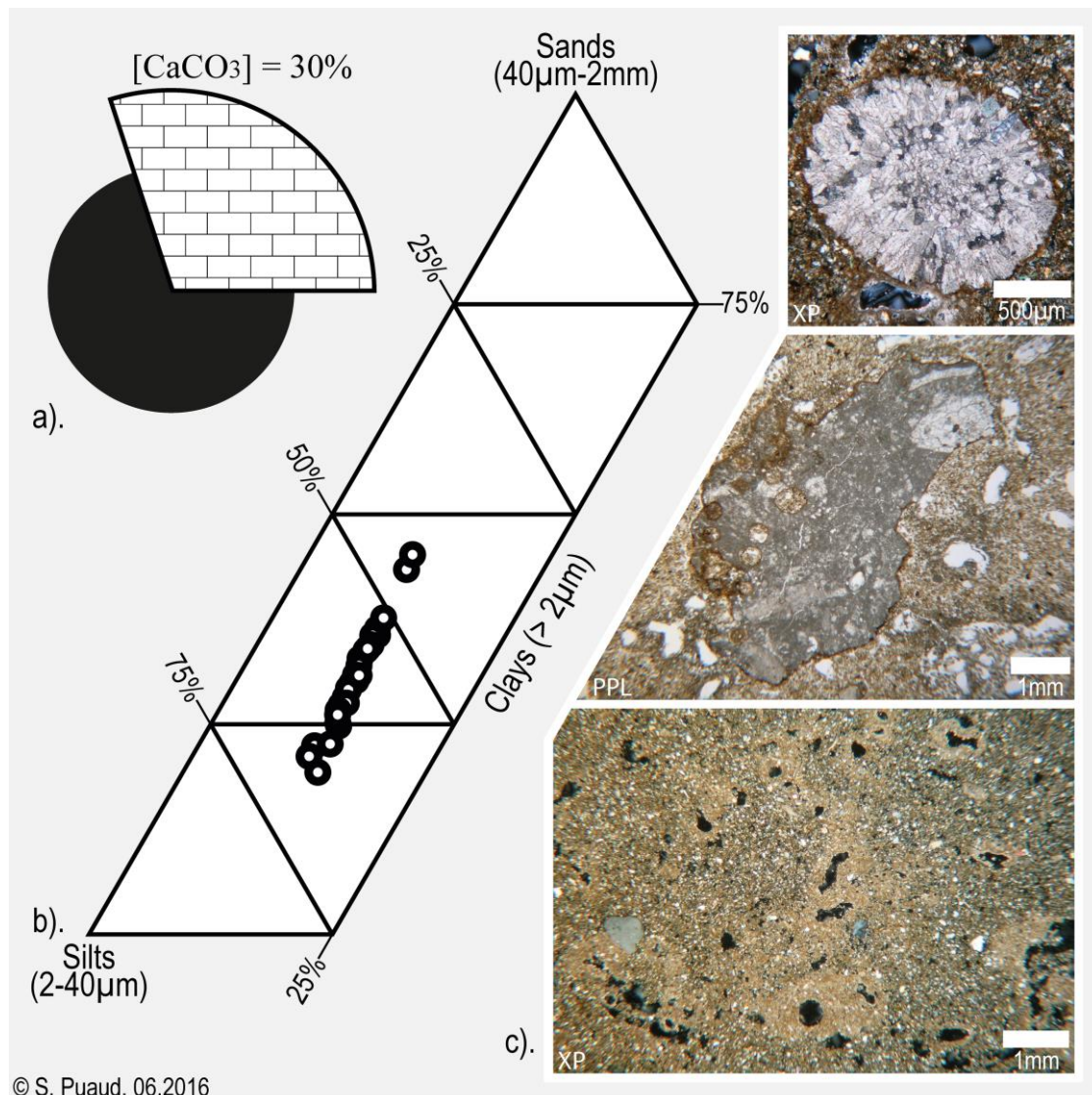


Figure S2. Distribution of bone fragments by size classes (intervals: 0-25 mm).

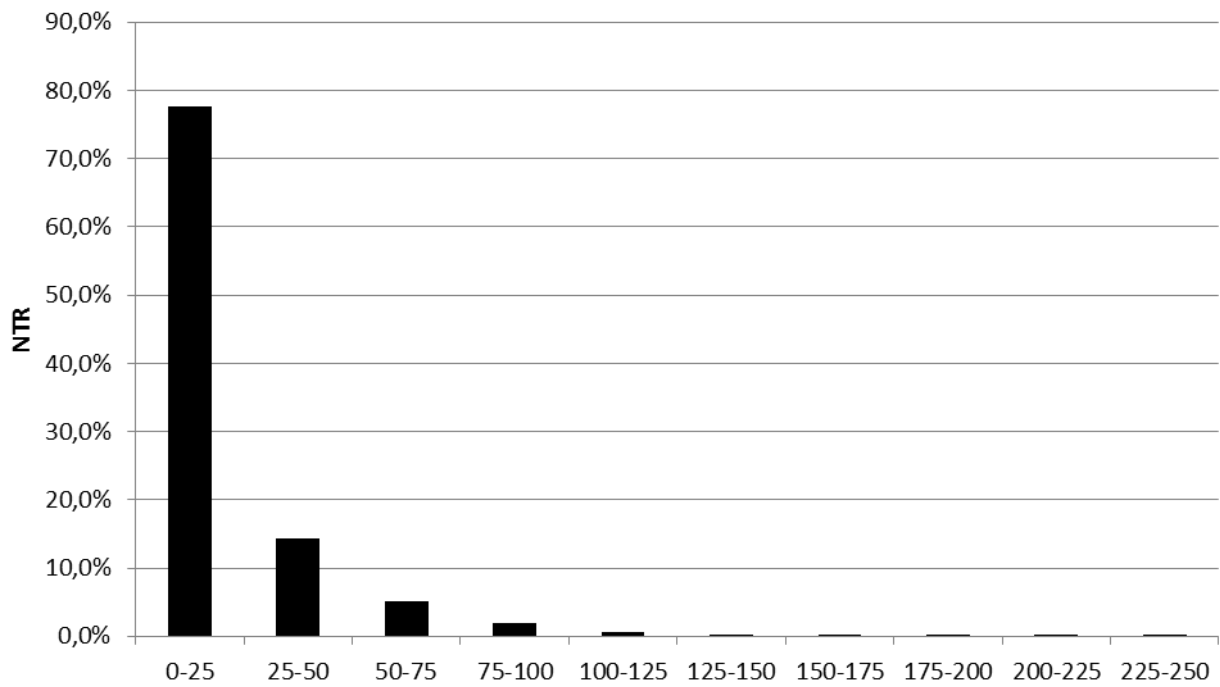


Figure S3. %MAU of the different reindeer long bone portions.

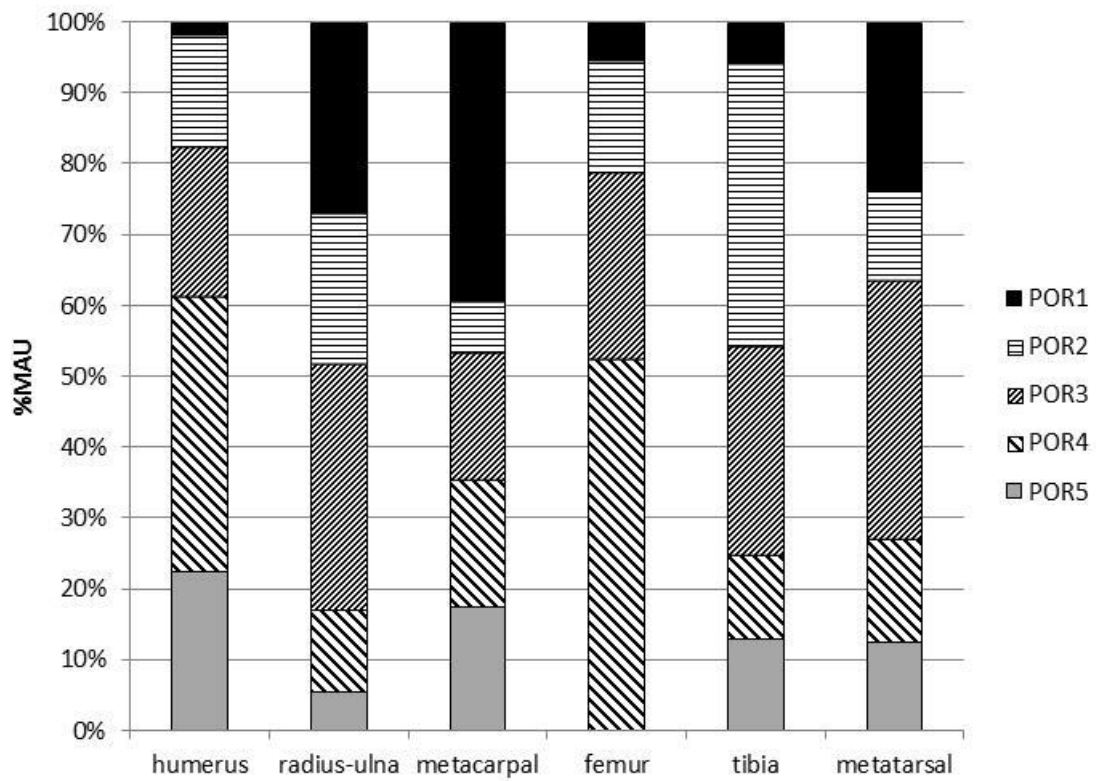


Figure S4. Three-dimensional bar diagram showing relative frequencies of shaft length and circumference (NR=1656).

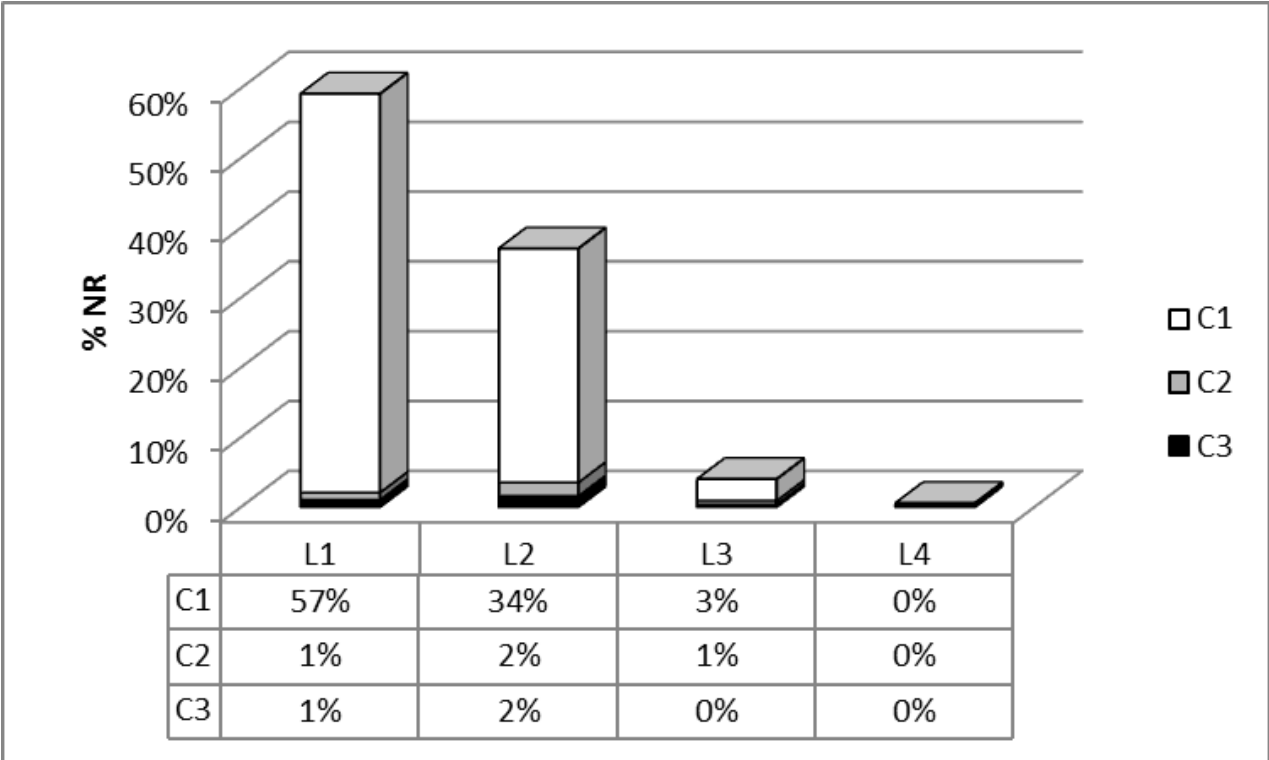


Figure S5. Distribution of the skeletal elements for reindeer according to the seven carcass pieces (%MAU).

