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NEANDERTHAL SUBSISTENCE STRATEGIES AT THE KARSTIC SITES OF COUDOULOUS IN THE QUERCY (SW FRANCE) – FROM MARGINAL SCAVENGING TO A KILL-BUTCHERY SITE, AND BACK

Abstract

This paper reports a long stratigraphic Pleistocene/Palaeolithic sequence from Marine Isotope Stage (MIS) (8)-7 to MIS 4-3, discovered in a karstic system in south-western France, where two chronologically complementary archaeo-palaeontological sites were uncovered. The sites provide a global overview of biological (*sensu lato)* events happening at the same locale over time, in which herbivores, carnivores and humans all played a role. Several multi-disciplinary studies have been conducted and a first synthesis is proposed, which greatly complements our knowledge about subsistence strategies in Early Neanderthal and in Neanderthal populations.

Keywords

Karstic sites, south-western France, natural trapping, predators, human subsistence, Neanderthal

INTRODUCTION

Karstic environments – caves and sinkholes – provide favored habitats for many vertebrate and invertebrate species. Predators in particular, both human and non-human, use these places on a regular basis, often for limited periods only, according to their seasonal cycles of activities. Their often-alternating occupations in the caves leaves waste, which tends to mix and form amalgams or palimpsests in the fossil record. It is therefore interesting to disentangle the succession of these occupations and their chronology, and to determine their modalities. The abundance, nature and condition of fossil remains, the presence of lithic artefacts and the completeness of their *chaîne opératoire* allows us to distinguish primary occupations from more marginal, secondary occupations.

In the study of fossil assemblages, taphonomic resolution is often low. Nevertheless, major events as well as accumulating agents can be identified. Caves (horizontal entrance) and sinkholes (vertical entrance) can record and also preserve long chrono-stratigraphic sequences and significant fossil records.

One such case is represented by the karst sites of Coudoulous I and II (Lot) located in the middle hilly region of the Quercy in south-western France. Two archeo-palaeontological sites from the same karstic complex enable us to follow a succession of various occupations in one locale during a long time period, from the end of the Middle Pleistocene to the Late Pleistocene, spanning the period of Marine Isotope Stages (MIS) (8)-7 to MIS 4-3.

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THE QUERCY REGION

The two sites of Coudoulous are located in the center of a mid-elevated limestone area (named *Causse*, ca. 350-450 m a. s. l.) in the Quercy region, which is dissected by east-north / west-south running rivers (Dordogne, Lot, Célé, Aveyron rivers), coming down from the margin of the Massif Central to the Aquitaine Basin. The landscape is mainly characterized by plateaus and relatively narrow valleys bordered by limestone cliffs. This region yields numerous Palaeolithic and palaeontological sites, mostly located in caves and rock-shelter (Jarry et al., 2013). The hydrographic network and geological nature (mainly Jurassic) of the region explains the particularly high density of karstic cavities, composing of mostly caves and sinkholes (Brugal et al., 2006). Most of these sites yield a more or less large quantity of fossil material, especially bones of large ungulates which have fallen into these natural traps. Large Pleistocene animal populations (of ten or more individuals) of horse, bison, and occasionally cervids are well known from this type of setting. The palaeobiological data that can be extracted from these locales are important for our understanding of past climatic conditions and the dynamics of mammalian communities during the Pleistocene (Brugal et al., 2013a). Together with two other categories of sites, i. e., dens and human occupations, these locales provide high resolution biotic frames which are important to better understand the precise subsistence (acquisition, consumption) and behavioral traits (competition) of human and non-human predators. Finally, human occupation in this region seems relatively continuous from the end of Middle Pleistocene to the Late Pleistocene (Jaubert, 1999, 2010; Jaubert et al., 2013).

THE COUDOULOUS SITES

Coudoulous is located near the edge of a limestone plateau, overhanging two rivers (Lot and its tributary the Célé) (**Fig. 1**) with alluvial terraces and surrounded by prominent vertical cliffs. Some topographical incisions provide a connection between the two biotopes. The alluvial terraces served as the main source of lithic raw materials for humans.

This site complex basically functioned as a sinkhole for the most part of its depositional history. Discovered in 1966, rescue excavations conducted by J. Clottes and E. Bonifay (1978-1980; e. g., Bonifay and Clottes,

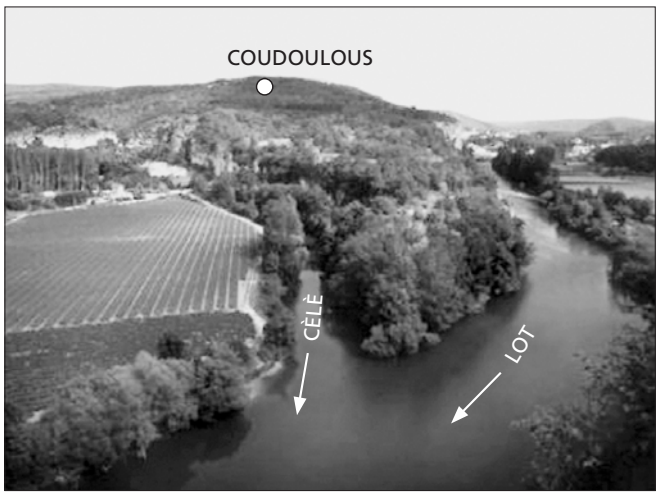

Fig. 1 Location of Coudoulous karstic sites on a plateau between the Lot and Celé rivers.

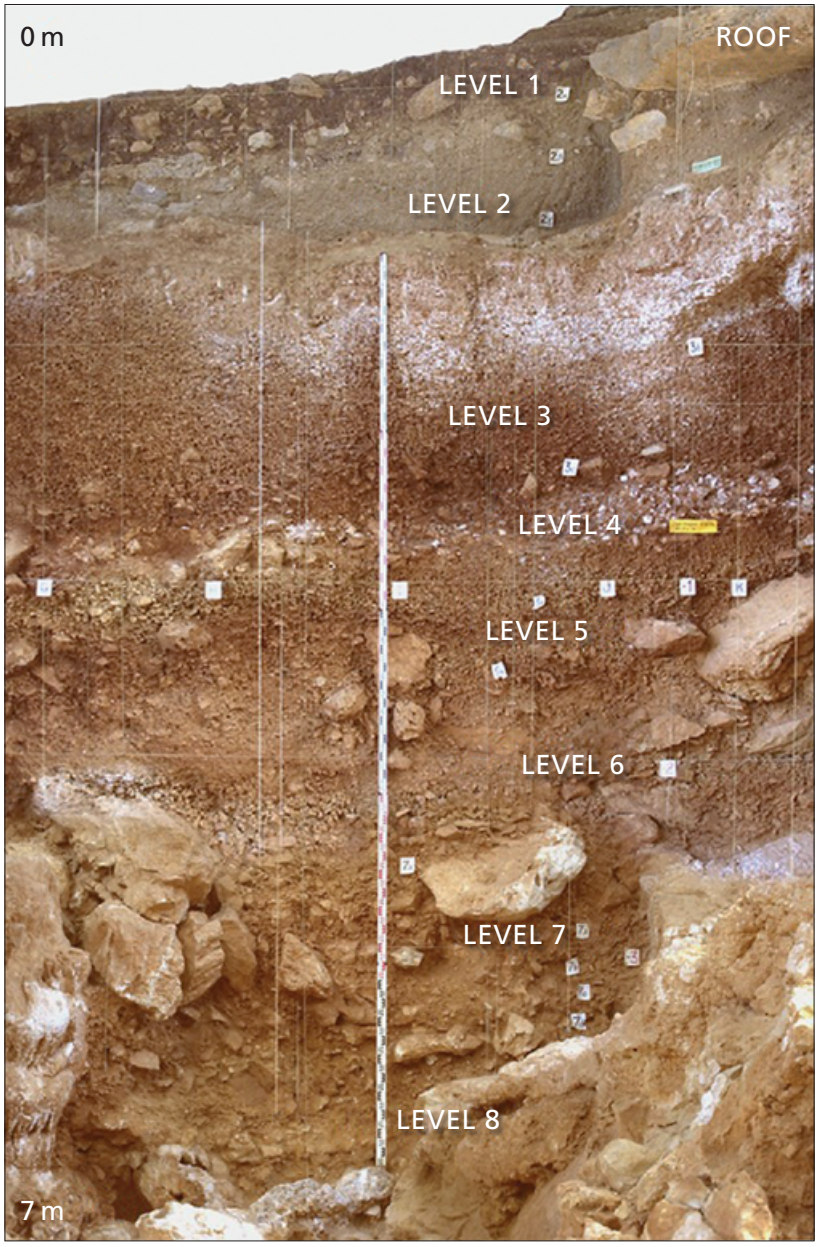

Fig. 2 Stratigraphic sequence of Coudoulous I.

1982) were followed by more intensive fieldworks (1993-2003) directed by the two authors of this paper. Interdisciplinary studies, undertaken during the field seasons, provided a general overview of the geological infilling and allowed us to determine the origins of the accumulations of bones and lithics, and their associations.

The combination of stratigraphic sequences from the two main deposits located in two distinct cavities provides a chrono-climatic record covering the time-span from ca. 300 ka to ca. 40 ka. The sequences yielded very rich and diversified faunal assemblages as well as different cultural layers that gave important new insights into both paleoenvironmental conditions and human subsistence strategies during at least MIS 7 to 3. Thus, Coudoulous provides the quite unique opportunity to follow the history of occupation of the locales in a diachronic perspective by studying the succession and interplay of biological and cultural agents.

Fig. 3 Example for bone (epiphysis) fragmentation with perpendicular fracture planes (Lower Unit – Coudoulous I).

Coudoulous I

Coudoulous I (see first synthesis in Jaubert et al., 2005) was partly destroyed by heavy quarry work. The geomorphology of the site, defined as a sinkhole resulting from the gradual collapse of the roof, constitutes a key-factor in explaining the occasional or more permanent occupations by carnivores and humans during the Middle Pleistocene. A complex sequence almost 8 m was subdivided into many strata and substrata representing four main units (**Fig. 2**): a basal part (levels 9-10) of karstic sterile clay; a complex lower part (levels 8 to 5) starting with a stalagmitic floor (basal sub-levels of level 8) and followed by detrital heterometric stones in clay-sandy matrix deposits (upper level 8 to level 5), a middle unit (levels 4 and 3) constituted of a rich assemblage of lithics and bones (level 4); and an upper unit starting with a thin stalagmitic layer and with levels 2 to 1. Only the lower and middle units yield diversified faunas and lithic artefacts. The chronostratigraphic scheme of this sequence is supported both by faunal remains (according to the degree of evolutive stage of some taxa, especially rodents) and radiometric dates (TL, ESR, TT-OSL and U/Th on speleothems of a stalagmite floor, and tooth enamel). The fossiliferous lower part of the sequence is bracketed between MIS 8-7 to 5, and level 4 clearly dates to MIS 6 (Jaubert et al., 2005; Couchoud, 2006; Hernandez et al., 2015; Fernandez et al., in press). The collapse of the limestone roof connected the endokarst with the outside, favoring sedimentation accompanied by the first evidence for animal and human activities (bottom of level 8). As the sinkhole became larger, making detrital sedimentation easier, the mid-part of level 8 to level 1 developed, until the complete filling of the cavity. The lower unit (levels 8 to 5) is characterized by the heavy impact of post-depositional processes (compaction, freeze-thaw action, flow-debris) as shown in the fauna by the low percentages of identifiable specimens (< 2,000), while more than 81,000 bones/teeth measuring less than 5 cm in length represent ca. 98 % of the total bone assemblage (levels 6b + 7abc yield the largest bone assemblages).

Bone breakage is very high and even epiphyses show perpendicular breakage patterns (**Fig. 3**). Micro fauna (studied by M. Jeannet, A. Louchart, O. LeGall) is very abundant (> 10,000 remains) and diversified (ca. 110

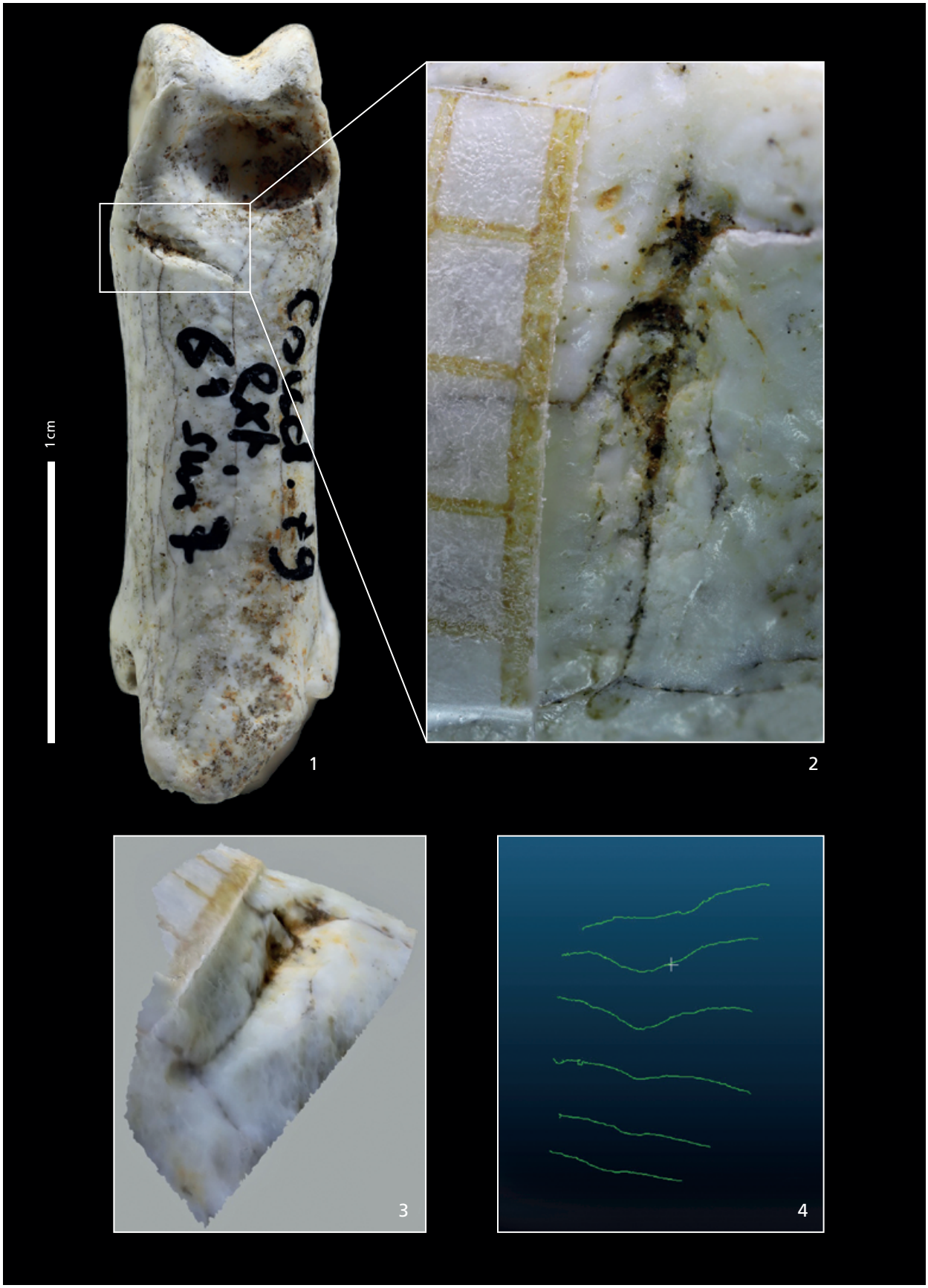

Fig. 4 Example for a cut-mark on a first phalanx of a raptor bird from Coudoulous I (level 6'/7).

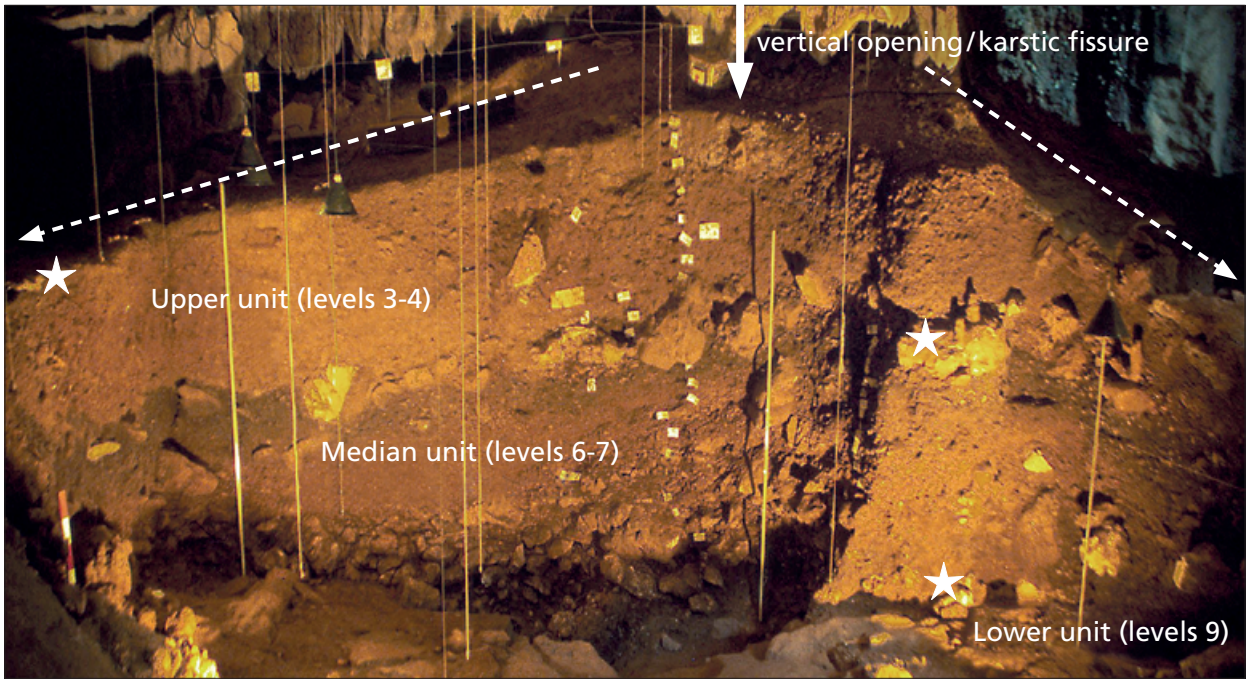

Fig. 5 Stratigraphic sequence of Coudoulous II. White star: Carbonate floor (from top to bottom = levels 2, 5 and 8).

rodent species, leporids, insectivores, chiropters, reptiles, amphibians, birds, fishes, mollusk). Ten herbivore species are represented, mainly comprising equids (*Equus c. mosbachensis*), bovines (*Bison priscus mediator*), cervids (*Cervus*, few *Capreolus* and *Dama*?) and caprids (*Hemitragus*, few *Rupicapra*), followed by a lower number of suid-, proboscid- (*Palaeoloxondon antiquus*) and rhinocerotid- (*Stephanorhinus*) remains. The main ungulates are represented by juveniles, adults and old adults. Of particular interest is the presence of fetus bones (especially from horse), indicating end of winter-early spring deaths. Twelve species of carnivores occurred, mainly represented by canid (*Canis l. lunellensis*: Boudadi-Maligne, 2010), *Cuon*, *Vulpes*] and Ursid (*U. deningeri*, very few *U. thibetanus*). Only rarely are felids (lion, leopard, lynx, wild cat) and mustelids (badger, polecat, weasel) documented. Some juvenile carnivores are present among the canids, ursids and felids (lion) and demonstrate use of the place during winter season for hibernation and reproduction. Coprolites have not been recorded, potentially due to taphonomic bias. Non-human predators are particularly abundant at the base of the sequence indicating a possible horizontal passage ('ghost' gallery) or at least easy entrance.

Both carnivores and humans occasionally left marks on the bone material. Few cut-marks were documented on bone shafts. Among these, a femoral condyle of a caprid (Brugal et al., 2006: Fig. 5) documents carcass dismemberment. A particularly deep cut-mark on a first phalanx of raptor bird (cf. *Bubo bubo*) also needs to be mentioned (**Fig. 4**). Only a few cases of bird exploitation have been reported for the Middle Pleistocene, becoming more frequent in later phases (e. g., Morin and Laroulandie, 2012; Romandini et al., 2014). Most of the bones are either complete, or show dry breakage. Green bone fracture and bone flakes are both rare, though their presence so far could indicate that humans interacted with the bones, as do few burnt black bones attesting to the use of fire (level 6b and 5). These data on faunal material reveals an opportunistic and discrete intervention by humans.

In the lower unit, lithic material is rare (around 100 pieces) and spatially dispersed. The strictly local and very diversified raw material used for lithic production (microgranite, quartz, quartzite, basalt, jasper, etc.)

derived from the alluvial terrace, 100 m down the valley. Among the lithics heavy-duty cutting tools produced on cobbles (hammers, cores, choppers, few flakes and one large cutting tool) are mostly represented. They can be attributed to the Acheulian of south-western France (Jaubert, 1995, 1999; Jaubert and Mourre, 1996; Mourre, 1996; Turq et al., 2010; Colonges et al., 2013). Predator dens and above all, natural deaths are responsible for the bioaccumulations. The stratigraphic sequence was interpreted to reflect a natural ungulate trap with only marginal scavenging.

Level 4 is the main anthropic level. The 30-50 cm thick deposit dates around 160 ± 20 ka and 148 ± 11 ka (MIS 6) and yielded a rich Early Middle Paleolithic (EMP) industry made on local quartz, quartzite (n > 3,000, discoid, bipolar on anvil) and flint (n = 108, Levallois) (Jaubert and Mourre, 1996; Faivre et al., 2013). Use wear analyses (n = 79 tools) demonstrated that the production of shape flakes mainly served butchering activities, but also woodworking and working of dry hide. Comparison with experimentally obtained data (Venditti, 2014) indicates that some of the pointed flakes were used as projectiles (spearheads). Some of these flakes show tip breakage that occurred together with localized, meat related use-wear.

Around 98 % of the associated fauna (plus a few remains of horse, wolf, red fox and beaver) represents steppe bison, with more than 230 individuals recorded in the 25 m^2 excavated. All parts of the skeleton are present (with a taphonomical bias toward axial and spongy parts such as cranials and horn-cores), and metric attributes show the presence of mostly female individuals. Bones in articulation are common and were especially represented by the distal parts of legs and dental series.

A catastrophic mortality pattern with a dominance of juveniles and young adults is evident (Brugal, 1999a; Brugal and David, 1993). Dental wear studies and skeletochronology (H. Martin, unpubl.) indicate recurrent late spring to early summer deaths. Finally, anthropic modifications are relatively numerous, with green bone fractures, cut-marked bones and few localized small burnt bones. This impressive evidence was analysed, with a combination of taphonomic and isotope data (Bernard et al., 2009) as well as studies of sex and age, with reference to eco-ethologic data as well as typo-technology and raw material studies (Bernard et al., 2009). Interpretation suggests several recurring seasonal hunting events on a single prey species by Early Neanderthal groups (Brugal, 1999b), by driving part of the herds into the pit-fall, which during this time period formed a wide opening, subsequently followed by focused exploitation. Such hunting events were part of organized planned activities of structured human groups.

Coudoulous II

Coudoulous II is a complex cavity, with a 3 m deposit showing a detrital cone (**Fig. 5**) coming from a vertical narrow opening, which is actually blocked (in comparison to Coudoulous I) (Brugal, 2006). Three main units are subdivided by three main speleothems: levels 2, 5 and 8 (from top to bottom) (Kervazo et al., 2008). They have been dated by U/Th series (Y. Quinif) and provide a chronological sequence bracketed between MIS 6 to the beginning of MIS 3. The middle part of the sequence contained a well-preserved interglacial deposit (MIS 5 *sensu lato*), with humic horizons, the presence of charcoal remains, as well as faunal and lithic material (see below). It is important to note that the Coudoulous II chronosequence completes and chronologically complements that of Coudoulous I.

The lower unit (level 9) represents a bone-bed with many complete bones, often found in semi-anatomical connection (Uzunidis and Brugal, 2018; Franch, 2020) (**Fig. 6**). Herbivores are dominant, and a morphometrical study and dental wear analyses were used to determine the precise evolutionary stage of several taxa as well as paleoenvironmental conditions. The ungulate species are *Bos primigenius trochoceros*, *Bison priscus*

mediator, *Equus* cf. *mosbachensis*, *Coelodonta antiquitatis*, *Stephanorhinus kirchbergensis*, *Mammuthus intermedius* (*sensu* Labe and Guerin, 2005), *Cervus elaphus* (of a large size), *Rangifer tarandus* and *Dama dama.* Carnivores are rare and mainly represented by wolf (bigger that the *lunellensis* form), red fox and steppe polecat (an almost complete articulated skeleton of *Mustela eversmanii*), with very few remains of bear, lion and cave hyena. Comparative analyses allowed us to infer the chronology of the level, attributed to the very end of the Middle Pleistocene. In this level, the large ungulates represent a faunal association with temperate and cold species indicating the transitional period between the Middle- (MIS 6) and Late Pleistocene (MIS 5e), a period still poorly known in the Quercy region and beyond. This level lacks evidence for hominid or carnivore activities and provides a clear picture for a natural bone deposit formed by carnivores and ungulates that had become trapped in the cavities.

The middle part of the sequence (levels 7 and 6) is attributed to MIS 5 (incl. its sub-stages), with temperate species dominating the bone assemblage, comprising of cervid species (red deer, fallow deer, roe deer), a few bovids, and suids. The material is dispersed and fragmented, with many juvenile specimens. With less than 5 %, carnivora are rare with canids (wolf, red fox), lynx and badger not known to accumulate bones. The natural presence of charcoal indicates a forested and mild environment with hornbeam (66 %), blackthorn (16.1 %), oak (9.4 %), and maple (7.1 %) (Théry-Parisot et al., 2008). All these bioaccumulations are interpreted as of non-anthropogenic origin. However, several lithic artefacts (n = 71) occurred in these levels, displaying a very diverse raw material spectrum with flint, quartz, metaquartzite, and granite. Some bones showing green fracture and scarce cut-marked bones (studies in progress), reveal a discrete human presence and minor carrion exploitation.

Fig. 6 Semi-articulated distal front leg (metapodials, phalanxes, sesamoids) from *Bison* from level 9 at Coudoulous I.

The upper unit (levels 4 and 3) forms a thick deposit of clay and clastic elements. The faunal analysis was based on the material from Brugal's excavations (NISP = 1,452, Costamagno, 1999). Herbivores represent 79.5 % NISP with ten species present. Among these cervids (*Cervus*, *Rangifer*, *Capreolus*), bovids, and caprids (*Rupicapra*) dominate, followed by Equids (mostly *E. hydruntinus*) and some suids. Juveniles are numerous (overall 17.9 %, including fetal bones). Carnivores are mainly represented by adults, and constitute 20.5 % NISP of the assemblage, comprising seven species: canids (*Canis*, *Vulpes*) and hyenids (*Crocuta*) are the most abundant species, then felids (*Panthera spelaea*), ursids (*U. arctos*) and Mustelids (*Meles*, *Putorius*). Such associations correspond to a cool and relatively dry environment (mosaic landscape) dated to MIS 4 and early MIS 3. During this period, the Quercy region is peculiar and during the Pleistocene the documented biocoenosis quite often shows a mixed picture (Brugal et al., 2013a). Taphonomical analysis demonstrates that the cavity was not used as a carnivore den even though around 18.3 % of the bones are tooth-marked (mainly deer and bovid bones and few bones of wolf and red fox). Less than 40 lithic artefacts of bad quality were documented and the fauna lacks clear evidence for human interference. The association of animals and artefacts could be purely accidental (cf. Villa and Soressi, 2000). Conclusions report a mainly natural accumulation formed by ungulates trapped in the cavity that attracted human- and non-human predators, which probably removed portions of meat from the cavity. For a more refined perspective complementary analyses are still needed to integrate material unearthed during fieldwork undertaken by Bonifay and Clottes.

DISCUSSION

Karst systems can yield bone- and/or lithic assemblages that reflect the use of the site by human groups for diverse purposes (base or seasonal camp, hunting place or bivouac). Carnivores equally use these systems, mostly for denning or hibernation. Moreover, some sites with vertical access/opening i. e., sinkholes or pitfalls are characterized by a huge amount of bone material originating from accidental deaths (trapping), particularly of ungulate individuals. Such natural accumulations are very common in limestone areas throughout the Neogene and the Pleistocene. They contain a huge number of individuals ('populations'), often well preserved, and thus are an important source for palaeontological studies. The Query region is particularly rich in karstic sites and many sinkholes, which are known to yield rich and diversified faunal records (e. g., Castel et al., 2018; Coumont et al., 2013).

Coudoulous (Coud I & II) are of particular importance as i) both sites represent sinkholes, with a wide (Coud I) or narrow opening (Coud II), ii) they display a long stratigraphic sequence (ca. 12 m cumulative thickness), iii) they cover the long chronological sequence from MIS 7 to MIS 3, iv) they yield abundant remains both of fauna and lithics, whose quantity and nature vary according to level. It is therefore possible to follow the biological dynamics (including humans) of these deposits over a long period of time at the same locality within a similar geomorphological context.

Table 1 summarizes the main characteristics of the material from the main levels at Coud I and II. Most of the bone assemblages are of natural origin with herbivores trapped in the pitfall. Five models for site use distinguished by different degrees of predator involvement have been postulated (Tab. 2). Level 4 - Coud I represents the only major archaeological layer with a predominance of a single prey species (bison), interpreted as a kill-butchery site. Complete or partial herds were driven into the sinkhole during repeated, unselective, but controlled communal and seasonal hunting episodes, and it might be possible that knowledge about site use was transmitted over several generations. Paleolithic large-Bovid assemblages are recognized throughout the Middle to Late Pleistocene (Jaubert and Brugal, 1990; Farizy et al., 1994; Gaudzinski, 1996,

		Coudoulous I				Coudoulous II		
		Layers 7+8	Layer 6	Layer 5	Layer 4	Layer 9	Layers 7-6	Layers 4-3
	MIS	(8)-7	7	7	6	6-5	5	4-(3)
	bones [n]*	12,500	6,000	3,500	> 10,000	3,500	2,500	11,000
	NISP [%]*	6	2	3	40	50-60	75	28
Carnivores	main species	canid + felid + ursid	canid	canid	(canid)	canid	canid (felid)	canid, hyenid
	gnawed bone	++	+	+	no	0	very few	18.3 % NISP
	coprolites	0?	0	0	0	0	0	4
Carnivore/ Human	green fracture	++	+	-	+++	no	very few	very few
Humans	lithics	50	20	34	> 3,200	0	71	35
	cut-marked bones	2	1	2	++	0	7	1?
	flaked bones	+	+	+	++	0	+	-
	burnt splinters	0	3	10	very few	0	3	0
Herbivores	main species	horse, bison, red deer, thar			bison	horse, bison, red deer	cervid	cervid, bovid
	main age structure	fetus + juv. + ad.			juv. to adults	adult	ad. (level 6) + juv. (level 7)	(fetus) + juv. + ad.

Tab. 1 Synthesis of main features from the main units at Coudoulous. MIS Marine Isotope Stage; NISP Number of Identified Specimens; juv. juvenile; ad. adult. * estimated value; canid = wolf, red fox.

2005; Brugal, 1999a, 1999b; Brugal et al., 1999), and Coud I probably accounts for one of the oldest testimonies of such monospecific game acquisition. The Quercy region is rich in Middle and Upper Paleolithic sites and bison seem to have been a regular and common prey-resource for various human groups and societies (Brugal et al., 2013b).

With the lower unit of Coud I and the median unit of Coud II, additional human site use patterns were documented. These levels yield very few lithic artefacts, and based on the analysis of the naturally accumulated bones, marginal and opportunistic scavenging is respectively suggested. Non-human predators were evidenced in the first case which implies higher risk and competition for humans whereas the other carnivore species were involved in opportunistic scavenging in the second case. Finally, two other hominid site use models are reported from Coud II. Layer 9 lacks any evidence for carnivore involvement, whereas in layers 4-3 several scavenging processes are visible. Hyenas were only documented in these levels, while mainly canids (wolves) typically play the major role in the remaining sequence. Canids are more regularly reported in the Middle and Upper Paleolithic sites in the Quercy region (Brugal et al., 2013a: tabl. 4).

This marginal exploitation strategy might relate to the frequent occurrence of herbivorous trapped in the karstic pitfall during different Pleistocene phases. With one sinkhole per 2 km² estimated, the density of sinkholes in the *Causse* limestone plateau bordering the French Massif Central is quite high (Brugal et al., 2006). Many of them contain fossil Pleistocene faunas. Human and non-human predators observed the regularly occurring accidental trapping of herbivores, which led to the primary exploitation of these karstic environments that were sometimes rich in well preserved carcasses. Compared to open-air sites where decay

is more rapid, these settings are favorable for scavenging, with their settings also allowing human groups to use these holes as traps to push and drive herds, as observed in the level 4 of Coud I.

Different pictures emerge, from marginal (and methodical) scavenging to active hunting (both in Coudoulous I), followed by the return to marginal scavenging (Coudoulous II) for Early Neanderthals/Neanderthal groups. We observe the co-occurrence of small lithic assemblages, comprising technologically simple stone tools made from local materials, and bones displaying few cut-marks (meat removal) and green bone breakage (marrow procurement) indicating potential food procurement. These lithics and bones are found in closed association with natural bone accumulations, and though a direct causality is difficult to demonstrate, the record at least shows the presence of humans around (and inside?) these sinkholes. But how can we explain this human presence? The numerous carcasses within the karstic traps may have been a discontinuous phenomenon, and were probably a seasonally occurring phenomenon. 'Occupations' by humans were probably very short, ephemeral and even discrete, without leaving clear trace of their activities. However, we think that these palaeontological sites with some lithic artefacts are relevant for assessing variabilities in hominid food-management and meat procurement by scavenging (for this hypothesis, cf. Brugal and Jaubert, 1991).

The adaptive framework of meat-eaters basically follows three strategies to exploit large ungulates (Houston, 1979: 265-266) 1) by predation: killing prey is often risky and requires time, energy, a strategy and hunting weapons; 2) by scavenging from a predator kill or predator accumulations (den): food is generally of low quality and it can be risky to frequent such places (higher interspecies competition); 3) by locating and scavenging from animals that died due to starvation, disease or accident (i.e., unconnected to predation), a strategy that introduces seasonal exploitation to this kind of mortality. Indeed, mortality is not uniform throughout the year. On the east African plains, two third of ungulate deaths fall into category 3, which delivers the main food supply for non-human predators during certain times of the year. Such a strategy can be applied to the modelled conditions prevailing at karstic systems on the European limestone landscape, with its combination of a high density of pitfalls and frequent incidents of animal trapping during the Palaeolithic/Pleistocene.

Such sites attracted all kind of predators, and in the case of the Quercy, large canids are the most common species and therefore an interdependence with human prehistoric groups could be assumed to some extent. These sites are concentrated in distinct areas and the risk of confronting other predators is highly possible (also called aggressive scavenging). An alternative view outlines the dynamics in these areas as an example for ecological interaction, expressed in the term *ecosystem service* for early humans (Moleon et al., 2014). The presence of canids around sinkholes where herbivores have been trapped helped to locate carcasses to benefit human groups (Moleon et al., 2014). In addition, these natural processes might have inspired humans to actively develop the use of these trap-sites within the frame of cooperative

	Coudoulous I		Coudoulous II		
	Layers 8-5	Layer 4	Layer 9	Layers 7-6	Layers 4-3
MIS	(8)-7	6	6-5	5	4-(3)
Origin	natural trap	hominid trap	natural trap	natural trap	natural trap
Hominid	low (scav.)	high (hunt)	0	low (scav.)	0
Carnivore	high (den + scav.)	0	0	0	high (scav.)

Tab. 2 Patterns recorded for the main units/layers at Coudoulous. MIS Marine Isotope Stage; scav. scavenging.

hunting (for a discussion on the origins of cooperation in hominins, cf. Smith et al., 2012). Among predators, the relationship between humans and wolves is very special, based on mutual fear and fascination. This relationship goes back to the "dawn of time", and might have begun with some extent from of commensalism and proto-domestication. 'Wolf' becoming 'dog' is one of the first and most ancient bonds between humans and animals.

CONCLUSION

The long Palaeolithic sequence of the two sites at Coudoulous constitutes a significant archive for our knowledge about the socio-economic dynamics of prehistoric groups and provides information about other non-human predators, mammal associations, and the paleoenvironment. Study of the main characteristics from the main units of the two chronologically complementary sites Coudoulous I and II, covering the long period between MIS 7 to 3, allows us to propose five distinct scenarios or patterns. These scenarios combine the origin of ungulate deaths (primarily natural) and two predators, carnivores and humans, against the context of the sites topography, i. e., cavities that functioned as pit-falls.

Geotopography is important when considering the location and accessibility of these features. This last point, accessibility, is especially relevant for quadruped and biped species. Humans are more easily able to ascent the vertical walls of a sinkhole. The mode and nature of bone accumulations is variable, with complete carcasses found in pits. Fragmented and dispersed material is expected in cave situations that are riskier due to the possibility of encountering other carnivores.

Finally, human involvement, in terms of degree of occupation and the resulting cultural debris, shows again a different picture. It can be assumed that the presence of humans in sinkholes would be short, encompassing just the necessary time to collect fresh portion of carcasses. Humans leave very few or no lithic artefacts or traces on bones. The examples given above supports the idea of discrete human involvement with some of the carcasses found in these natural accumulations. The chronology of the record from Coudoulous starts with some cases of marginal scavenging followed by an intense hunting event, with a later return to marginal scavenging. This evidence demonstrates the regular, non-exclusive use of these two strategies, with a significance of these strategies for the course of human evolution not evident.

Hominid food acquisitions using animals trapped in sinkholes could be considered as an original subsistence behavior, marked by the systematic monitoring of small karstic territories on a regular and seasonal basis. These sites with vertical entrances are hardly accessible to quadrupedal (carnivore) animals, while bipeds are more able of climbing and exploiting carcasses that have fallen into these wells. In addition, these cavities could function like fridges, promoting preservation and benefiting the body/nutrient conservation (Brugal et al., 2006: 8). These factors must be considered during food exploitation, especially when animal resources were scarce. However, for past human groups this opportunistic tactic does not serve as a reliable foraging strategy throughout the year, as humans adapt according to context, using various and complementary strategies (hunting, scavenging or simply collecting) to ensure their subsistence.

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