

The Chronometric Dating and Subsistence of Late Neanderthals and Early Anatomically Modern Humans in the Central Balkans Insights from Šalitrena Pećina (Mionica, Serbia)

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Eastern Europe, particularly the Balkans, played a major role as a likely cul-de-sac for late Neanderthal survival and as a gateway to Europe for Anatomically Modern Humans (AMH) during the Middle to Upper Paleolithic transition. Despite the importance of the region, the known archaeological record during this period is still very limited, with little available site information. The recently excavated site of Šalitrena Pećina (Mionica, Serbia), south of the Danube River, contains archaeological evidence of late Mousterian, Aurignacian, and Gravettian occupations and presents an opportunity for understanding the behavior of both human populations in this eastern European region. Here we present the first radiocarbon dates for Neanderthal and AMH occupations in Serbia, as well as preliminary evidence on subsistence strategies obtained from the Mousterian and Aurignacian macrofaunal assemblages in Šalitrena Pećina. Radiocarbon dates indicate that Neanderthal and AMH groups may not have coexisted and interacted in this site. Nevertheless, zooarchaeological and taphonomic results show that both human populations were the main depositional agents of macrofaunal accumulation at the cave. The general compositions of the faunal assemblages reflect subtle differences between both human types and point to the necessity of further multidisciplinary research in southeastern Europe to increase our knowledge about human behavior and the causes of the demise of the Neanderthals in the Balkans.

Key words: Neanderthals, Anatomically Modern Humans, [Subsistence](#), Šalitrena Pećina, Serbia, [Radiocarbon](#) dates

The Middle to Upper Paleolithic transition in Europe is a key period in human evolution directly linked to late Neanderthal and early Anatomically Modern Human (AMH) populations. The Neanderthal extinction is recognized as a regionally diverse

Submitted March 14, 2016; accepted November 17, 2016; published online Month XX, 2017.
Journal of Anthropological Research (Fall 2017). © 2017 by The University of New Mexico.
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phenomenon rather than a uniform pan-European event. The reasons behind their demise and the survival of AMH are still unknown and hotly debated. Current prevailing hypotheses are diverse and inconclusive, deriving from the study of the archaeological record from different theoretical perspectives. Existing theories include: dietary differences between the two types of hominins (Bocherens and Drucker 2006; Hockett and Haws 2003; Richards and Trinkaus 2009), Neanderthal technological inefficiency (Pettitt 1999; Shea and Sisk 2010), demographic imbalances (Flores 1998; Mellars and French 2011; Zubrow 1989), environmental shifts (Finlayson 2004; Stewart 2004), competition with modern humans (Banks et al. 2008), decline in genetic diversity (Green et al. 2010), and cognitive differences (Mellars 1991; Soffer 1994), among others (see Villa and Roebroeks 2014 for an update of the debate).

Neanderthals and AMH were contemporaneous in various regions of Eurasia for several millennia. However, Neanderthals failed to survive, disappearing within no more than ca. 5,000 years of their first encounters with AMH (Higham et al. 2014). Methodological advances in radiocarbon dating (Bronk Ramsey et al. 2004; Higham et al. 2006a) have removed young carbon contamination from old organic samples up to the limit of the method at ~50,000 years ago, a crucial time when the transition between the two human species took place, allowing for a more precise temporal identification of the replacement than was previously possible. Now, even the very existence of southwestern (i.e., Iberian) refugia for Neanderthal populations toward the end of Marine Isotope Stage 3 (MIS3 ~57–27 ka) (Higham et al. 2014; Wood et al. 2013) has been challenged.

Modern humans rapidly colonized Europe, from the Near East to Iberia, with the earliest Aurignacian cultural evidence identified at ~47–45 ka (GI-12) (Müller et al. 2011). Although the taxonomic status of the makers of these earliest phases of the Upper Paleolithic is poorly documented, AMH expansion has been traced through the so-called Initial Upper Paleolithic (IUP; i.e., Protoaurignacian and Aurignacian complexes) and some “transitional” technological industries (Uluzzian, Lincombian-Ranisian-Jerzmanowician [LRJ], Szeletian, and Châtelperronian in various regions of Europe). These industries suggest cultural contacts between local and immigrant populations and presage the onset of the Upper Paleolithic in western and central Europe (Hublin 2015).

The dispersal of Proto-Aurignacian and Aurignacian technologies likely shows a rapid advance of AMH along two main routes: up the Danube Valley (Conard 2002; Mihailović et al. 2011; van Andel et al. 2003) and along the Mediterranean coast (Mellars 2011). This relatively fast migration may have coincided with the displacement of Neanderthal populations toward more patchy and previously unexploited regions either because of direct and unsuccessful competition with modern humans (Stewart 2004) or because they failed to adapt to unsuitable MIS3 environmental conditions and climatic instability (Finlayson 2009; Stewart 2007), despite their previous success at surviving climatic crises.

In spite of the fact that the Balkan region has long been considered a likely gateway to Europe for AMH (Conard and Bolus 2003; Kozłowski 1998, 2006; Mihailović et al. 2011; Roebroeks 2008), very few sites dated to the Middle to Upper Paleolithic transition have been found, particularly in Serbia (see Mihailović, ed. 2014 and Mihailović et al. 2011 for an updated synthesis for the Central Balkans). Possible reasons for this include the political upheavals of the 1990s, the lack of systematic archaeological surveys, and a very limited Paleolithic research history in this area (Mihailović et al. 2011). To date, no Aurignacian sites have been found in the mountainous zone between Croatia and Bulgaria, and only a few Mousterian sites have been recorded in Serbia (Smolucka Pećina, Malisina Stijena, Hadzi Prodanova Pećina and Tabula Traiana) and Montenegro (Crvena Stijena: Basler 1975; Morley and Woodward 2011). None of these provide information about diet and subsistence, either because of the lack of preserved bone or because, when bones are preserved, they can be attributed to carnivore (mainly hyena) accumulations (Mihailović and Mihailović 2009). The available information about fossil mammal assemblages of the Upper Pleistocene consists of paleontological studies that only indicate the relative abundance of each species and general ecological considerations (Dimitrijević 1997). Only in recent years have faunal accumulations begun to be investigated from an archaeozoological point of view (Dimitrijević et al. 2014).

To date, the only Paleolithic human bone found in Serbia is a mandible (BH-1) from Mala Balanica with primitive characteristics comparable to Early Pleistocene mandibular specimens, associated with a minimum radiometric date of 113,000 +72,000/−43,000 years ago (dated by U/Th series). It does not appear to exhibit any derived Neanderthal traits (Roksandic et al. 2011).

Recent excavations offer, for the first time, an outstanding opportunity to explore a territory that lies between the two proposed routes of colonization of Europe by AMH. Much of Serbia is characterized by mountainous landscape and, despite being crossed by secondary fluvial valleys, is somewhat isolated. Although Europe in the second half of MIS3 was climatically unstable, the Balkans might have served as a refugium for plant and animal species due to the favorable conditions present, especially in the west of the peninsula, where the humidity was higher (Griffiths et al. 2004; Tzedakis 2004; Tzedakis and Bennett 1996; Weiss and Ferrand 2007). As a result, Neanderthal populations inhabiting the region may have escaped the negative influences of climatic change that provoked shifts in ecological zones between the northwest and the southeast of Europe (Dogandžić et al. 2014; Mihailović 2009; Mihailović et al. 2011).

Šalitrena Pećina, located southwest of the Danube River in central Serbia, has been the subject of ongoing excavation since 2004. This cave is the only site in Serbia with a complete stratigraphic sequence from the late Mousterian to the Gravettian, containing abundant macrofaunal assemblages and diagnostic artefact industries. Here we present AMS-dates using ultrafiltration and preliminary zooarchaeological results from the Mousterian- and Aurignacian-age faunal remains, which suggest the successive pres-

ence of late Neanderthal and early AMH populations in Serbia and offer the first evidence about their respective diets, subsistence strategies, and ecological adaptations in the region.

THE SITE, INDUSTRIES, AND RADIOMETRIC CHRONOLOGY

Šalitrena Pećina

Šalitrena Pećina is located near the village of Breždje, in the canyon of the Ribnica River, around 100 km southwest of Belgrade (Figure 1). The cave is on the left bank at 277 masl. Preliminary excavations began in the 1980s (Jez and Kaluderovic 1985), although it was not until 2004 when, under the direction of B. Mihailović, excavations were carried out using modern techniques and intensive recovery methods (B. Mihailović 2008, 2013; Mihailović et al. 2014). Excavations are still ongoing. The cave entrance is 20 m wide, facing west, overlooking (and 20 m above) the present-day river course. It is divided by a large rock into two passages of nearly 40 m in length. The interior of the cave is around 600 m², with a total length of 135 m. Rich archaeological assemblages have been retrieved from an excavated area totalling 40 m², subdivided into three main zones (Figure 2): the cave mouth (divided into six trenches: B, C, D, E, G and EG), the interior (12 m from the entrance, with two trenches: H and HSP), and near the southwest corner (Trench F).

Industries

Evidence of Paleolithic human activity is found in the cave mouth in level 3, which together with level 4 is attributed to the Gravettian (Mihailović and Mihailović 2007)



Figure 1. Location of Šalitrena Pećina (Mionica, Serbia). Exterior view of the cave and view of the excavation area in the cave mouth.

Šalitrena Pečina

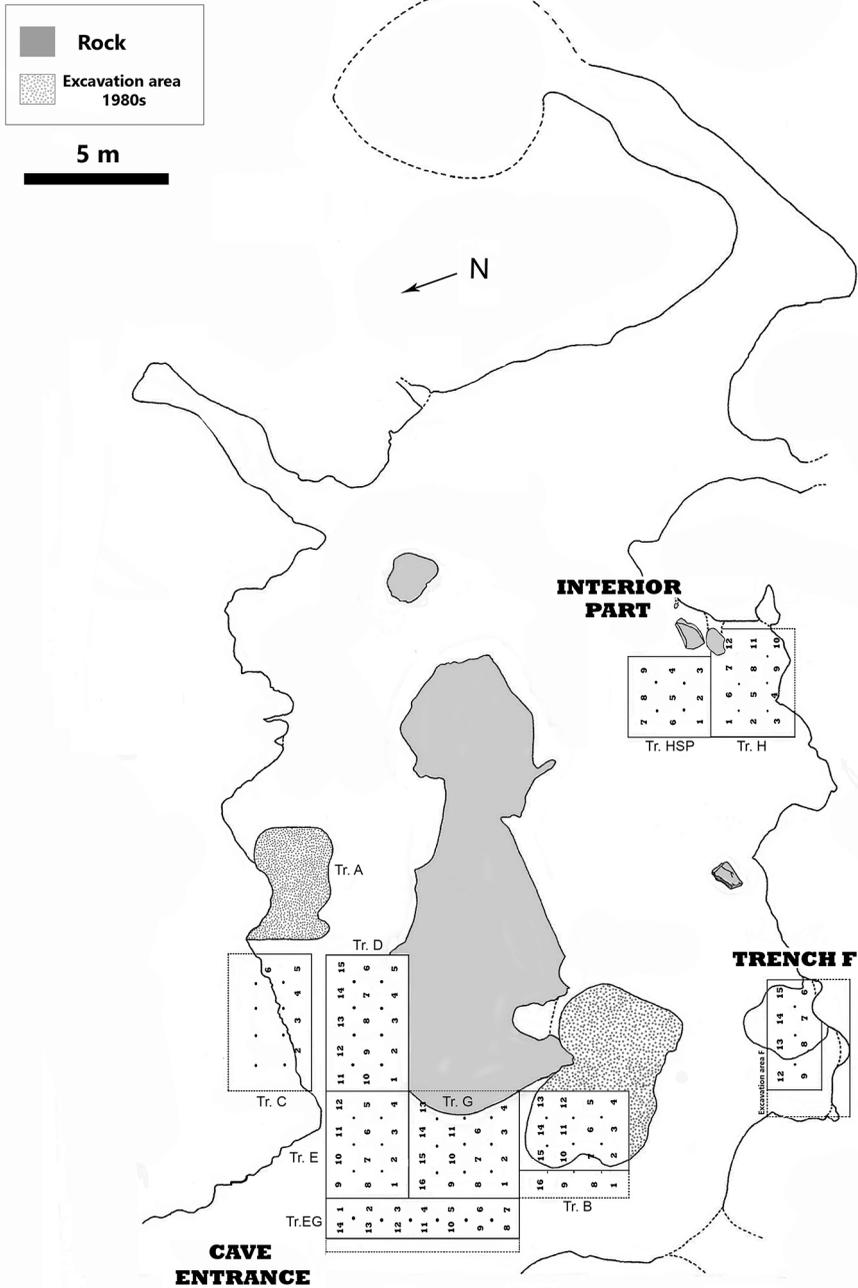


Figure 2. Plan of Šalitrena Pečina showing excavation areas. (redrafted by L. Agudo from original by J. Marković)

(Figure 3). Level 5a contains Aurignacian artifacts and levels 5b, 5c, and 6 contain Middle Paleolithic ones. Lithic assemblages from levels 5b, 5c, and 6 can be ascribed to the typical Balkan Mousterian with side scrapers, Mousterian points and Levallois artifacts. This type of industry is present at many sites in northern Bosnia and western Serbia (D. Mihailović 2008). During the 2014 season of excavation, Middle Paleolithic assemblages with leaf-like points were found. The identification of such leaf-point techno-complexes indicates that they were distributed not only in central Europe and the eastern Balkans, but also in the peri-Pannonian area (Mihailović et al. 2014). The Aurignacian industry from level 5a is distinctive and differs from other Aurignacian sites in northern Bosnia, and in Romanian and Serbian Banat (Mihailović et al. 2011), given a high percentage of carinated endscrapers, burins, and retouched and unretouched bladelets. The composition, technological, and typological characteristics of the artifacts indicate this industry can be more closely associated with the early Aurignacian in central and western Europe. Aurignacian level 5a also contains mineral pigments, a dentalium (*Antalis* sp.) shell bead (Mihailović and Mihailović 2009), and several bone tools, particularly bone points. In the Mousterian levels several retouched bones (fragments of large and medium-sized mammal diaphyses) were found. The study of bone technology is currently ongoing.

Unlike in the cave mouth, Aurignacian level 2 in the interior area of the cave does not contain bladelets and instead has larger tools, including typical Aurignacian long-blades and endscrapers on blades. Whether these differences are the result of different activities or represent different periods of use is still being explored. Level 3 industries in the interior of the cave are similar to those of the Mousterian in the cave mouth area. Between the exterior and interior areas, Trench F (near the southwest corner) has yielded a distinctive Aurignacian assemblage in one level (Level 5). The presence of cave bear remains and carnivore evidence (hyena gnaw marks) in the interior part of the cave is noteworthy. Cave bear is commonly found in karstic deposits in Serbia, as speleological, paleontological, and archaeological explorations have shown in the past few decades (Cvetković and Dimitrijević 2014).

Radiocarbon Dates

Nine radiocarbon measurements have been obtained from the Mousterian and Aurignacian levels of Šalitrena Pećina, sampled from both the cave mouth and interior areas. Of these radiocarbon dates, eight were from faunal bone/tooth collagen and one from a shell (*Antalis* sp). Ultrafiltration techniques were used for the bone measurements and CarDS methodologies were applied to the shell specimen as described in Bronk Ramsey et al. (2004) and Douka et al. (2010), respectively. Of the radiocarbon samples, two measurements are beyond the range of the radiocarbon method (Table 1). Mousterian-level dates at Šalitrena Pećina indicate a presumed Neanderthal occupation ranging between 42.8 and 39.3 cal BP, whereas probable modern human occupation at the cave is dated to between 36.7 and 33.8 cal BP. According to these

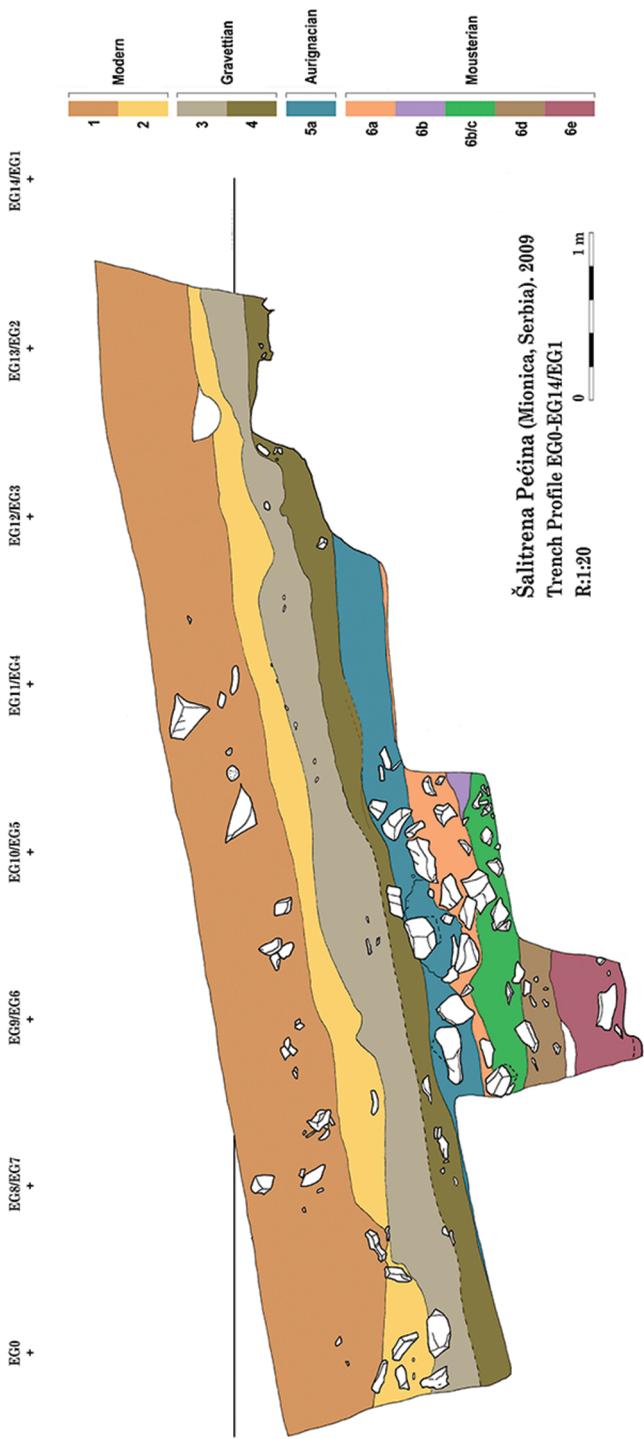


Figure 3. Stratigraphic profile at the cave mouth –Trench EG. (redrafted by L. Agudo from original by J. Marković).

Table 1. Radiocarbon dates. Conventional ages expressed in ^{14}C years BP and calibrated in Oxcal platform 4.2 (Bronk Ramsey 2009) using the IntCal 13 curve (Reimer et al. 2013).

Techno-complex	Area	Level	Square	Lab code	^{14}C age	\pm	Cal yr BP (95.4%)		$\delta^{13}\text{C}$	Material	Species
							From	To			
Aurignacian	Outside	5a	I2	Beta-237688	31980	360	36671	35051	-19.1	bone	Mammal
			L3A	Beta-224720	30190	400	34941	33626	-20.8	bone	Mammal
			M2C	OxA-27975	29700	340	34512	33196	-19.7	bone	Mammal; worked bone
			M4A	OxA-27683	30150	150	34531	33877	0.92	shell	<i>Antalis</i> sp.
Musterian	Outside	2	X21A	Beta-237684	29980	280	34590	33638	-19.5	bone	Mammal
		5b	M2	Beta-237690	37760	520	42821	41358	-19.8	bone	Mammal
		5c	L4A	OxA-27682	>50200	—	—	—	-21.1	bone	<i>Bos/Bison</i> sp.
Musterian	Inside	6a	L4A	OxA-27829	>45700	—	—	—	-19.9	bone	Large mammal
		3	W20C	OxA-27948	36150	750	42104	39286	-19.8	tooth	<i>Megaloceros</i> sp.

Beta-Analytic samples were collected during the excavation project led by B. Mihailović. OxA-27975, OxA-27683, OxA-27682, and OxA-27829 were conducted under the FP7-PEOPLE-2012-CIG (Ref.N 322112) and Spanish Ministry of Economy and Competitiveness (HAR2012-33956) grants to Marín-Arroyo; OxA-27948 was conducted under the NERC Late Quaternary Megafaunal Extinctions grant to A. J. Stuart and A. M. Lister.

radiocarbon dates, there would have been a depositional hiatus of several thousand years between cave mouth levels 5b (Mousterian) and 5a (Aurignacian).

The modeled age for the end of the European Mousterian has been estimated as lying between 41 and 39 ka cal BP based on material from the sites of Spy (Belgium) and Bombrini (northwestern Italy) (see Higham et al. 2014: Supplementary Information). Current dating evidence supporting a late Neanderthal survival only in southern latitudes (e.g., Vindija, Zafarraya, Gorham's Cave) is now regarded as problematic (Higham et al. 2006b; Wood et al. 2013). Therefore, the Mousterian occupations at Šalitrena Pećina might support the hypothesis of a withdrawal of Neanderthal groups from the fluvial Danube plains into the mountainous territories to the south (Mihailović et al. 2011).

In addition, an earlier presence of AMH in Europe has been confirmed for the Uluzzian in the Italian Peninsula (between 45 and 40 ka cal BP; Douka et al. 2014), the Aurignacian of northern Iberia (c. 42 ka cal BP; Zilhão 2006; Wood et al. 2014), the southwest German site of Geißenklösterle (between 43 and 41 ka cal BP; Higham et al. 2012), and the directly dated KC4 maxilla of Kent's Cavern in the UK (between 44.2 and 41.5 ka cal BP; Higham et al. 2011). All of these evidence suggests that the spread of AMH throughout Europe was rapid and that the period of coexistence with Neanderthals was shorter than previously thought, potentially even within the error ranges of chronological models (Wood et al. 2014). The Danube Valley could have been a major colonization route into central and western Europe from the Near East, as evidenced by the sites of Temnata and Bacho Kiro (Layer 11) in Bulgaria with radiocarbon dates slightly older than those of the Uluzzian levels at the Grotta del Cavallo (Douka et al. 2014; Mellars 2011). In Serbia, Tabula Traiana Cave, located in the Danube Gorge, provided the first radiocarbon dates of the early Aurignacian ranging between 41.5 to 34.5 ka cal BP (Borić et al. 2012), with a small lithic and faunal assemblage attributed to short human occupations, whereas the dates at Šalitrena Pećina indicate a later and more intense occupation by modern humans. Nevertheless, the hiatus between levels 5b and 5a in Šalitrena Pećina might suggest no interaction between Neanderthals and AMH here during a period of ca. 6,000 years (assuming that in Serbia the Aurignacian only represents AMH, notwithstanding the lack of associated human fossils).

Here, archaeozoological evidence of macromammals recovered at Šalitrena Pećina offers an exceptional, albeit preliminary, opportunity to unravel the diet and subsistence strategies carried out by both human species and to reconstruct the paleoecological niches exploited in this eastern European region.

Zooarchaeological Analyses

The zooarchaeological analyses were conducted at the National Museum of Belgrade, where the material is currently curated. Only macromammalian remains from the cave mouth and Trench F that are securely attributed to the Aurignacian (level 5a in the cave mouth and level 5 in Trench F) and to the Mousterian (levels 5b, 5c, and 6

in the cave mouth) are analyzed here. The comparative collection at the Department of Archaeology at the University of Belgrade and the fossil collection from the Natural History Museum in London were used to determine taxa and skeletal elements. Each bone recovered during the excavation was spatially attributed to the square, sub-square, and archaeological level where it was found, complete with an individual identification number. Dry sieving during the excavation allowed the recovery of small anatomical elements as well.

Owing to small sample sizes, the Mousterian and Aurignacian assemblages were each grouped to permit preliminary comparison. The identified bones were quantified by applying the following indices: Number of Identified Specimens (NIS), Minimum Number of Individuals (MNI), Minimum Number of Skeletal Elements (MNE) following Marín-Arroyo (2009b), and Minimum Animal Units (MAU; Binford 1978). Biomass calculations were made by multiplying values of useable meat (following the methodology applied in Marín-Arroyo and González Morales 2009) using MNI. Because of the high degree of fragmentation, the specimens that could not be identified taxonomically by any distinctive landmark were grouped by size into megafauna (rhinoceros/megaloceros), large (bovine/horse), medium (red deer/ibex), and small (chamois/roe deer) ungulates. Unidentifiable carnivore remains were also grouped into large (cave bear, cave lion, leopard), medium (wolf, hyena, lynx), and small (fox, wild cat, mustelids).

Every skeletal element >2 cm long was examined under a LEICA S8 APO stereoscope with 10 × eyepieces to identify any biostratigraphic and diagenetic alterations, such as cut marks (grouped into skinning, dismembering, and defleshing categories following Binford 1981 and Pérez Ripoll 1992), hammerstone percussion marks [including conchoidal notches (Bunn 1981; Capaldo and Blumenschine 1994; Pickering and Egeland 2006), type and angle of fracturing (fresh green vs. old dry following Villa and Mahieu 1991), and thermoalterations. Carnivore and rodent gnaw marks and traces of digestion were also identified, as well as other biological and chemical alterations, such as weathering (Behrensmeyer 1978), root etching, insect/fungus activity, carbonate deposits, polishing (Fisher 1995; Lyman 1994; Shipman 1981), and dissolution or mineral coatings (mainly mineral manganese; see Marín-Arroyo et al. 2008, 2014).

Ungulate mortality patterns (i.e., juvenile, prime, or older individuals) were determined by using both dental eruption and wear stages of pd_4 , P_4 , and M_3 , following Stiner (1991, 2005). Dietary breadth and the degree of anthropogenic use of the environment have been evaluated using the inverse of Simpson's index. This index can vary between 1 and the number of hunted species, the former when the abundance of one species is overwhelming and the latter when all species are equally consumed.

Differential transport of carcasses and the related functionality of the site were investigated using bivariate correlations of %MAU with utility (in terms of %MGUI, following Binford 1978) and bone survivorship (represented by bone mineral density, following Lam et al. 1999). Correspondence analysis was used to compare the skeletal profiles found in the assemblages with theoretical profiles deriving from different kinds

of carcass butchery practices at kill sites and various degrees of attrition (Marín-Arroyo 2013). This method enables comparative evaluation between species and periods. When resources were scarce in the vicinity of a site and changing residency is not likely to improve the situation, mobility and catchment areas would have to increase. As travelling times become longer, differential transport of carcasses will intensify to maximize the energy contributed to the base camp (Cannon 2003; Marín-Arroyo 2009a). The possible ways in which human groups might have processed carcasses at kill sites are summarized in Table 2. Once elements were discarded and deposited at the base camp, they undergo attritional processes of varying intensity, characterized by a parameter (β) that can vary between 0 and 8. Thus, the likelihood of survival of a single element, in the absence of better estimates, is obtained as an exponential function of the bone density (Rogers 2000). A value of $\beta=1$ would indicate that only half the bones survive, whereas if $\beta=2$, the survival percentage is reduced to 25%, and so on.

Finally, the relationship between the consumed fauna and ecological niches was investigated by estimating the catchment areas associated with the site, characterizing the local relief, following the methodology described by Marín-Arroyo (2009a). A digital model of the terrain around the sites was produced, including the continental shelf (ASTER GLOBAL DEM and ETOPO1 data). Travelling times across the territory were estimated with empirical formulas depending on distance, slope angles, movement direction (uphill or downhill), and the existence of nearly insurmountable barriers (Marín-Arroyo 2010). To define the preferred biotopes for plains and montane species, within the boundaries determined by the catchment area, a threshold value of 10% slope has been fixed to differentiate areas related to one or the other group of taxa. Beyond that value, grazing suitability is depleted (Holeček et al. 1998)

Table 2. Proposed strategies of carcass processing at a kill site and transport to a basecamp.

P can take a value of 0, 0.2, 0.4, 0.6, 0.8, or 1. The head is represented by mandibles; the axial skeleton, by vertebrae, ribs, pelvis, and sacrum; the forelimb, by scapula, humerus, radius/ulna, metacarpals, carpals, and phalanges; and the hindlimb, by femur, tibiae, metatarsals, astragalus, calcaneum, tarsals, and phalanges.

Strategy	Probability	Transport to the site			
		Head	Axial	Forelimb	Hind limb
Complete contribution	1	Yes	Yes	Yes	Yes
	P	Yes	Yes	Yes	Yes
Axial processing at the kill site	(1-P)/2	No	No	Yes	Yes
	(1-P)/2	No	No	No	Yes
	P	Yes	Yes	Yes	Yes
Appendicular processing at kill site	(1-P)/2	No	Yes	No	Yes
	(1-P)/2	No	Yes	No	No

RESULTS

Quantification of the Faunal Assemblage

The Mousterian and Aurignacian levels collectively yielded 2,604 faunal remains (bones and teeth), 14% of which were identifiable to taxa and 34% to anatomical part. Owing to the state of fragmentation of the assemblage, a minimum number of only 463 anatomical elements (MNE) were quantified (18% of NISP). The total MNI represents 75 different ungulate, carnivore, rodent, leporid, and bird taxa. The distribution of NISP, MNE, and MNI values per level and species is presented in Table 3. The assemblage composition of ungulate and carnivores is similar in the Mousterian and Aurignacian levels. Ungulates represent 64% in the Mousterian and 54% in the Aurignacian, while 35% of the assemblage in each cultural period is attributable to carnivores. Other taxa, such as leporid, rodent, bird, and fish remains, represent 2% in the Mousterian and 11% in the Aurignacian levels, respectively.

Origin of the Deposit

Determining the taphonomy of the deposit is essential for identifying the agents involved in the formation of the assemblage, and it is crucial to ascertain before any interpretation about subsistence can be made (Lyman 1994). First, to determine if the deposit was accumulated primarily by humans or carnivores, the percentage of long bones with cut marks and gnawing marks was calculated. As shown in Figure 4, experimental and ethnographic results from control samples have been combined with the aim of distinguishing the agent of accumulation of large and medium-sized mammal bones in Šalitrena Pečina. To do so, typical cut-mark percentage data have been obtained from previous studies by Dominguez-Rodrigo (1997: Table 2), Selvaggio (1998: Table 6), Capaldo (1998: Table 12), Lupo and O'Connell (2002: Table 6), Dominguez-Rodrigo and Barba (2005: Table 3); the tooth-mark data were taken from Blumenschine (1995: Table 3), Capaldo (1998: Table 12), Selvaggio (1998: Table 6), and Marean et al. (2000: Table 3).

The results show that long bones from large and medium-sized mammals from both Aurignacian and Mousterian levels were clearly brought to the cave by humans, as they have significantly more butchery marks than those originating from carnivore activity. In particular, medium-sized mammal bones from Mousterian level 6 fall within the typical range of being accumulated first by humans and later scavenged by carnivores, whereas those from level 5c are not clearly attributed to humans because there is an overlap between "carnivore to human" and "human to carnivore" patterns (Figure 4). As well as those occurring on long bones, cut marks were found on other skeletal elements, such as crania, axial elements, metapodials, and phalanges. Thus, for large mammals, the percentage of butchery marks is 13.6% in the Mousterian assemblages and 6.9% in the Aurignacian ones, and for medium-sized mammals, such anthropogenic marks were found on 5% and 2.7% of the Mousterian and Aurignacian assemblages, respectively. Carnivore marks on large mammals are

almost identical during the Mousterian (3.7%) and Aurignacian (3.8%), and for medium-sized mammals the percentage is lower during the Mousterian (0.7%) than in the Aurignacian (2.7%). Among small mammal bones, neither cut marks nor gnaw marks were found, and no evidence of small, fast game exploitation has been identified in either period. In summary, the deposit is clearly linked to human activity and can be interpreted as evidence of human subsistence.

In addition to butchering marks identified on large and medium-sized mammals, other anthropogenic modifications have been recognized in the assemblage (Table 4). In particular, 30% of the ungulate bones in the Mousterian levels and 17% in Aurignacian levels show evidence of fresh bone fractures. Flake scars on the medullary surface were identified on 9% of the bones in Mousterian and 8% in Aurignacian levels. Signs of thermoalteration on ungulate remains were found on 4% of the bones in Mousterian and 4% in Aurignacian levels. Figure 5 shows some of the biostratigraphic modifications identified on animal bone surfaces.

There are abundant signs of marrow extraction in all levels. The degree of fragmentation (measured as the quotient between NISP and MNE) correlates positively and significantly with the Marrow Index (1) for medium-sized mammals in the Mousterian (levels 5b and 5c) and (2) for large mammals in all of the Mousterian and Aurignacian levels, except in Trench F (Table 5).

Within the Aurignacian level in Trench F, anthropogenic activity, although apparent, is more infrequently observed within the assemblage, whereas gnawing marks were identified in a larger percentage than in other strata. The location of this trench, toward the interior and close to the south wall, made it a suitable place for carnivore denning and, at the same time, made it less appealing for human activities, serving for human groups more as an area of transit to the rear part of the cave. Three different cave bear individuals (one infantile, one prime-age and one old) were identified in the trench in addition to hyena and fox remains. This sheltered zone could have been used both by cave bears and as a location where secondary carnivore scavenging activities took place. Therefore, Trench F has been excluded from further human subsistence analysis and interpretation.

Other biostratigraphic and diagenetic alterations are summarized in Table 6. Within the cave mouth, Mousterian levels 5b, 5c, and 6 are less sheltered than areas deeper the cave, so these levels might have suffered several episodes of ponding and water flow, with intensive washing being indicated by the larger number of bones showing evidence of dissolution. Thus, the substantial number of bones with weathering suggests that there were significant changes in temperature/humidity at the times that levels 5b and 6 were being deposited. The trampling activity in level 6 could be a result of human activity, as well as the great abundance of detritus that fell from the roof of the cave during the Mousterian period, which is indicative of a cold period. Finally, in Trench F, the high proportion of polished bones (up to 19%) is likely due to cave bear trampling, as this area served as a corridor to the interior of the cave.

Table 3. Description of faunal assemblage (NISP, MNE, MNI) by level.

	Aurignacian						Mousterian							
	Trench F		Level 5a		Level 5b		Level 5c		Level 6					
	NISP	MNE	MNI	NISP	MNE	MNI	NISP	MNE	MNI	NISP	MNE	MNI		
<i>Diceroelobius hemitoechus</i>							2	2	1			6	5	1
<i>Bos/Bison</i> sp.	3	2	1	24	16	1	20	16	2	45	22	1	11	7
<i>Bison prisus</i>							3	3	1					
<i>Equus ferus</i>	1	1	1	2	2	1	12	7	1	2	2	1	7	5
<i>Cervus elaphus</i>				7	7	3	8	7	2	2	2	1	5	4
<i>Capreolus capreolus</i>							2	2	1					
<i>Capra ibex</i>	5	3	1	7	6	2	7	6	2	16	4	1	11	10
<i>Rupicapra rupicapra</i>							5	3	1				2	2
<i>Crocuta spelaea</i>	2	2	1										1	1
<i>Ursus spelaeus</i>	13	11	3	7	6	3	8	8	2	1	1	1	21	12
<i>Canis lupus</i>				3	2	1	3	3	1	1	1	1	2	2
<i>Vulpes vulpes</i>	1	1	1	5	5	1	19	19	1	5	5	1	16	13
<i>Panthera leo</i>				1	1	1								
<i>Panthera pardus</i>				1	1	1							1	1
<i>Felis silvestris</i>							2	2	1	2	2	1	3	3
<i>Lynx lynx</i>										2	2	1		

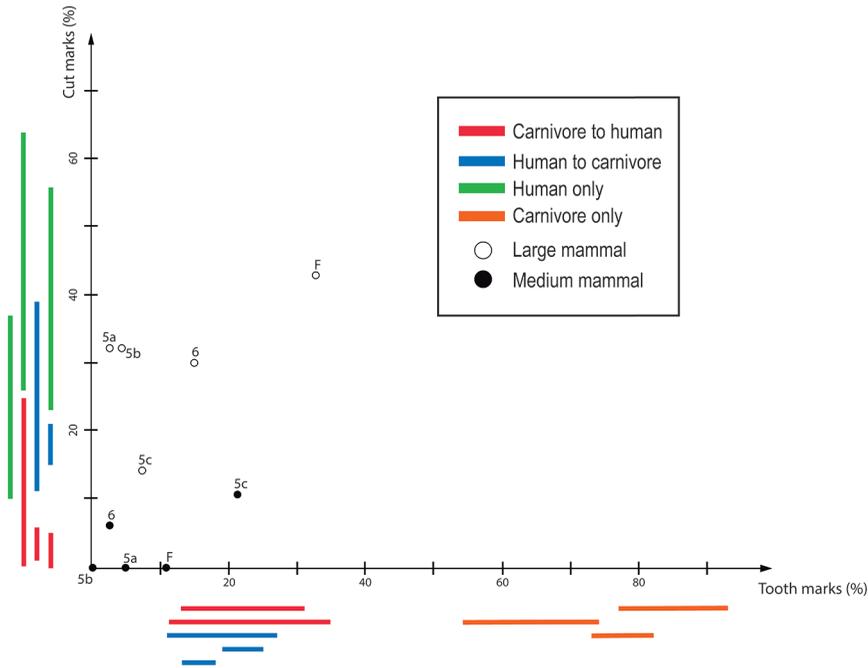


Figure 4. Percentages of large and medium-size mammal long bones with cut and tooth marks in the Mousterian (5b, 5c, 6) and Aurignacian (5a and F) levels at Šalitrena Pečina, compared with findings from ethnographic and actualistic studies. Sources are listed in the text.

Subsistence Strategies and Ecological Niche Exploitation

Table 7 shows the taxonomical representation of ungulates at Šalitrena Pečina in terms of NISP and biomass. On the one hand, in terms of NISP, bovines (followed by ibex, horse, and deer) are the most abundant taxa in the Mousterian assemblage, which is consistent with the topographic location of the cave very close to open plains. Those flat areas were the favored habitat for the bovines (Figure 6a), whereas the habitat of ibex is around a 2-hour walk from the site. Other identifiable ungulates, which appear in relatively small numbers, are rhinoceros and small mammals, such as roe deer and chamois. In the Aurignacian deposit, bovines are the most important taxa, with higher percentages than in the Mousterian assemblage, followed by red deer and ibex, with horse being scarcely represented. However, the differences in terms of NISP between the Mousterian and Aurignacian are nearly imperceptible when comparing the size of the prey. Medium-sized mammals are slightly more abundant during the Aurignacian, and small mammals were only identified in Mousterian assemblages.

On the other hand, when considering the biomass contributed by the different species in each cultural assemblage, there are some differences vis-à-vis those shown by NISP figures (Table 7). First, when rhinoceros is present (only during the Mous-

Table 4. Summary of occurrence (NISP) of key taphonomic traits by mammal size classes

		NISP w/o teeth	Cut marks	Spiral fracture	Impact scars	Burning	Tooth marks	Digestion
Aurignacian	Trench F							
	Large	39	7	8	2	0	10	0
	Medium	53	1	3	0	0	4	0
	Small	1	0	0	0	0	1	0
	Total	93	8	11	2	0	15	0
	Level 5a							
	Large	76	13	31	12	5	1	0
	Medium	111	7	8	9	8	4	2
Small	11	0	0	0	0	0	1	
Total	198	20	39	21	13	5	3	
Mousterian	Level 5b							
	Large	187	39	56	26	7	10	1
	Medium	63	7	10	3	7	0	0
	Small	11	0	4	2	1	0	0
	Total	261	46	70	31	15	10	1
	Level 5c							
	Large	134	24	71	18	0	17	0
	Medium	17	6	7	1	3	5	0
	Small	1	0	0	0	0	0	0
	Total	152	30	78	19	3	22	0
	Level 6							
	Large	170	32	46	6	2	10	1
	Medium	111	22	17	7	5	14	0
	Small	5	0	0	0	0	0	0
Total	286	54	63	13	7	24	1	

terian), it could represent, in theory, the most important part of the diet. However, the number of skeletal elements of rhinoceros is relatively small and, in this case, we consider that the MNI is inflating the real representation of this taxon. Therefore, excluding rhinoceros, 63% of the Neanderthals' diet was based on bovines, the taxon that provided the greatest amounts of meat, grease, and fat to the diet. It was followed by horse (15%) and red deer (16%) and, to lesser extents, by ibex (6%) and chamois and roe deer (0.4%). The AMH diet was composed of 41% bovines, followed by 36% red deer, 15% horse, and 7% ibex (Table 7). Thus, both Neanderthals and modern humans in Šalitrena Pećina relied on the exploitation of bovines, although the percentage of medium-sized mammals (red deer) is higher in the Aurignacian (36%)



Figure 5. Examples of taphonomic alterations and bone tools. (A) Mousterian (top to bottom) a bovid rib with cut marks; a deer metapodial used as a bone retoucher; a burnt flat bone with cut marks; (bottom left) gnawing marks on a ibex femur; and (bottom right) an ibex astragalus with dismemberment marks. (B) Aurignacian: *Antalis* sp. bone shaft with deliberate modification and use wear (dated OxA-27/683); four different views of a grooved bone point fragment (dated OxA-27/975); and a likely spatula point made from a long bone shaft.

Table 5. Spearman's correlation (ρ_s) between NISP/MNE and Marrow Index for mammals by size class (significant if $p < 0.05$). Positive and significant correlations are shaded.

	Large	Medium	Small
Aurignacian			
Trench F-Level 5	0.126	0.058	0.27
	0.548	0.784	0.192
Level 5a	0.628	0.205	0.202
	0.001	0.325	0.344
Mousterian			
Level 5b	0.54	0.405	0.036
	0.005	0.045	0.864
Level 5c	0.46	0.609	-0.195
	0.021	0.001	0.35
Level 6	0.502	0.333	0.206
	0.011	0.104	0.324

than the Mousterian (16%). There are no significant differences between the Mousterian and Aurignacian assemblages in the exploitation of horse and ibex, as those taxa show similar percentages.

The inverse Simpson index (Figure 7) indicates higher values in Mousterian levels 5b and 6, which could be interpreted as a wider diet at that time. However, Mousterian level 5c and Aurignacian level 5a show lower values, indicating a narrower diet (Figure 7). Hence, we cannot reject the possibility that the change observed in taxonomical composition between the different levels could have been caused by other factors, such as the season of occupation, site function, group size, or archaeological

Table 6. Diagenetic modifications reported by %NISP (in relation to the total NISP of the assemblage)

Source/Type of Modification	Aurignacian	Mousterian		
	Level 5a	Level 5b	Level 5c	Level 6
Rodent	14.8	0.7	0	0
Insect/fungus	17.3	1.9	0	0
Root etching	0.6	0.7	0	0
Carbonate	7.9	1.8	0.3	3.2
Coating	12.9	37.5	6.6	44.8
Dissolution	5.8	12.1	0.6	3.8
Trampling	1.4	1.9	0.3	17.8
Polishing	18.6	3.1	0	4.9
Weathering	1.2	15.1	1.2	19.7

Table 7. Taxonomical representation (by species and size class) of ungulates in terms of %NISP and %biomass (in relation to the total ungulate assemblage)

	% NISP		% Biomass		
	Aurignacian	Mousterian	Aurignacian	Mousterian	Mousterian (w/o rhinoceros)
By Species					
<i>Dicerorhinus hemitoechus</i>	0	5	0	43	0
<i>Bos/Bison</i> sp.	59	48	41	36	63
<i>Equus ferus</i>	5	13	15	9	15
<i>Cervus elaphus</i>	20	9	36	9	16
<i>Capreolus capreolus</i>	0	1	0	0	0
<i>Capra ibex</i>	17	20	7	3	6
<i>Rupicapra rupicapra</i>	0	4	0	0	0
By Size Class					
Large	63.4	64.1	56.6	84.7	52.0
Medium	36.6	30.4	43.4	15.1	15.1
Small	0.0	5.5	0.0	0.3	0.3

sampling biases, rather than a clear difference in subsistence strategy between two hominin species.

As a whole, although ibex is well represented in terms of NISP in both cultural assemblages, large mammals clearly played the most important role in the diet during both Mousterian and Aurignacian occupations in Šalitrena Pečina. Both Neanderthals and modern humans intensively exploited the fluvial plain biotopes, located less than 1.5 hours' walking distance from the site. In addition, the presence of ibex reflects the exploitation of mountain environments by both human species (Figures 6a and 7).

The presence of beaver during Mousterian could be related to a natural death, given the proximity of the cave mouth to the Ribnica River, as the remains do not show evidence of human modification.

Finally, although the macromammals recovered at the site are not very sensitive to climatic change because of their plasticity vis-à-vis warmer and colder environments, the spectrum of ungulates is typical of both forested and grassland habitats, which is in agreement with the modelled temperatures and the paleoenvironmental reconstructions of the MIS3 in eastern Europe. In fact, climatic simulations of Greenland Stadial 12 (-46 ka cal bp) with a regional climatic model (RCA-3) coupled with a dynamic vegetation-terrestrial ecosystem model (LPJ-GUESS) show that the region was then dominated by semi-open areas, with a tree cover of ca. 50–60% (Kjellström et al. 2010) (Figure 6b).

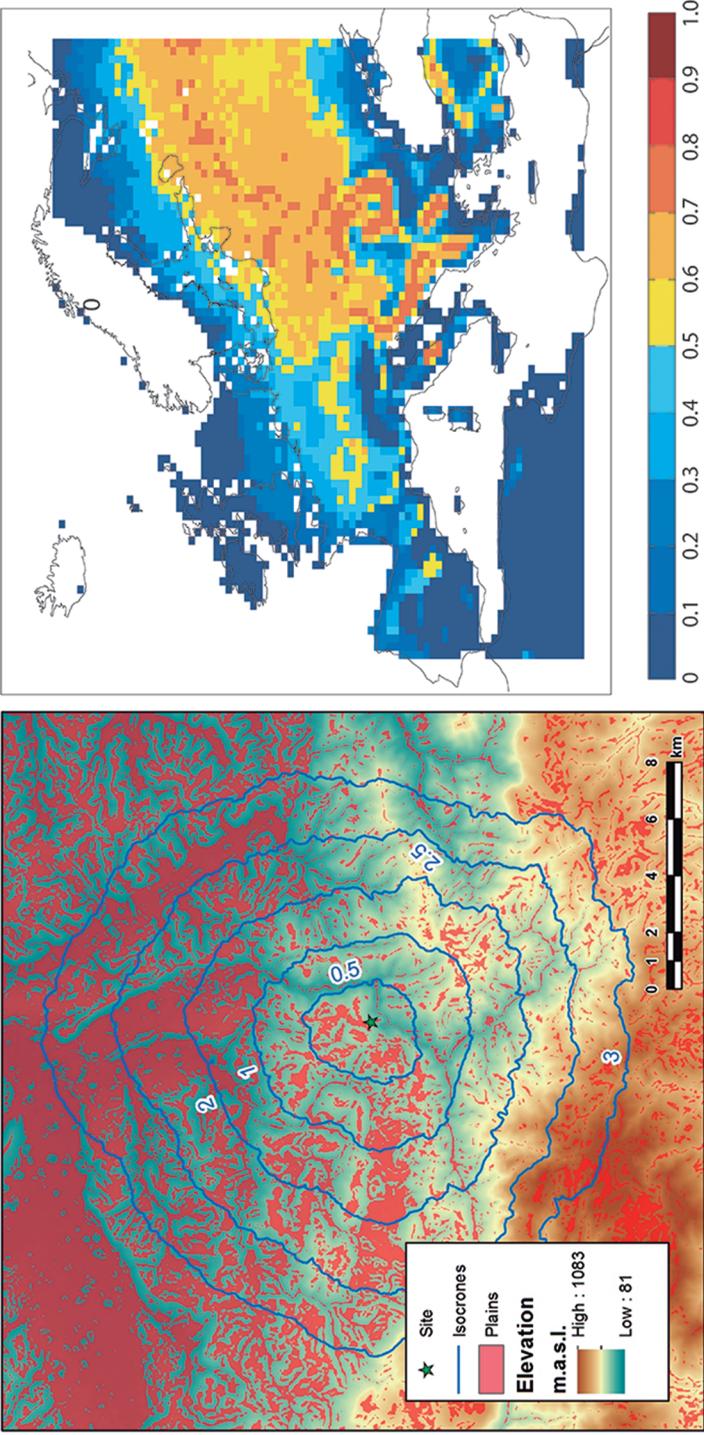


Figure 6. (Left) Catchment areas up to 3 hours walking distance from Šalitrena Pečina. (Right) Proportion of environment represented by forest as simulated for the MIS3 stadial by LPJ-GUESS (in Kjellström et al. 2010: Fig. 12, p. 447)

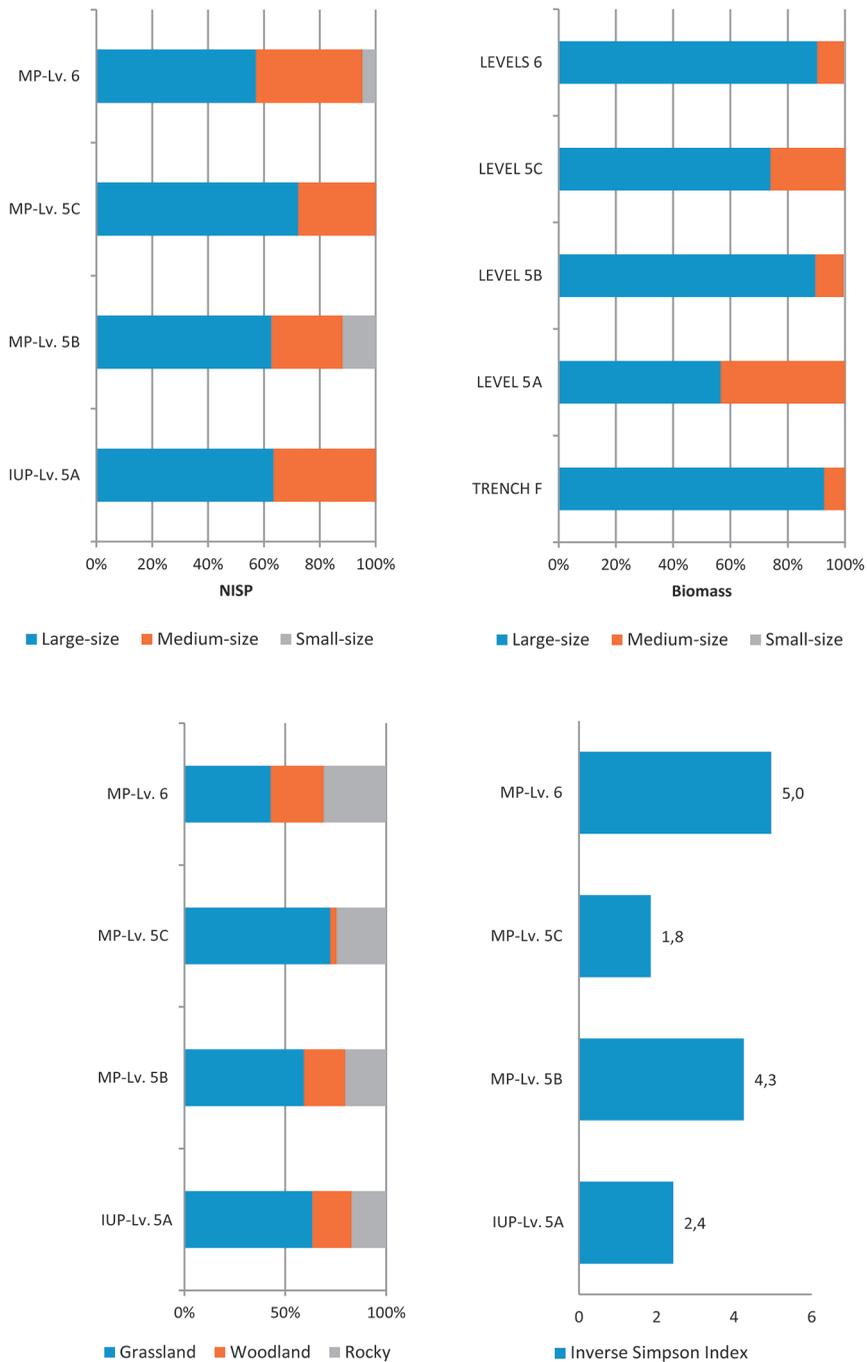


Figure 7. Diet comparison in terms of NISP and biomass for large, medium-size, and small ungulates in relation to habitat biotopes and inverse Simpson Index in Šalitrena Pečina. MP: Middle Palaeolithic, IUP: Initial Upper Palaeolithic.

Ungulate Mortality Profiles and Seasonality

In general, the percentage of juvenile, prime-age, and older individuals in both the Mousterian and Aurignacian assemblages is consistent with live herd profiles. In both periods, there is a clear predominance of prime-age individuals. Specifically, in Mousterian level 5c, only prime-age individuals were selected (Figure 8). The differences in the representation of juvenile and older individuals could reflect different activities at the site, the local population densities of the respective animals, or the site's location via-à-vis the herds at different times. Seasonality was difficult to assess, owing to the small sample sizes, although hints of an autumn occupation are present in Aurignacian level 5a.

Mobility Patterns

The relationship between human groups and the territory they inhabited is crucial for identifying mobility patterns (Marín-Arroyo 2013) and assessing whether they exploited available resources in an efficient way (Lupo 2006), thereby enhancing their chances for survival (Kaplan and Hill 1992). Topographic characterization of nearby

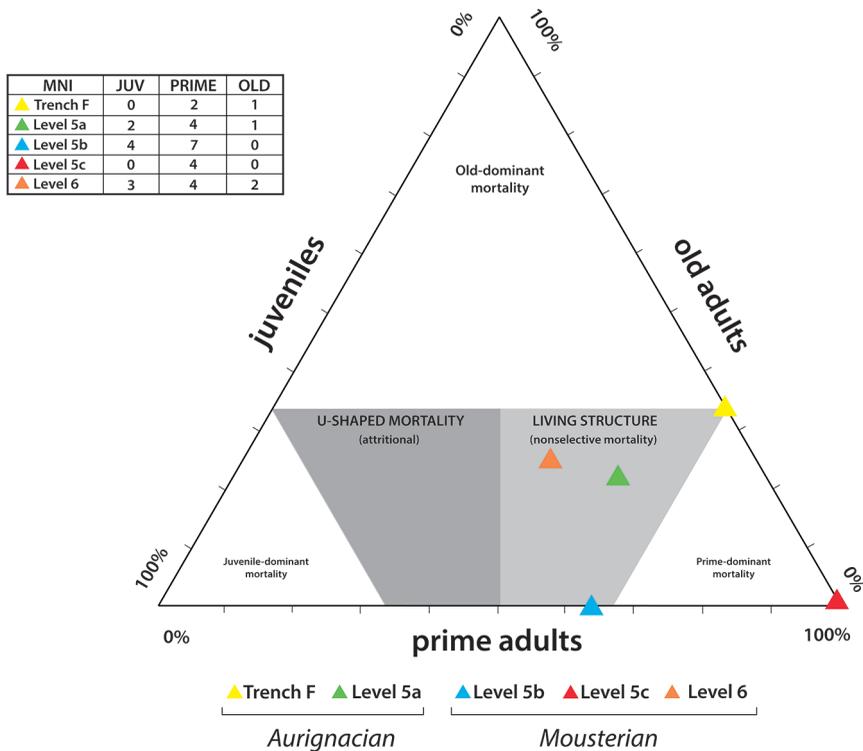


Figure 8. Mortality profiles of ungulates at Šalitrena Pećina during the Aurignacian and Mousterian.

Table 8. Occurrence (km²) and ratio of plains and hilly environments within easy walking distance of Šalitrena Pečina

Travel time (h)	Plains (km ²)	Hills (km ²)	Ratio Plains:Hills
0.5	2.9	7.7	0.37
1	11.9	31.6	0.38
1.5	31.7	72.4	0.44
2	62.0	130.0	0.48
2.5	104.9	202.3	0.52
3	163.2	290.3	0.56

catchment areas in comparison with the type of animals consumed is especially useful (Marín-Arroyo 2010). Figure 6a shows the catchment areas corresponding to different travel times around Šalitrena Pečina. The surface areas of plains and montane biotopes, as identified by a 10% slope threshold, is presented in Table 8. Figure 6a shows the catchment areas up to 3 hours' walking distance from Šalitrena Pečina.

Access to the plains increases after a 1.5-hour walk from the site, meaning that both human populations had to travel that far to exploit the large and medium-sized mammals that inhabit the grasslands and woodlands and that dominate the hominin diets. This energetic expenditure should be reflected in the differential transport of skeletal remains if an optimal strategy was followed. Table 9 presents the results of the bivariate correlations between %MAU and both MGUI and bone density, showing that there is no significant correlation with the utility index. On the contrary, the

Table 9. Correlations between %MAU and both MGUI and bone density (ρ_s is significant if $p < 0.05$). Positive and significant correlations are shaded.

	Level	Mammal Size Class					
		Large		Medium		Small	
		ρ_s	p	ρ_s	p	ρ_s	p
%MAU-MGUI							
Aurignacian	5a	0.344	0.116	0.010	0.963	0.102	0.650
Mousterian	5b	0.126	0.577	0.205	0.359	0.170	0.450
	5c	0.160	0.477	0.011	0.961	0.249	0.264
	6	0.095	0.674	0.382	0.080	-0.193	0.390
%MAU-Bone density							
Aurignacian	5a	0.735	0.000	0.448	0.042	0.038	0.869
Mousterian	5b	0.591	0.005	0.669	0.001	0.047	0.838
	5c	0.569	0.007	0.617	0.003	-0.148	0.523
	6	0.656	0.001	0.643	0.002	-0.046	0.842

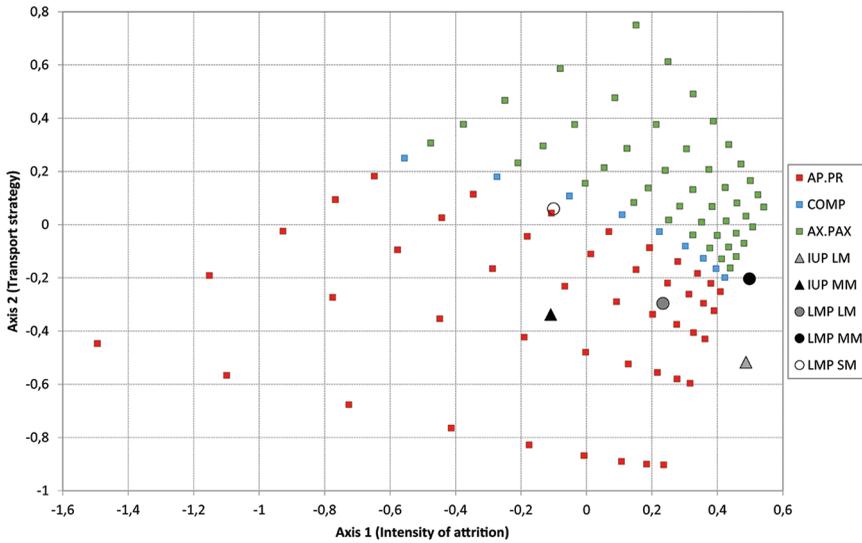


Figure 9. Correspondence analysis between recorded and theoretical skeletal profiles for large (LM) and medium-size (MM) mammals in Šalitrena Pećina during the Late Middle Palaeolithic (LMP) and the Initial Upper Palaeolithic (IUP). Axis 1 accounts for the degree of attrition, with larger numbers representing greater attrition. Axis 2 accounts for the transport strategy, with smaller numbers indicating more appendicular processing at the kill site. PAP: appendicular processing at the kill site, COMP: complete transport of the carcass, PAX: axial processing at the kill site.

role played by attrition in the deposit is quite notable, a fact that led to a skewing of the original anatomical representation of the skeletons, complicating inferences as to hypothesized human subsistence behavior. Outcomes related to small mammals are inconclusive because of the limited sample available for analysis.

In Figure 9, the transport strategy presumably carried out by each human species is explored by comparing the existing anatomical element representations with the outcomes from different theoretical strategies and potential degrees of attrition. During the Aurignacian, a greater degree of appendicular skeleton processing of large and medium-sized mammals took place at the kill sites, in addition to greater levels of attrition. During the Mousterian, medium-sized mammals were being brought to the site almost complete, whereas large mammals might have been processed at the kill site, as in the Aurignacian. Neanderthals might have processed the appendicular skeleton of larger prey at the kill site, but perhaps to a lesser extent in comparison with modern humans' butchering strategy.

DISCUSSION

Despite the rapid climatic oscillations during the MIS3, the central area of the Balkan Peninsula may have acted as a relatively short-term refugium for Neanderthals to

withdraw after the arrival of AMH into Europe. The particular ecological conditions, with short river valleys and steep mountain areas with karstic caves and rockshelters, might have favored their retreat into this area south of the Danube River. For Serbia, the first chronometric dates for late Neanderthal and early AMH occupations are presented in this paper (Table 1). On the one hand, the late Middle Paleolithic dates of Šalitrena Pećina, ranging between 42 and 39 ka cal bp, are in agreement with the current modelled age for the end of the European Mousterian (Higham et al. 2014). Thus, evidence at Šalitrena Pećina would support late Neanderthal survival in southern European latitudes. In the southeast, they could have been forced to move south of the Danube, toward the mountainous part of the Balkan Peninsula. On the other hand, the Aurignacian dates at Šalitrena Pećina are relatively recent in comparison with the first dates of the presumed arrival of AMH into the continent (Douka et al. 2012; Szmidi et al. 2010), but they are significant to help unravel the activities of both populations in the region. In summary, our results show a chronological succession of Mousterian and Aurignacian occupations in this cave. No evidence of transitional industries between late Mousterian and Early Upper Paleolithic culture is found in Šalitrena Pećina. The hiatus between cultural complexes of ca. 7,000 years, previously suggested by Mihailović (2009), seems to indicate that Neanderthal and AMH groups did not coexist and interact in this particular region.

Our poor knowledge of the Middle to Upper Paleolithic transition in the central Balkans, because of the scarcity of sites, the lack of well-dated archaeological sites, and the absence of zooarchaeological and taphonomic studies, highlights the relevance of the data obtained at Šalitrena Pećina for understanding this complex transition between Neanderthal and early AMH in the Balkan region. Consequently, despite the small size of the faunal assemblages, the zooarchaeological results obtained in this study are meaningful as they provide the first data about the subsistence strategies and ecological niche exploitation of both late Neanderthal and early modern human populations in Serbia. Results indicate that both human species exploited the same ecosystems and hunted the same prey with only slight differences in the representation of each taxon, as is evidenced in other European regions (Boyle 2000; Grayson and Delpech 1998; Patou-Mathis 2000). Bovines are the most common taxa within the Neanderthal diet, followed by other large and medium-sized mammals (although those were supplementary), whereas modern humans exploited bovines as well as red deer, with very similar percentages of biomass. Although there is no clear evidence of a narrower diet breadth during the Aurignacian, Neanderthals did target a wider range of prey, including some low-ranked ones, such as chamois and roe deer, which are unrepresented in the Aurignacian levels. The representation of these smaller mammals could be interpreted as a more opportunistic pattern (Bar-Yosef 2004). Diversification at the end of the Middle Paleolithic has been attributed either to demographic pressure (Stiner et al. 1999) or to less productive hunting (Hortolà and Martínez-Navarro 2013), but in Šalitrena Pećina diversification is debatable since the percentage of small prey is relatively low. In addition, there are no significant shifts in mortality profiles

during the Middle to Upper Paleolithic transition, whereas mortality data for ungulates suggest that adults were preferentially selected. These different taxonomic and age profiles could be a result of several factors, such as group size and functionality, animal population density, seasonality and settlement organization, among others, rather than by intentional choice of different subsistence strategies. Therefore, it is difficult to specify whether cognitive, technological, or social abilities could best explain these differences.

Regarding anatomical element representation, Neanderthals brought whole carcasses of medium-sized mammals back to the site, whereas modern humans processed the same prey more intensively at the kill sites and brought back to the cave mostly appendicular elements. The topographic location of Šalitrena Pećina, surrounded by extensive fluvial plains that provided the bulk of the diet in both periods, is key to understanding the potential energetic yield that each human species managed to reach. The fact that AMH practiced a more intensive processing of the appendicular skeleton at the kill site could be a reflection of larger catchment areas (Lupo 2006; Marín-Arroyo 2013; O'Connell et al. 1988; Rabinovich and Hovers 2004), perhaps due to lower animal density resulting from climatic instability. This processing behavior may have been a response to a need to maximize the energetic contribution to the camp, due to either a larger population to sustain or lower resource availability. Whereas Neanderthals might have had greater energetic needs (De Groot 2011), AMH would have possessed lower basal energetic costs because of their smaller body size and more efficient locomotion owing to their longer lower limbs (MacDonald et al. 2009; Steudel-Numbers and Tilkens 2004; Weaver and Steudel-Numbers 2005). These physiological features might explain some of the strategies they adopted, although the small size of the archaeofaunal sample precludes drawing definitive conclusions. The lack of a seasonal signal in the timing of hunting events might emphasize the great flexibility in Middle Paleolithic subsistence (Boyle 2000; Gaudzinski and Niven 2009; Grayson and Delpech 2006; Morin 2004). Nevertheless, Neanderthal hunting efficiency, as measured by time and effort expended to kill their prey, may have been lower than that of early modern humans in Europe and in Africa (Marean 2005; Villa and Roebroeks 2014).

There is not yet enough evidence, at least in this particular region, to attribute Neanderthal extinction to subsistence issues. The differences observed in the Šalitrena Pećina faunal assemblages are not large enough to identify nutritional stress from lower carrying capacity or climatic instability. The representation of ungulates and the anthropogenic marks on the bones do not reflect a climatic change either, unlike in Roc de Marsal and Pech de l'Azé IV, where Neanderthals were processing faunal remains more heavily during glacial periods as a response to increased nutritional stress (Hodgkins et al. 2016). In summary, despite the intense current fieldwork and analyses to find Paleolithic human occupations and to provide information about the behavior of both human species during the Middle and Upper Paleolithic, more multidisciplinary studies such as micromorphology, micromammals, pollen, and stable isotope analyses are needed not only for Šalitrena Pećina, but also throughout Serbia and the Balkans.

CONCLUSION

The late Mousterian occupations of Šalitrena Pećina, located in the central Balkans, a likely mountainous refugium for Neanderthals during the rapid dispersal of Anatomically Modern Humans throughout Europe along the Danube corridor, fills an important gap in the study of the Middle to Upper Paleolithic transition in the southeastern part of Europe. The zooarchaeological analysis of the admittedly small faunal assemblages has allowed us to begin to reconstruct the subsistence strategies carried out by both human species in Serbia. Despite the climatic fluctuations during MIS3, the differences in subsistence between Neanderthals and AMH are narrow, as they were exploiting the same habitats and prey. Future research should focus on discovering contemporaneous sites where human remains might be found, investigating the role of other dietary resources, and reconstructing the climatic and environmental conditions at that time. All these data will help us to understand human behavior during Late Pleistocene in Serbia, and in the Balkans in general.

NOTE

Thanks are due to P. Miracle for introducing the first author to the Balkans Paleolithic and especially to Prof. R. Foley and M. Lahr for their support during the initial part of this research at the University of Cambridge. The authors want to acknowledge the National Museum in Belgrade and the Natural History Museum in London for the facilities provided during the study of Šalitrena Pećina material. V. Dimitrović kindly welcomed ABMA to her Laboratory of Bioarchaeology at the University of Belgrade. ABMA warmly appreciates the significant help of M. Lopčić and S. Milošević during her research stays in Belgrade. Thanks to K. Douka for the shell pretreatment, J. Jones and the *JAR* editor for English language correction, and L. Agudo for her technical support with some of the figures. This revised version of the paper profited from the criticism and advice of three anonymous reviewers and especially the editor, L. G. Straus. ABMA has a contract with the Ramón y Cajal Research Program (RYC-2011-00695) and wants to thank D. Ocio for his constant support. This research has been supported by a British Academy PDF (2011) and a Small Research Grant (SG102618) and by funds from the McDonald Institute for Archaeological Research in Cambridge during 2010/11. Currently, the research is involved in projects funded by the European Commission through FP7-PEOPLE-2012-CIG (Ref.N 322112) and by the Spanish Ministry of Economy and Competitiveness (HAR2012-33956). Since 2004, excavation in Šalitrena Pećina has been financed by the Ministry of Culture and Information of the Republic of Serbia.

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