



The exploitation of rabbits for food and pelts by last interglacial Neandertals

Maxime Pelletier, Emmanuel Desclaux, Jean-Philip Brugal, Pierre-Jean Texier

► To cite this version:

Maxime Pelletier, Emmanuel Desclaux, Jean-Philip Brugal, Pierre-Jean Texier. The exploitation of rabbits for food and pelts by last interglacial Neandertals. *Quaternary Science Reviews*, 2019, 224, pp.105972. <10.1016/j.quascirev.2019.105972>. <hal-02510413v2>

HAL Id: hal-02510413

<https://hal.science/hal-02510413v2>

Submitted on 20 Jul 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons CC BY-NC 4.0 - Attribution - Non-commercial use - International License

The exploitation of rabbits for food and pelts by Last Interglacial Neandertals

Maxime PELLETIER^{1, 2,*}, Emmanuel DESCLAUX^{3, 4}, Jean-Philip BRUGAL², Pierre-Jean TEXIER²

¹Department of Archaeology, History, Culture and Communication Studies, Faculty of Humanities, University of Oulu, Oulu, Finland

²Aix Marseille Univ, CNRS, Minist Culture, LAMPEA, Aix-en-Provence, France

³Laboratoire départemental de Préhistoire du Lazaret, Nice, France

⁴Université Côte d'Azur, CNRS, CEPAM, Nice, France

*Corresponding author; e-mail address: maxime.pelletier@oulu.fi (M. Pelletier)

Abstract

The exploitation of small game, especially rabbits, by Neandertals as sources of food or for utilitarian purposes is no longer a subject of debate given increasing evidence for such practices in Europe from the Middle Paleolithic onwards. Instead, focus is now on whether rabbits were an occasional prey or were fully integrated into the socio-economic system of these human groups. Here we address this issue based on a detailed analysis of rabbit remains from the Mousterian deposits of Pié Lombard (Tourrettes-sur-Loup, Alpes-Maritimes, France). Dated to the last interglacial period (Marine Isotope Stage 5), rabbit remains (*Oryctolagus cuniculus*) are the most abundant species throughout the site's Mousterian sequence. Our multi-aspect taphonomical analysis combining mortality profiles, skeletal-part representation, breakage patterns, and bone surface modifications revealed a high incidence of human involvement, demonstrating the rabbit assemblage from Pié Lombard to have been primarily accumulated by Neandertals. Multiple lines of evidence indicate a recurrent and optimised exploitation of carcasses directly on the site, both as sources of meat (preferentially eaten roasted) and marrow as well as for their pelts, which appear to have been transported away from the site. The high frequency of rabbits in the Pié Lombard Mousterian assemblage, comprising at least 225 individuals, is unique for this period and probably reflects the location and function of the rock-shelter. The capture of such a high number of this small mammal potentially required sophisticated acquisition techniques formerly known only from Upper Palaeolithic contexts. Finally, our results shed new light on the subsistence practices, settlement systems and socio-economic behavior of Neandertals in Western Europe during MIS 5.

Keywords: Neandertal subsistence strategies, Marine Isotope Stage 5, Middle Palaeolithic, Mousterian, *Oryctolagus cuniculus*, small prey, taphonomy.

1. Introduction

The behavioural complexity and flexibility of the Neandertals, as well as their cognitive capacities compared with anatomically modern humans, continues to attract significant attention from paleoanthropologists and prehistorians. Changes in subsistence strategies or the development of symbolic practices amongst Neandertal societies are commonly considered as evidence for the emergence of so-called "modern" behaviours. Increasing evidence of the behavioral, social and cultural "modernity" of Neandertals is in part due to new fieldwork at previously excavated sites and the re-evaluation of old collections using new analytical techniques. We now know that these groups developed remarkably similar behaviours to anatomically modern humans, including the burial of their dead (Pettitt, 2002, 2011; Rendu et al., 2014), personal ornaments (Zilhão et al., 2010; Finlayson et al., 2012; Radovčić et al., 2015), pigment processing (Soressi and d'Errico, 2007; Roebroeks et al., 2012; Hoffmann et al., 2018a; Dayet et al., 2019, Pitarch Martí et al., 2019), the manufacture of bone tools (d'Errico et al., 2012; Soressi et al., 2013), rock art (Rodríguez-Vidal et al., 2014; Hoffmann et al., 2018b), frequent aquatic resource exploitation (Trinkaus et al., 2019), and the construction of complex structures deep within karstic cave systems (Jaubert et al., 2016). In terms of subsistence practices, although the majority of evidence suggest Neandertals primarily focused on ungulates (e.g., Richards and Trinkaus, 2009; Discamps et al., 2011; Rendu and Morin, 2018), recent research indicates a more substantial contribution of small game to the diet, including leporids (e.g., Brown et al., 2011; Blasco and Fernández Peris, 2012; Cochard et al., 2012; Hardy et al., 2013), birds (Blasco et al., 2014, 2016; Romero et al., 2017; Gómez-Olivencia et al., 2018), small terrestrial carnivores (Soulier and Mallye, 2012; Gabucio et al., 2014; Gómez-Olivencia et al., 2018), tortoises (Blasco, 2008; Nabais and Zilhão, 2019), and marine resources (Stringer et al., 2008; Brown et al., 2011; Gutiérrez-Zugasti et al., 2018).

Amongst these small preys, the European rabbit (*Oryctolagus cuniculus*) is of particular interest, as they sometimes occupied an important, if not central role in Palaeolithic socio-economic systems in Western Europe. The remains of leporids are frequently found in archaeological sites and are in some cases the most abundant species (e.g., Pelletier, 2018). The first European evidence for the exploitation of these small mammals dates to the Middle Pleistocene, around 400-350 kyr BP (Desclaux, 1992; El Guennouni, 2001; Sanchis and Fernández Peris, 2008; Blasco and Fernández Peris, 2012). However, whether Middle Palaeolithic hunter-gatherers regularly exploited rabbits remains an open question. Several studies have highlighted the systematic acquisition (hunting and / or trapping) and consumption of rabbits to be uniquely associated with Upper Paleolithic anatomically modern humans (Stiner, 1994; Villaverde et al., 1996; Stiner et al., 1999, 2000; Aura et al., 2002; Hockett and Haws, 2002; Cochard and Brugal, 2004; Pérez Ripoll, 2004; Lloveras et al., 2011; Fa et al., 2013). For example, Stiner et al. (1999) argue that the significant increase of leporids in the human diet at the end of the Upper Paleolithic is related to the demographic growth of human groups. The gradual increase in the density of rabbit remains in different Upper Paleolithic techno-complexes would equally reflect profound cultural changes in the socio-economic organization of human groups (Cochard and Brugal, 2004). In fact, despite the typically low return rates compared to ungulates (Speth and Spielmann, 1983; Ugan, 2005), the socio-economic potential of leporids is also reflected by the fact that both their bones and pelts can be exploited (e.g., Hockett, 1994; d'Errico and Laroulandie, 2000; Fontana, 2003; Cochard, 2005).

The regular incorporation of small game in subsistence strategies during earlier periods, particularly the Middle Paleolithic, has been questioned by some researchers who argue that Neandertals, unlike modern humans, lacked the cognitive capacity and / or a sufficiently well-developed technology for regularly exploiting small game (Stiner et al., 1999; Fa et al., 2013). While it is now clear that Neandertal groups did consume rabbits (Gerber, 1973; Blasco, 1995; Sanchis and Fernández Peris, 2008; Brown et al., 2011; Blasco and

Fernández Peris, 2012; Cochard et al., 2012; Hardy et al., 2013; Rufà et al., 2014; Pérez et al., 2017; Carvalho et al., 2018), in several cases a significant portion of the rabbit remains found in sites can be tied to accumulation by carnivores or raptors (El Guennouni, 2001; Lloveras et al., 2010, 2011; Sanchis Serra, 2012; Rufà et al., 2014). Understanding the agent(s) responsible for the accumulation of rabbit remains in Middle Paleolithic contexts is thus essential for providing insights on this aspect of Neandertal subsistence behavior.

Given its small size and weight (1 to 2 kg), the rabbit is currently the preferential prey of more than 40 predators in Western Europe (Delibes and Hiraldo, 1981). Because this species is known for its burrowing behaviour and ability to produce complex and substantial underground warrens (Pelletier et al., 2016, 2017), determining the nature of leporid bone accumulations can be problematic. For example, the presence of rabbit bones in a fossil assemblage can be connected to three different accumulation agents: 1) non-human predators (terrestrial carnivores, nocturnal or diurnal birds of prey); 2) humans; or 3) natural accumulations without any evidence of predation (accidental deaths in natural traps or attritional deaths in burrows). Moreover, these agents are non-exclusive in the formation of leporid assemblages within a same deposit. In order to derive valid paleo-ethnographic and palaeoenvironmental interpretations, it is therefore essential to reliably demonstrate the origin of an archaeological rabbit accumulation, especially in cases when rabbits represent the most abundant species in a given stratigraphic sequence.

This is the case with the Pié Lombard rock-shelter; a Mousterian site in southeastern France dated to the transition between Marine Isotope Stages (MIS) 5 and 4 (Texier et al., 2011). Here we present a detailed taphonomical and zooarchaeological analysis of the assemblage of rabbit bones recovered from this Middle Palaeolithic site with the goal of evaluating the exact role Neandertals or other accumulation agents played in the formation the assemblage. Our results provide key contextual information for discussing the role of this small prey

species in the socio-economy of late MIS 5 Neandertal groups and for interpreting the site's function within the regional Mousterian settlement system.

2. Material and Methods

2.1. Pié Lombard rock-shelter

The site of Pié Lombard is located near the town of Tourrettes-sur-Loup (Alpes-Maritimes, France), on the east bank of the Loup River, 9 km from the Mediterranean Sea and 15 km south of the Alpine foothills (Fig. 1). Situated 200 meters a.s.l, this small rockshelter in Bajocian-Bathonian (Middle Jurassic) limestone was exposed following karstic erosion. Discovered in 1962 by an amateur prospector (A. Mellira), the site yielded Mousterian lithics and Upper Pleistocene faunal remains (Lumley-Woodyear, 1969). Excavations at the site were directed by one of us (P.-J.T.) as part of a larger analysis of the region's Middle Palaeolithic archaeological record (Texier, 1972, 1974). The exhaustive excavation of the rockshelter's archaeostratigraphic sequence, which included the systematic wet-sieving of sediments (using 5, 2 and 0.4 mm sieve meshes), was carried out mainly between 1971 and 1975, accompanied by fieldwork in 1983 and 1985, and a final excavation season in 1996. This work recovered a significant amount of lithic and bone remains accumulated in a diacalse at the front of the rock-shelter. The three-meter deep archaeological sequence was documented in a four meter long and less than one metre wide trench (Fig. 2).

Although the site was excavated by archaeological levels, the uneven configuration of the diacalse, as well as small volume of excavated sediment and limited number of piece-plotted pieces per level, meant that the sequence was separated into two stratigraphic complexes (Texier et al., 2011; Fig. 2):

• An Epipaleolithic complex (ensemble I) comprising three layers (*a*, *b* and *c*) and dated by Accelerator Mass Spectrometry (AMS) between 20,639 - 20,167 cal BP or 22,581 - 22,073 cal BP (Tomasso, 2014). The exact cultural attribution of this occupation remains difficult to characterize due to the low density of material ($n=81$), which is also poorly preserved. Some 180 faunal remains were also collected, with a significant part of the dental elements represented by carnivores, while herbivores are mainly represented by the Alpine ibex (*Capra ibex*) and a limited number of red deer (*Cervus elaphus*);

• A Mousterian complex (ensemble II) (1,000 lithics and fauna per m²) subdivided into 5 lithological layers (*d*, *e*, *e1*, *f*, *g*) and attributed to the MIS 5 to 4 transition based on a thermoluminescence (TL) date of 70 ± 8 kyr BP (Valladas et al., 1987). Stalagmites supporting Mousterian sediments returned two Electron Spin Resonance Dating (ESR) dates of 147 ± 10 kyr and 130 ± 20 kyr BP (Yokoyama et al., 1983). The Mousterian lithic industry comprises 902 pieces, including cores, fragments and flakes > 2cm. The retouched pieces ($n = 172$) occupy a significant portion (37.2%) in the corpus ($n = 462$) where Levallois products have a particularly high transformation rate. Semi-local and allochthonous raw materials are most common, with transfer distances not exceeding 40 km. However, several microquartzite and jasper pieces derive from sources found 60 and 240 km, respectively, from the site (Porraz, 2005). In terms of faunal remains, 16 species of large mammals have been identified (Table 1) from around 2,500 identifiable elements and several thousand bone splinters (Texier et al., 2011; Romero et al., 2017). Among herbivores, Alpine ibex (*Capra ibex*) and red deer (*Cervus elaphus*) dominate the Mousterian complex, representing 63% and 30% (NISP) of the assemblage, respectively, and are accompanied by a limited number of chamois remains (*Rupicapra rupicapra*; 4%). The carnivore assemblage is dominated by panther (*Panthera pardus*), wolf (*Canis lupus*) and lynx (*Lynx spelaea*) and includes juvenile remains of panther and brown bear (*Ursus arctos*). Preliminary zooarchaeological data indicate that, while Neandertal groups are clearly responsible for the introduction of several deer and ibex carcasses, it is impossible to exclude a contribution from other predators (e.g.

wolf, leopard, and lynx) to the ungulate assemblage. Except for the lagomorphs, which are represented by a single species, the European rabbit *O. cuniculus*, the Mousterian deposits yielded a relatively diversified small vertebrates collection comprising 45 species (Table 1; 1 lagomorph, 2 reptiles, 1 amphibian, 2 insectivores, 5 bats, 10 rodents, and 24 birds). A combination of malacological, palynological and faunal data is consistent with colder climatic conditions than experience today in the region and typified by wooded and open areas with a marked Mediterranean influence. Finally, the site produced two deciduous incisors attributed to a Neandertal individual of between 2 and 4 years of age (Texier et al., 2011).

Pié Lombard was initially interpreted as a potential fur and skin processing site given the abundance and especially the diversity of small and large carnivore species in the Mousterian assemblage (Brugal and Jaubert, 1996); however, no clear evidence was provided to support such an interpretation. It is very likely that carnivores used the rockshelter as a long-term den (natural death, reproductive place) and during different periods (Texier et al., 2011; Romero et al., 2017). Despite the difficult access to the site during the Pleistocene, Neandertals nevertheless imported deer or ibex carcasses for immediate consumption in the rock-shelter. It is likely that Pié Lombard functioned as a seasonal basecamp incorporated within a well-developed territorial system rather than as short stay hunting camp (Texier et al., 2011). In addition, it has been recently demonstrated that Neandertals were equally responsible for part of the bird remains from Pié Lombard primarily as a food source and potentially for the use of their feathers (Romero et al., 2017).

2.2. The rabbit assemblage

The rabbit assemblage from the Mousterian complex consists of more than 16,000 bones, which were conditioned and stored by anatomical part during the exhaustive sorting of the small vertebrate remains. The near-absence of coxal bones is noteworthy; only a limited number of coxal bone fragments (NISP=50) were found mixed with the other previously

sorted anatomical elements. This pattern suggests that coxal bones were in fact present during excavations and the subsequent conditioning of the material, meaning that the limited number of specimens is highly unlikely to reflect a taphonomic bias. We assume that the box containing the missing coxal bones was lost during the relocation of the collections. In order to avoid biases when comparing the Pie Lombard assemblage with other studies, we excluded this element from all analyzes.

As multiple taphonomical criteria are shared by several accumulating agents (e.g., Cochard, 2007, 2008; Lloveras et al., 2010; Pelletier et al., 2016), it remains difficult to reliably identify the origin of rabbit assemblages recovered from archaeological sites. This being the case, we integrated four types of data to investigate the nature of the accumulation: mortality profiles, skeletal-part representation, bone breakage and bone surface modifications.

2.2.1. Mortality profile of rabbits

Age at death was estimated from the degree of long bone (humerus, radius, ulna, femur, and tibia) ossification. In rabbits, adult size is reached at five months (Biadi and Le Gall, 1993), while ossification is complete at the age of eight months (see synthesis in Jones, 2006). According to Pelletier et al. (2016), four age classes can usually be distinguished:

- “Infants”: aged up to two weeks and characterized by their small size, no epiphyseal ossification, an incomplete diaphyseal ossification, as well as unerupted or erupting adult teeth;

- “Juveniles”: aged between 2 weeks and 3 months with unfused epiphyses that have not yet reached their adult size;

- “Subadults”: aged between 3 and 8 months, who, although having reached their adult size, nevertheless display incompletely fused epiphyses;

- “Adults”: aged more than 8 months with all epiphyses fused.

It has recently been shown that age structure models of rabbit populations can help to identify acquisition strategies, predator behaviors or the type of accumulation (Pelletier et al., 2016, 2017). Although age distributions may depend on the size of the predator, the season of capture and / or geography (e.g., Cochard 2004b, 2008; Lloveras et al., 2012a; Arriaza et al., 2017), and that several accumulator agents (e.g., foxes and eagle-owls) produce very similar mortality profiles; they nevertheless rule out certain predators that prey almost exclusively on adult individuals, such as medium-to-large sized carnivores (i.e., badgers, dholes, lynx), large birds of prey (i.e., eagles, vultures), and humans (Hockett, 1991; Cochard, 2004a, 2007; Mallye et al., 2008; Lloveras et al., 2011, 2014a, 2016, 2017; Cochard et al., 2012; Pelletier et al., 2016, 2017). Age structure can also be useful for identifying or excluding several potential species known to prey on rabbits. For this study, we used ternary diagrams (Stiner, 1990) modified after Discamps and Costamagno (2015) and specifically adapted for rabbit populations by Pelletier et al. (2016).

Finally, we omitted sex data for the Pie Lombard assemblage given the recent demonstration that commonly employed models (Jones, 2006) for determining the sex-ratio of rabbit populations (Cochard et al., 2012; Blasco et al., 2013; Rufà et al., 2014, 2017; Martínez-Polanco et al., 2017) do not accurately distinguish males from females in a reproducible manner (Pelletier et al., 2015). Sexing rabbit remains is further complicated by the fact there is no sexual dimorphism in this species (Pelletier, 2019).

2.2.2. Anatomical representation of rabbits

The number of identified specimens (NISP), minimum number of skeletal elements (MNE) and the minimum number of individuals (MNI) were calculated for each skeletal element (Reitz and Wing, 1999; Lyman, 2008). Relative abundance (RA) was calculated using the formula proposed by Dodson and Wexlar (1979):

$$\bullet \quad \%RA = [MNE / (MNI * E)] * 100$$

where MNE equals the minimum number of skeletal elements, MNI equals the minimum number of individuals based on the greatest number of any single element in the assemblage subdivided by age cohort, and E is the number of elements present in one skeleton (adapted here without the coxal bone).

The proportion of skeletal elements for all rabbit age classes was calculated using adjusted ratios based on the work of Andrews (1990) and Lloveras et al. (2008), and slightly modified by Pelletier et al. (2016). For our study, these ratios were adapted to reflect the exclusion of coxal bones from the analysis:

$$\bullet \quad \mathbf{PCRT/CR\%} = [(PCRT * 32) / ((PCRT * 32) + (CR * 182))] * 100$$

where PCRT is the total number of postcranial elements (limbs, vertebrae, and ribs) and CR the total number of cranial elements (mandibles, maxilla, and teeth);

$$\bullet \quad \mathbf{PCRAP/CR\%} = [(PCRAP * 32) / ((PCRAP * 32) + (CR * 112))] * 100$$

with PCRAP being the total number of limb elements (long bones, scapula, patella, metapodials, carpals, tarsals, and phalanges);

$$\bullet \quad \mathbf{PCRLB/CR\%} = [(PCRLB * 32) / ((PCRLB * 32) + (CR * 10))] * 100$$

with PCRLB calculated as the total number of long bones (humerus, radius, ulna, femur, and tibia);

$$\bullet \quad \mathbf{AUT/ZE\%} = [(AUT * 12) / ((AUT * 12) + (ZE * 98))] * 100$$

with AUT comprising autopodia (metapodials, carpals, tarsals, and phalanges) and ZE zygopodia and stylopodia (tibia, radius, ulna, humerus, femur, and patella);

$$\bullet \quad \mathbf{AN/PO\%} = [(AN * 12) / ((AN * 12) + (PO * 16))] * 100$$

with AN representing the number of scapula, humerus, radius, ulna, and metacarpals, and PO being the femur, tibia, and metatarsals;

$$\bullet \quad \mathbf{Z/E\%} = [(Z * 4) / ((Z * 4) + (E * 6))] * 100$$

with Z grouping zygopodia (tibia, radius, and ulna) and E stylopodia (femur and humerus).

2.2.3. Bone breakage and surface modifications

To help discern rabbit assemblages resulting from natural deaths from those produced by predators, the percentages of complete elements, isolated teeth and articulated elements were calculated (Cochard, 2004a). In this regard, the percentage of shaft cylinders was also recorded for comparison with anthropic accumulations (e.g., Hockett, 1991; Pérez Ripoll, 2004). The type and nature of breaks (green or dry bone) were recorded for each long bone fragment based on morphological criteria provided by Villa and Mahieu (1991) and applied to small mammals by Armstrong (2016a, 2016b).

335 Break type was equally recorded for each bone element following Lloveras et al. (2008) and
336 applied in several subsequent studies (e.g., Lloveras et al., 2009a, 2012b, 2014a, 2016):

337

338 • Cranium were recorded as complete (C) or represented by the incisive bone (IB),
339 incisive bone and maxilla (IBM), maxilla (M), zygomatic arch (ZA) or neurocranium (NC);

340

341 • Mandibles were recorded as complete (C), incisive part (IP), mandible body and
342 incisive part (MBI), mandible body (MB), mandible body and branch (MBB) or condylar
343 process (CP);

344

345 • Scapula were recorded as complete (C), glenoid cavity (GC), glenoid cavity and neck
346 (GCN), glenoid cavity, neck and fossa (GCNF), neck and fossa (NF) or fossa (F);

347

348 • Long bones (humerus, radius, ulna, femur, tibia), metacarpal and metatarsal bones
349 were classified as complete (C), proximal epiphysis (PE), proximal epiphysis and shaft
350 (PES), shaft (S), shaft and distal epiphysis (SDE) or distal epiphysis (DE);

351

352 • Vertebrae were recorded as complete (C), vertebral body (VB), vertebral epiphysis
353 (VE) or spinous process (SP);

354

355 • Phalanges were recorded as complete (C), proximal fragment, (P), distal fragment (D)
356 or fragment (F);

357

358 • Patella, carpals, tarsals (calcaneus, talus, cuboid, cuneiform, and navicular), ribs and
359 teeth were classified as complete (C) or fragmentary (F). For teeth, breakage was recorded
360 separately depending on whether teeth were found isolated or still set in the mandible
361 (Fernández-Jalvo and Andrews, 1992).

362

363 All remains were observed under a light-reflecting microscope (40x magnification) in order to
364 systematically describe bone surface alterations. Evidences of non-human predation (i.e.,
365 digestion, tooth/beak marks) were counted for each element, as were traces of human
366 modifications such as cut-marks or burning.

367

368 **3. Results**

369

370 *3.1. Mortality profile*

371

372 The rabbit assemblage recovered from the Mousterian complex is well preserved and
373 comprises 16,084 bone elements (NISP), corresponding to a minimum of 225 individuals.
374 Epiphysation of the distal end of the humerus demonstrates at least 219 individuals to be
375 older than 3 months (97%), with the non-epiphyseal proximal end of the tibia reflecting the
376 presence of 34 subadult individuals. Overall, long bones correspond to at least 6 juveniles,
377 34 subadults, 185 adults. No infant remains were identified in the Mousterian rabbit
378 assemblage.

379

380 The Pié Lombard profile is distinct from those generated by solitary small-predators, such as
381 foxes or eagle-owls, who preferentially prey upon juveniles with smaller body sizes (Fig. 3). It
382 is also substantially different from modern warrens, which are characterised by higher
383 numbers of both juvenile individuals and infants (Pelletier et al., 2016). Moreover, age
384 profiles produced by solitary predators and typical of warrens are also characterized by
385 greater proportions of immature individuals. This is not the case with the Pié Lombard profile,
386 which is much more similar to those generated by larger predators such as badgers, dholes,
387 or humans. In fact, the Pié Lombard mortality profile falls within the “old” (O) zone of the
388 ternary diagram, which is consistent with the selection of the most profitable prey and

considered evidence for a targeted hunting strategy (Stiner, 1990; Discamps and Costamagno, 2015).

3.2. Anatomical representation

The Pié Lombard Mousterian assemblage produced all elements of the rabbit skeleton, a pattern consistent with a large proportion of complete skeletons having been introduced to the site. Phalanges, metapodials, vertebrae and teeth are most common (%NISP), while the smallest elements, such as carpals/tarsals, sternebrae, sesamoids, and patellae, are less well represented (Table 2). The relative abundance mean value (43%) is low, which indicates a significant loss of bony elements in the assemblage. The best-represented anatomical elements are the humerus (95%), calcaneus (94%), and talus (86%), whereas sternebrae, ribs, carpals, vertebrae and cuneiform are less abundant (1% to 8%).

The assemblage produced relatively similar proportions of cranial and postcranial elements (PCRT/CR%=48%), although the latter are underrepresented compared with long limb bone elements (i.e., PCRAP/CR% and PCRLB/CR%; Table 3). The AUT/ZE% index shows a deficit of the autopodia compared to the zygopodia (39%), and relatively equal proportions of lower and upper limb elements (Z/E%=51%) as well as anterior and posterior members (AN/PO%=46%). The patterns of skeletal part representation documented for the Pié Lombard assemblage differs substantially from either modern reference collections or other fossil rabbit assemblages (Fig. 4). The proportion of postcranial and cranial elements is somewhat similar to skeletal profiles generated by birds of prey (PCRT/CR% and PCRAP/CR%). However, the high degree of variability in skeletal part profiles produced by humans does not exclude this type of accumulation. For example, the under-representation of autopodials in the Pié Lombard assemblage is a typical signature of birds of prey but shared with the clearly anthropic assemblage from Gazel cave (Fig. 4). The balance between the anterior and posterior elements allows a clear link with the anthropogenic accumulations.

417

418 3.3. Bone breakage: frequency and type

419

420 While overall bone fragmentation is relatively high (46% complete bones), it varies according
421 to bone element and size. The smallest bones (i.e., carpals/tarsals, patellae, phalanges, and
422 teeth) 86% are complete, while long bones display a significantly higher breakage rate, with
423 an average of only 0.2% complete bones (only two humerus, two radius and one tibia are
424 complete).

425

426 Skulls and mandibles are never found complete and are mainly represented by the maxilla
427 (M) and mandible body (MB), respectively (Table 4). Nearly half of the teeth (49%) were still
428 recovered in the mandible and were generally complete (90%), just like isolated teeth (88%).
429 Only one complete scapula is present and most fragments include the glenoid cavity (GC).
430 Metacarpals and metatarsals are complete in 38% and 11% of the cases, respectively.
431 Carpals (98%), cuneiforms (99%), cuboids (92%), and naviculars (84%) are more frequently
432 complete than talus (71%) and calcaneus (58%). Only 70% of proximal phalanges are
433 complete, while 91% and 99%, respectively, of mesial and distal phalanges are complete.
434 Vertebrae are complete in 13% of cases, primarily represented by the vertebral body (VB),
435 while ribs are almost always fragmented (98%).

436

437 In terms of long bones, all breakage categories were found among which fragments of
438 diaphysis are most abundant. Humerus and tibia are most often represented by distal
439 epiphyses, while proximal epiphyses of radius, ulna and femur fragments are more frequent
440 (Table 4). Thirty-five percent of all long bones are represented by shaft cylinder fragments,
441 with nearly 20% representing the humerus, femur and tibia (Fig. 5). Most long bone fractures
442 concern green bone (Table 5) and are characterized by an oblique fracture angle (68%) and
443 a V-shaped profile (70%). Dry bone breaks with a right fracture angle (17%) and a transverse
444 fracture profile (15%) are less common, and result from post-depositional processes (e.g.,

pressure and sedimentary movements, roof collapse, weathering). Approximately 15% of bone breakage is recent, probably occurring during excavation and/or cleaning.

3.4. Bone surface modifications

Bone surfaces are very well preserved and bear no signs of weathering or alterations by abiotic agents. Traces of digestion are evident on less than 3% of the rabbit assemblage (Table 6), with metacarpals, metatarsals, talus, calcaneus and phalanges the most commonly affected. Pits and punctures are present on 33 bones (0.2% of NISP) and mostly occur on the scapula (n=8), femur (n=6), calcaneus (n=4), metatarsals (n=3) radius (n=2) and mandible (n=2). Carnivore tooth marks, likely a relatively small-sized predator such as fox, wild cat or lynx are concentrated around the glenoid cavity (n=4), the proximal part of the femur (n=2) and ulna (n=1), as well as on the mandible body (n=1).

Most of the bone surface modifications can be attributed to human activity. A total of 481 bone elements (3% of NISP), primarily long bones (n=219), display cut-marks (Fig. 6; Table 6). Cut-marks are also frequent on metacarpals (n=43) and metatarsals (n=107), and concern mainly lateral metapods, such as the metacarpal II (n=10) and V (n=16), and metatarsal II (n=26) and V (n=31). A significant number of cutmarks were also recorded on the calcaneus (n = 54), talus (n = 12) and scapula (n = 14). On the long bones, most cut-marks were located on shafts and near the epiphyses and are almost always transverse to the principal axis of the bone. Traces of burning are evident on 9% of NISP and are not concentrated on any particular portion of the skeleton; 15% of cases concern the epiphyses, with long bones, the calcaneus, talus, metapodials and phalanges most commonly affected (Table 6). However, we did not record any traces of human teeth on the bones, although reliably identifying such marks is difficult (e.g., Cochard, 2004; Lloveras et al., 2009b).

4. Discussion

473

474 4.1. *The origin of the Pié Lombard rabbit assemblage*

475

476 Despite differences in the relative abundance of certain skeletal elements, the overall
477 anatomical representation of rabbits at Pié Lombard suggests whole carcasses were
478 introduced to the site. Most potential rabbit predators transport whole carcasses and can
479 produce the same pattern than an attritional mortality typically observed for warrens. Infants
480 only leave the warren 2 to 3 weeks after birth (Biadi and Le Gall, 1993), and the presence of
481 their remains could suggest a warren and the potential bioturbation of archaeological layers
482 (Pelletier et al., 2016, 2017). However, most predators, including humans, lynx, dholes,
483 eagles or badgers, tend to focus primarily on adults, who generally comprise at least 80% of
484 an assemblage (Hockett, 1991; Hockett and Bicho, 2000; Jones, 2004; Cochard, 2004a,
485 2007; Brugal, 2006; Mallye et al., 2008; Lloveras et al., 2011, 2016, 2017; Cochard et al.,
486 2012; Rillardon and Brugal, 2014; Rosado-Méndez et al., 2015; Arriaza et al., 2017; Rufà et
487 al., 2017). Taken together, the absence of infant remains at Pié Lombard and an assemblage
488 dominated by adult individuals (82%) is in good overall agreement with an accumulation
489 produced by a large predator.

490

491 Despite some variation in skeletal part representation, anatomical profiles produced by
492 terrestrial predators are generally similar, especially when complete carcasses are
493 transported. In the anthropogenic assemblages, the best-represented elements are generally
494 mandibles, long bones, scapula and coxal bones (Hockett, 1991; Hockett et Haws, 2002;
495 Cochard, 2004a; Brugal, 2006; Lloveras et al., 2016), which is the case with the Pié Lombard
496 assemblage (except for coxal bones, which were excluded from our study; see section 2.2).
497 In the case of accumulations generated by lynx, skeletal profiles tend to be very similar,
498 characterised by a higher abundance of cranial remains and an over-representation of
499 forelimb bones compared to those of the hindlimbs (Lloveras et al., 2008). The Pié Lombard
500 profile clearly departs from this pattern, particularly in the under-representation of cranial

elements, and resembles accumulations produced by some raptors, who tend to focus essentially on immature individuals (Sanchis Serra, 2000; Cochard, 2004b; Lloveras et al., 2009a; Sanchis Serra et al., 2014) and sever the limbs and / or head before transporting the most nutritious parts for consumption elsewhere (Donazar, 1988).

Can this particular skeletal-part representation of Pié Lombard be connected to the differential preservation of bone remains? According to Pavao and Stahl (1999), in cases of differential preservation, density differences between hindlimb (more dense) and forelimb (less dense) elements should be reflected in femur and tibia outnumbering humerus, radius and ulna. At Pié Lombard, all of these elements are present in similar proportions, which is consistent with an overall good preservation of the assemblage. The underrepresentation of the extremities of the paws (phalanges, carpals/tarsals, and metapodials) is generally due to their small size and that these elements are frequently overlooked during excavations or lost during sieving when using large mesh sizes (Shaffer and Sanchez, 1994; Cannon, 1999; Val and Mallye, 2011a). A systematic water sieving protocol using less than 5 mm meshes during excavations at Pié Lombard exclude recovery biases affecting skeletal-part profiles. The absence of the differential transportation or preservation of rabbit remains at Pié Lombard reflects a particular context, with the skeletal representation of the remains suggesting humans to be responsible for the accumulation. The Pié Lombard assemblage falls between the anthropogenic accumulations from the Mousterian occupation of Les Canalettes (Cochard et al., 2012), the Late Aurignation at Arbreda cave (Lloveras et al., 2016) or the Late Magdalenian at La Faurélie II (Cochard, 2004a), where rabbits were exploited uniquely as a source of food, and the anthropogenic accumulation from Gazel Cave, where leporids were captured both for their fur and meat (Fontana, 2003).

Bone breakage linked to marrow extraction produces numerous epiphyseal and shaft-cylinder fragments (e.g., Hockett, 1991; Cochard, 2004a; Pérez Ripoll, 2004). With few exceptions, rabbit accumulations from Upper Paleolithic contexts generally contain less than

15% (of NISP) of shaft cylinders (Hockett and Bicho, 2000; Cochard, 2004a; Cochard and Brugal, 2004; Brugal, 2006; Lloveras et al., 2011, 2016; Rillardon and Brugal, 2014; Rufà et al., 2017). In this regard, the proportion of shaft cylinders at Pié Lombard (35%) is more similar to the Middle Paleolithic assemblage of Les Canalettes (39%; Cochard et al., 2012), which as dates to the same period (i.e., MIS 5-4). The percentage of complete long bones (0.2%) is equally consistent with anthropogenic accumulations (e.g., Cochard et al., 2012; Lloveras et al., 2016; Rufà et al., 2017) and lower than that observed for modern predators (Sanchis Serra, 2000; Lloveras et al., 2008, 2009a, 2012b, 2014a, 2017; Mallye et al., 2008). Moreover, fauna accumulations generated by non-human predators are characterized by very high percentages of digested remains (>60%). At Pié Lombard, less than 3% of NISP show traces of digestion and only 33 elements bear carnivore teeth-marks (0.2%), reflecting an extremely limited impact of non-human predator on the Pié Lombard rabbit assemblage. The skinning and defleshing of rabbit carcasses leaves clear evidence in the form of cut-marks and traces of burning on the distal ends of long bones (Vigne et al., 1981; Vigne and Marínval-Vigne, 1983; Lloveras et al., 2009b). At Pié Lombard, 3% of bones are cut-marked and 9% show traces of burning, a pattern consistent with what is observed in anthropogenic accumulations (for a synthesis, see Lloveras et al., 2016).

Moreover, the accumulation of small vertebrates at Pié Lombard is characterized by a very high proportion of rabbits (Table 1). Such an overrepresentation has never, to our knowledge, been encountered in any Pleistocene natural death assemblage or mixed accumulation (rock shelter or cave sites; e.g., Andrews, 1990; Desclaux et al., 2011) or in any modern coprocoenosis (e.g., Géroutet, 1984; Bayle, 1992; Lloveras et al., 2014a, 2014b, 2017; Sanchis Serra et al., 2014). This further underlines the unique nature of the Pié Lombard Mousterian assemblage, which results from the acquisition and processing of small game, primarily rabbits as well as birds, by Neandertal groups. The presence of a limited number of digested remains and carnivore-gnawed bones shows that another agent, probably a small terrestrial carnivore, contributed only marginally to the accumulation.

557

558 *4.2. Function of the Pié Lombard site*

559

560 Pié Lombard was alternately occupied by small, medium and large carnivores during
561 particular periods as well by Neandertal groups as part of a seasonal mobility system (Texier
562 et al., 2011). Both predators introduced large herbivores as well as small vertebrate remains
563 to the site. A recent taphonomic analysis of the bird remains from the Mousterian complex
564 showed that multiple agents were responsible for the accumulation (Romero et al., 2017):
565 birds of prey (i.e., nocturnal raptors) transported their prey (usually choughs) to the rock-
566 shelter, where they were consumed and subsequently regurgitated; small terrestrial
567 carnivores (i.e., lynx or red fox) also occasionally hunted birds; as did Neandertals, who
568 focused almost exclusively on pigeons, partridges, and choughs, mainly for their meat and
569 perhaps also for the use of their feathers.

570

571 Unlike the mixed origin of the avian assemblage, the rabbit remains from Pié Lombard were
572 primarily transported to the site by Neandertal groups. The Pié Lombard assemblage
573 demonstrates whole carcasses have been brought and butchered on-site and bones broken
574 to access marrow. At Les Canalettes, the low rate of burned bones (<1%) led Cochard
575 (2004a) to suggest that carcasses were boiled rather than roasted. At Pié Lombard, the
576 relatively high rate of burned bones (9%) suggests that rabbit carcasses were roasted rather
577 than boiled. Rabbits can be roasted directly after being skinned without having to first
578 dismember the carcass (Rufà et al., 2017). Moreover, disarticulation and defleshing are, in
579 fact, easier after roasting, and do not require the use of tools, which could explain the low
580 number of cut-marks observed on the remains.

581

582 Although it is still difficult to definitely demonstrate the processing of leporid pelts by
583 prehistoric hunter-gatherers (e.g., Cochard, 2004a; Mallye et al., 2018), numerous cut-marks
584 potentially unrelated to meat consumption are present. Generally, skinning carcasses for

pelts leaves abundant evidence on bone, primarily on the skull (Lloveras et al., 2009b; Val and Mallye, 2011b). Although rabbit skull elements are too heavily fragmented and poorly represented at Pié Lombard to observe traces clearly referable to skinning, other lines of evidence are suggestive of this process. Metapodials alone bear nearly 31% of all recorded cut-marks, which are concentrated on the lateral sides of metacarpals (II and V) and metatarsals (II and V), suggesting the removal of the skin (Val and Mallye, 2011b). The under-representation of these elements, as well as the phalanges, compared to the numerous tarsals, including the calcaneus and talus, which also carry numerous cut-marks resulting from skinning and disarticulation processes, could also testify to the transport of pelts for tanning beyond the excavated area. In this scenario, a large portion of tarsal elements (calcaneus, talus) would remain in the area where carcasses were processed for food, while the metapodials and phalanges would be transported still attached to the skin. Such a hypothesis was previously proposed by Cochard (2004a) for the Middle Paleolithic site of Les Canalettes. Finally, the very limited number of caudal vertebrae (NISP=14) equally suggests the removal of the tail with the skin (Fontana, 2003).

The importance of leporid fur for Upper Paleolithic societies remains a subject of considerable debate (Jullien and Pillard, 1969; Soffer, 1985; Alhaique, 1994; Charles and Jacobi, 1994; Morel and Muller, 1997; West, 1997; Pokines, 1998; Fontana, 2003; García-Argüelles et al., 2004). This is in no small part due to difficulties in reliably inferring skinning processes and the fact that cut-marks alone are not sufficient evidence for the removal of skins (Cochard, 2004a). Other taphonomic characteristics, such as skeletal-part representation, provide additional evidence for skin processing. For example, the under-representation of the autopodial and caudal vertebrae at a butchery or consumption site can provide indirect evidence for such activities. At Pié Lombard, the limited number of these small elements does not reflect either differential preservation processes or biases connected to sieving (i.e., mesh sizes). Traces of digestion on the autopodial could suggest that a scavenger influenced anatomical representation. However, although digested bones

are present at Pié Lombard, the impact of a terrestrial carnivore, such as red fox, wildcats, or lynx (Table 1), is low (2.6% and 0.2 %, respectively, of bones bear evidence of digestion or tooth-marks). This indicates that, while these species may have scavenged remains left by humans, their presence is too limited to account for the under-representation of the autopodial.

Whether rabbits were sought specifically for their pelts or first and foremost as a source of food remains an open question. In any event, the working of skins leaves very little trace on bones themselves, and wear on non-perishable tools is often the only evidence of this activity (Beyries, 2008). While bone and stone tools from Middle Palaeolithic contexts have been linked to the processing of skins (e.g., Chase, 1990; Texier et al. 1996; d'Errico et al., 2012; Soressi et al., 2013), no such evidence was recovered from Pié Lombard. With this being the case, tanning may have occurred outside the excavated area or at another site, as indicated by the under-representation of the metapodials and phalanges (cf. supra). Likewise, demonstrating fur processing at Pié Lombard to have been related to the manufacturing of clothes, either for group members or as trade goods, is also difficult. Substantial ethnographic and archaeological evidence, however, attests to the importance of leporid pelts for human societies (Teit, 1906; Emmons, 1911; Rogers, 1963, 1973; Oberg, 1973; Speck, 1977; Rogers and Smith, 1994; Charles, 1997; Kennedy and Bouchard, 1998; Lahren, 1998; Beyries, 2008), whether utilitarian purposes, such as the use of long bones to produce needles (Soffer, 1985; McComb, 1989; Leesch, 1997; Cochard, 2005) or personal ornaments manufactured from long bone shaft cylinders (Hockett, 1994; d'Errico and Laroulandie, 2000). There now exists robust evidence of personal ornament use by Neandertals, including raptor terminal phalanges (Morin and Laroulandie, 2012; Finlayson et al., 2019), bird feathers (Peresani et al., 2011; Finlayson et al., 2012; Fiore et al., 2016; Finlayson et al., 2019), small to medium carnivore teeth (Caron et al. 2011; Soulier and Mallye, 2012), and shells (Stringer et al., 2008; Mellars, 2010; Zilhão et al., 2010). In view of the high number of rabbit remains present at Pié Lombard, it is reasonable to assume that

641 this small prey played an important role in the socio-economic practices of Neandertal
642 groups in southern France during MIS 5-4.

643
644 Taken together, there is sufficient evidence from Pié Lombard demonstrating rabbits to have
645 been roasted and consumed on the site, with their pelts subsequently processed and
646 transported away from the site. Moreover, the numerous cut-marks, burnt bones and shaft
647 cylinders are all consistent with what is commonly found on Upper Paleolithic sites and is
648 readily comparable with the Mousterian rabbit assemblage from Les Canalettes. The
649 Neandertal groups who occupied Pié Lombard therefore exploited rabbits in the same way
650 as Upper Paleolithic anatomically modern humans. Interestingly, while it is generally
651 accepted that rabbits were of secondary importance in the Neandertal diet due to a
652 significantly lower caloric return compared to ungulates (Table 7), at Pié Lombard, the large
653 number of rabbits provided at least 226 kg of meat, representing more than 7% of the
654 group's overall caloric intake (Table 8). This value is much higher than what is known on
655 other Mousterian sites. Indeed, rabbit generally constituted less than 1% of the energy intake
656 of the Mousterian groups, with its role in the human diet increasing significantly in the Upper
657 Paleolithic, especially during the Magdalenian (Table 8). The exploitation of small game
658 (rabbits and birds) at Pié Lombard departs markedly from this pattern. The large number of
659 rabbits (Table 1) suggests they were the principal focus of Neandertal subsistence practices
660 at Pié Lombard and may reflect difficulties in accessing the rockshelter and hence an
661 emphasis on more easily transported small game rather than large herbivores.

662 663 *4.3. The exploitation of rabbits by Neandertal societies: a regional and repetitive* 664 *phenomenon?*

665
666 Prior to the Upper Paleolithic in southwestern Europe, it is generally assumed that small
667 game was rarely exploited by humans (Stiner, 2013). Consequently, the place of rabbits in
668 the Neandertal diet has been the subject of considerable debate. When present in Middle

669 Paleolithic assemblages, taphonomic analyses have generally demonstrated rabbits to have
670 been primarily accumulated by carnivores or raptors (Defleur et al., 1994; Blasco, 1995;
671 Martínez-Valle, 1996; Fernández-Jalvo and Andrews, 2000; El Guennouni, 2001; Hockett,
672 2006; Lloveras et al., 2011; Sanchis Serra, 2012). Evidence of human modifications on rabbit
673 remains is rare, and Neandertals are commonly considered to have played very minor role in
674 their accumulation. For example, while the Mousterian assemblages from Bolomor Cave
675 (NISP=457, MNI=49; Blasco and Fernández-Peris, 2012), Arbreda Cave (NISP=1,317,
676 MNI=43; Lloveras et al., 2010), Les Canalettes (NISP=1,627, MNI=58; Cochard et al., 2012),
677 Columbeira Cave (NISP=1,784; Carvalho et al., 2018), El Salt (NISP=1,789; Pérez et al.,
678 2017), or Teixoneres Cave (NISP=3,964, MNI=49; Rufà et al., 2014) contain a limited
679 number of rabbit remains, only Bolomor Cave and Les Canalettes produced robust evidence
680 for a rabbit accumulation linked to more long-term, repetitive Neandertal occupations. In this
681 respect, the over 16,000 rabbit remains and the presence of least 225 individuals make the
682 Pié Lombard assemblage not only unique for the Middle Palaeolithic but readily comparable
683 to anthropogenic accumulations found from Upper Paleolithic sites such as Les Cendres
684 Cave (NISP=14,976, MNI=337; Real, 2016), La Faurélie II (NISP=15,569, MNI=87; Cochard,
685 2004a), Arbreda Cave (NISP=17,700, MNI=43; Lloveras et al., 2016) or Molí del Salt
686 (NISP=22,627, MNI=445; Rufà et al., 2017). With this being the case, how best to interpret
687 the exceptional number of rabbits in Middle Paleolithic assemblage from Pié Lombard? It is
688 often argued that Upper Palaeolithic hunter-gatherers most likely adapted their subsistence
689 strategies 1) depending on the availability of different preys in the landscape; 2) as response
690 to increasing group size and social structure; or 3) following profound changes in socio-
691 economic organization in connection with settlement patterns and resource management
692 (e.g., Stiner et al., 1999, 2000; Aura et al., 2002; Cochard and Brugal, 2004). Similar
693 behaviours have partially been demonstrated for several Middle Paleolithic sites in
694 southwestern Europe based on the zooarcheological analyses of large (e.g., Discamps et al.,
695 2011; Morin et al., 2014; Rendu and Morin, 2018) and / or small mammals (e.g., Sanchis
696 Serra and Fernández Peris, 2008; Blasco and Fernández Peris, 2012; Blasco et al., 2014).

These research call into question the idea that the diversification and intensification of subsistence strategies were coincident with Middle to Upper Palaeolithic transition (e.g., Stiner et al., 2000; Hockett and Haws, 2002; Aura et al., 2002). Pié Lombard provides additional evidence for the regular exploitation of small prey around 70-75 kyr, some 25-30 kyr before the emergence of the Upper Palaeolithic.

In addition, rabbits were abundantly available in the Mediterranean region of Western Europe from MIS 5 until the beginning of MIS 4. During this period of temperate environmental conditions associated with substantial forest cover (Pelletier, 2018), rabbits only occasionally formed part of the Neandertal diet (Gerber, 1973; Blasco and Fernández Peris, 2012; Cochard et al., 2012; Hardy et al., 2013; this study). During MIS 4 to 2, although environmental and climatic changes led to a decline in rabbit populations and their retreat into several refugia in the Iberian Peninsula (Branco et al., 2002; Pelletier, 2018), rabbits were continuously exploited in these areas (Blasco, 1995; Sanchis Serra and Fernández Peris, 2008; Lloveras et al., 2010; Brown et al., 2011; Rufà et al., 2014; Pérez et al., 2017; Carvalho et al., 2018). During MIS 3 (around 45 kyr BP), Europe witnessed a genuine “cultural revolution” (Mellars, 1996; Bar-Yosef, 1998, 2002), as Middle Palaeolithic cultural traditions gave way to Upper Palaeolithic technological and symbolic innovations (McBrearty and Brooks, 2000; d’Errico, 2003; Henshilwood and Marean, 2003; Zilhão, 2011). This transition equally coincided with substantial biological change as the Neandertals were gradually replaced by dispersing anatomically modern humans (Trinkaus, 1986, 2007; Stringer and Andrews, 1988; Stringer, 2002). Despite these profound cultural and biological changes, rabbits continued to be exploited at the beginning of the Upper Paleolithic in the Iberian Peninsula by Aurignacian (between 40 and 30 kyr BP; Rosado-Méndez et al., 2015; Lloveras et al., 2016; Sanchis et al., 2016), Gravettian / Solutrean (Brugal, 2006; Hockett and Haws, 2009; Lloveras et al., 2011; Aura et al., 2012; Manne et al., 2012; Sanchis et al., 2016), and Magdalenian societies (Aura et al., 2002; Sarrión et al., 2008; Rufà et al., 2017; Yravedra et al., 2018). On the other hand, no clear evidence for the exploitation of rabbits is

currently available for southern France during the early Upper Paleolithic (Cochard and Brugal, 2004). This is likely explained by the absence of this species in this region until the end of the Late Glacial (Pelletier, 2018). The reincorporation of rabbit in post-Late Glacial subsistence strategies accompanied the return of more temperate climatic conditions in the region (Séronie-Vivien, 1994; Cochard, 2004a; Jones, 2006; Rillardon and Brugal, 2014).

The distribution and density of rabbit populations in southwestern Europe during the Middle and Late Pleistocene was therefore relatively discontinuous and largely dependent on climatic conditions (Pelletier, 2018). When rabbits were available, they were consumed by both Neandertals and anatomically modern humans. Thus, the diversification of the human diet towards the end of the Upper Paleolithic, notably the inclusion of leporids, cannot be tied uniquely to cognitive, cultural or economic changes but better tracks palaeobiogeographic factors modifying the range of this species. If the exploitation of small prey during the Middle Paleolithic now appears uncontested, several authors nevertheless maintain that changes in the importance of rabbit in human subsistence strategies was not due to prey availability and / or ecological or climatic variations but reflects a clear cultural choice (Lloveras et al., 2010, 2016; Sanchis et al., 2016). Despite the continuous presence of this species on the eastern coast of the Iberian peninsula, significant differences are evident in the exploitation of rabbits between Mousterian and Aurignacian groups at Arbreda Cave (Lloveras et al., 2010, 2016) or between Aurignacian and Gravettian groups of Malladetes Cave (Sanchis et al., 2016), differences potentially due to the socio-economic organization of these human groups. Finally, the integration of leporids in the diet, especially at the Middle-Upper Paleolithic transition, could be the result of multiple factors integrating both prey availability and human choice, whose relative impact would have varied between regions (i.e., the eastern coast of Spain versus southern France).

In addition to Romero et al's (2017) recent demonstration of the exploitation of birds at Pié Lombard, our data, combined with evidence from Les Canalettes (Cochard et al., 2012),

demonstrates that around 70-75 kyr Neandertal groups in southern France had a diversified subsistence strategy that sometimes incorporated a significant proportion of small game. This pattern suggests that these groups had both a clear working knowledge of the landscape and mobilised specific acquisition strategies. Two modes of acquisition are generally cited to explain the presence of high numbers of rabbits in Paleolithic assemblages (Jones, 2006): 1) a mass collection near burrows or warrens, where immature individuals are often abundant; or 2) an opportunistic capture of solitary individuals in the landscape, which is reflected in the prevalence of adult individuals. Although these arguments (Jones, 2006) have recently been questioned (Pelletier et al., 2015; Pelletier, 2018, 2019), the large number of rabbits at Pié Lombard suggests the use of specific acquisition methods to capture multiple individuals. The near-absence of immature individuals can probably be explained by their low energy return or that rabbits were procured outside the birthing season (Cochard et al., 2012). Ethnographic and historical sources report the use of several techniques to hunt large numbers of small prey, such as leporids, including bows and arrows, throwing weapons, nets, snares, or individual or collective traps (Nelson, 1973; Bean, 1974; Oswalt, 1976; Callou, 2003; Lupo and Schmitt, 2005). Although the perishable nature of these technologies makes it difficult to identify them archaeologically, their use is regularly attributed to Upper Paleolithic hunter-gatherers (e.g., Stiner et al., 1999; Hoffecker, 2005; Rufà et al., 2017) as well as the Middle Stone Age of South Africa (Wadley, 2010). The pattern of Middle Palaeolithic rabbit exploitation documented at Pié Lombard currently finds no equivalent in Europe for this period and provides indirect evidence for the development of advanced hunting strategies by Neandertals during MIS 5-4 as well as their advanced cognitive capacities.

5. Conclusion

Given current debates concerning the diet and cognitive capacities of Neandertals, demonstrating the primary accumulation agent responsible for faunal assemblages,

especially those dominated by small mammals, as at Pié Lombard, is fundamental. Our taphonomic analysis shows the rabbit remains at the site to have been primarily accumulated by Neandertals, who sought both the meat and pelts of these small mammals. The intense exploitation of rabbit at Pié Lombard reveals Neandertals were not only able to exploit their environment but also maximize the return of available resources. Moreover, the high numbers of rabbits potentially suggests that a variety of trapping techniques were likely developed during the Middle Paleolithic, well before the arrival of modern humans in Western Europe.

Over the last decade, the number of studies focusing on the behavioural variability and lifestyle of Neandertals has increased exponentially, providing new evidence for the advanced cognitive capacities and social organisation of these groups. Neandertals repeatedly exploited small game, whether for their meat, fat, bones, teeth, feathers or furs. Evidence from Pié Lombard, Les Canalettes and Bolomor Cave provide new insights into the diet and socio-economic organisation of Middle Paleolithic human groups in southwestern Europe during MIS 5.

Finally, the intense and regular use of locally abundant small game that potentially required sophisticated acquisition techniques is no longer limited to the end of Upper Paleolithic. The exploitation of small animals seems to have been above all influenced by environmental conditions and social factors, rather than by biological and cultural differences between Neandertals and modern humans.

Declarations of interest

None.

Funding sources

809

810 This research did not receive any specific grant from funding agencies in the public,
811 commercial, or not-for-profit sectors.

812

813 **Acknowledgments**

814

815 We wish to thank Marie Matu and Patrice Courtaud for granting us access to the
816 “Ostéothèque de Pessac” to study some of the material. We thank the LAMPEA for their help
817 and support of this research. We are very grateful to Brad Gravina, the Editor José S. Carrión
818 and two anonymous reviewers for their constructive comments that greatly improved the
819 quality of the manuscript.

820

821 **Author contributions**

822

823 **Maxime Pelletier:** Conceptualization, Methodology, Formal Analysis, Investigation, Writing –
824 Original Draft. **Emmanuel Desclaux:** Conceptualization, Formal Analysis, Investigation,
825 Writing – Original Draft. **Jean-Philip Brugal:** Writing – Original Draft, Supervision. **Pierre-**
826 **Jean Texier:** Resources, Writing – Original Draft, Supervision, Project Administration.

827

828 **References**

829

830 Alhaique, F., 1995. Sfruttamento dei piccoli mammiferi e dei carnivori nel paleolitico superiore di
831 Grotta Polesini. In: Peretto, C., Milliken, S. (Eds.), L'Adattamento umano all'ambiente. Passato e
832 presente, XI Congresso Degli Antropologi Italiani. Associazione Antropologica Italiana 2, Isernia,
833 pp. 209-219.

834

835 Andrews, P., 1990. Owls, Caves and Fossils: Predation, Preservation and Accumulation of Small
836 Mammal Bones in Caves, with an Analysis of the Pleistocene Cave Faunas From Westbury-Sub-
837 Mendip, Somerset, U.K. University of Chicago Press, Chicago.

838

839 Armstrong, A., 2016a. Eagles, owls, and coyotes (oh my!): Taphonomic analysis of rabbits and guinea
840 pigs fed to captive raptors and coyotes. *J. Archaeol. Sci. Rep.* 5, 135-155.
841 <https://doi.org/10.1016/j.jasrep.2015.10.039>

842

843 Armstrong, A., 2016b. Small mammal utilization by Middle Stone Age humans at Die Kelders Cave 1
844 and Pinnacle Point Site 5-6, Western Cape Province, South Africa. *J. Hum. Evol.* 101, 17-44.
845 <https://doi.org/10.1016/j.jhevol.2016.09.010>

846

847 Arriaza, M.C., Huguet, R., Laplana Conesa, C., Pérez-González, A., Márquez, B., Arsuaga, J.L.,
848 Baquedano, E., 2017. Lagomorph predation represented in a middle Palaeolithic level of the
849 Navalmaíllo Rock Shelter site (Pinilla del Valle, Spain), as inferred via a new use of classical
850 taphonomic criteria. *Quatern. Int.* 436 (Part A), 294-306.
851 <https://doi.org/10.1016/j.quaint.2015.03.040>

852

853 Aura, J.E., Villaverde, V., Pérez Ripoll, M., Martínez-Valle, R., Guillem, P., 2002. Big Game and Small
854 Prey: Paleolithic and Epipaleolithic Economy from Valencia (Spain). *J. Archaeol. Method. Th.* 9,
855 215-268. <https://doi.org/10.1023/A:1019578013408>

856

857 Aura, J.E., Jordá, J.F., Pérez Ripoll, M., Badal, E., Avezuela, B., Morales, J.V., Tiffagom, M., Wood,
858 R., Marlasca, R., 2012. El corredor costero meridional: los cazadores gravetienses de la cueva de
859 Nerja (Málaga, España). In: Heras, C. de las, Lasheras, J.A., Arrizabalaga, Á., Rasilla, M. de la
860 (Eds.), *Pensando el Gravetiense: nuevos datos para la región cantábrica en su context peninsular*
861 *y pirenaico*, Monografías del Museo Nacional y Centro de Investigación de Altamira, pp. 104-113.

862

863 Bar-Yosef, O., 1998. On the Nature of Transitions: the Middle to Upper Palaeolithic and the Neolithic
864 Revolution. *Cam. Arch. Jnl.* 8, 141-163. <https://doi.org/10.1017/S0959774300000986>

865

866 Bar-Yosef, O., 2002. The Upper Paleolithic Revolution. *Annu. Rev. Anthropol.* 31, 363-393.
867 <https://doi.org/10.1146/annurev.anthro.31.040402.085416>

868

869 Bayle, P., 1992. Le Hibou grand-duc *Bubo bubo* dans le Parc National du Mercantour et ses environs.
870 Rapport du Parc National du Mercantour, Nice.

871

872 Bean, L.J. 1974. Mukat's people. The Cahuilla Indians of Southern California. University of California
873 Press, London.

874

875 Beyries, S., 2008. Modélisation du travail du cuir en ethnologie : proposition d'un système ouvert à
876 l'archéologie. *Anthropozoologica* 43, 9-42.

877

878 Biadi, F., Le Gall, A., 1993. Le lapin de garenne. Vie Gestion et chasse d'un gibier authentique. Office
879 national de la chasse. Hatier, Paris.

880

881 Blasco, M.F., 1995. Hombres, fieras y presas. Estudio arqueológico y tafonómico del yacimiento del
882 Paleolítico medio de la cueva de los Moros de Gabasa 1 (Huesca). *Monografías Arqueológicas* 38,
883 Zaragoza.

884

885 Blasco, R., 2008. Human consumption of tortoises at Level IV of Bolomor Cave (Valencia, Spain). *J.*
886 *Archaeol. Sci.* 35, 2839-2848. <https://doi.org/10.1016/j.jas.2008.05.013>

887

888 Blasco, R., Fernández Peris, J., 2012. A uniquely broad spectrum diet during the Middle Pleistocene
889 at Bolomor Cave (Valencia, Spain). *Quatern. Int.* 252, 16-31.
890 <https://doi.org/10.1016/j.quaint.2011.03.019>

891

892 Blasco, R., Rosell, J., Fernández Peris, J., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E.,
893 2013. Environmental availability, behavioural diversity and diet: a zooarchaeological approach from

the TD10-1 sublevel of Gran Dolina (Sierra de Atapuerca, Burgos, Spain) and Bolomor Cave (Valencia, Spain). Quat. Sci. Rev. 70, 124-144. <https://doi.org/10.1016/j.quascirev.2013.03.008>

Blasco, R., Finlayson, C., Rosell, J., Sánchez Marco, A., Finlayson, S., Finlayson, G., Negro, J.J., Giles Pacheco, F., Rodríguez Vidal, J., 2014. The earliest pigeon fanciers. Scientific Reports 4, 5971. <https://doi.org/10.1038/srep05971>

Blasco, R., Rosell, J., Rufà, A., Sánchez Marco, A., Finlayson, C., 2016. Pigeons and choughs, a usual resource for the Neanderthals in Gibraltar. Quatern. Int. 421, 62-77. <https://doi.org/10.1016/j.quaint.2015.10.040>

Branco, M., Monnerot, M., Ferrand, N., Templeton, A.R., 2002. Postglacial dispersal of the European rabbit (*Oryctolagus cuniculus*) on the Iberian peninsula reconstructed from nested clade and mismatch analyses of mitochondrial DNA genetic variation. Evolution 56, 792-803. <https://doi.org/10.1111/j.0014-3820.2002.tb01390.x>

Brown, K., Fa, D.A., Finlayson, G., Finlayson, C., 2011. Small Game and Marine Resource Exploitation by Neanderthals: The Evidence from Gibraltar. In: Bicho, N.F., Haws, J.A., Davis, L. (Eds.), Trekking the Shore: Changing Coastlines and the Antiquity of Coastal Settlement, Interdisciplinary Contributions to Archaeology. Springer, New York, pp. 247-272.

Brugal, J.-P., 2005. Typologie des classes de taille chez les mammifères : implications paléoécologiques, taphonomiques et archéozoologiques. In: Costamagno, S., Fosse, P., Laudet, F. (Eds.), La Taphonomie : des référentiels aux ensembles osseux fossils. Round-Table, Toulouse.

Brugal, J.-P., 2006. Petit gibier et fonction de sites au Paléolithique supérieur. Paléo 18, 45-68.

Brugal, J.-P., Jaubert, J., 1996. Stratégie d'exploitation et mode de vie des populations du Paléolithique moyen : exemple des sites du Sud de la France. In: Mohen, J.-P. (Ed.), La vie préhistorique. Fatou, Paris, pp. 148-155.

924

925 Callou, C., 2003. De la garenne au clapier: étude archéozoologique du lapin en Europe occidentale.
926 Mémoires du Muséum national d'Histoire naturelle, Publications scientifiques du Muséum, Paris.

927

928 Cannon, M.D., 2003. A model of central place forager prey choice and an application to faunal
929 remains from the Mimbres Valley, New Mexico. J. Anthropol. Archaeol. 22, 1-25.
930 [https://doi.org/10.1016/S0278-4165\(03\)00002-3](https://doi.org/10.1016/S0278-4165(03)00002-3)

931

932 Caron, F., d'Errico, F., Del Moral, P., Santos, F., Zilhão, J., 2011 - The Reality of Neandertal Symbolic
933 Behavior at the Grotte du Renne, Arcy-sur-Cure, France. PLoS ONE 6, e21545.
934 <https://doi.org/10.1371/journal.pone.0021545>

935

936 Carvalho, M., Peireira, T., Manso, C., 2018. Rabbit exploitation in the Middle Paleolithic at Gruta Nova
937 da Columbeira, Portugal. J. Archaeol. Sci. Rep. 21, 821-832.
938 <https://doi.org/10.1016/j.jasrep.2018.09.003>

939

940 Charles, R.E., 1997. The Exploitation of Carnivores and Other Fur-bearing Mammals during the North-
941 western European Late and Upper Paleolithic and Mesolithic. Oxford Journal of Archaeology 16,
942 253-277. <https://doi.org/10.1111/1468-0092.00040>

943

944 Charles, R.E., Jacobi, R.M., 1994. The Lateglacial fauna from the Robin hood cave, Creswell crags: a
945 reassessment. Oxford Journal of Archaeology 13, 1-32. [https://doi.org/10.1111/j.1468-](https://doi.org/10.1111/j.1468-0092.1994.tb00029.x)
946 [0092.1994.tb00029.x](https://doi.org/10.1111/j.1468-0092.1994.tb00029.x)

947

948 Chase, P.G., 1990. Tool-Making Tools and Middle Paleolithic Behavior. Curr. Anthropol. 31, 443-447.
949 <https://doi.org/10.1086/203869>

950

951 Cochard, D., 2004a. Les léporidés dans la subsistance paléolithique du sud de la France. Ph.D.
952 Dissertation, University of Bordeaux I, Talence.

953

- Cochard, D., 2004b. Influence de l'âge des proies sur les caractéristiques des accumulations de léporidés produites par le hibou grand-duc. In: Brugal, J.-P., Desse, J. (Eds.), *Petits animaux et sociétés humaines. Du complément alimentaire aux ressources utilitaires*, Actes Des XXIV^{ème} Rencontres Internationales D'archéologie et D'histoire d'Antibes. APDCA, Antibes, pp. 313-316.
- Cochard, D., 2005. Les lièvres variables du niveau 5 du Bois-Ragot: Analyse taphonomique et apports paléo-ethnologiques. In: Chollet, A., Dujardin, V. (Eds.), *La grotte du Bois-Ragot à Goux (Vienne) Magdalénien et Azilien. Essais sur les hommes et leur environnement. Mémoire de la Société Préhistorique Française XXXVIII*, Paris, pp. 319-337.
- Cochard, D., 2007. Caractérisation des apports de Léporidés dans les sites paléolithiques et application méthodologique à la couche VIII de la grotte Vaufray. In: Evin, J. (Ed.), *Un siècle de construction du discours scientifique en Préhistoire*, Actes du Congrès du "Centenaire de la Société Préhistorique Française. Mémoire de la Société Préhistorique Française, Paris, pp. 467-480.
- Cochard, D., 2008. Discussion sur la variabilité intraréfèrentiel d'accumulations osseuses de petits prédateurs. *Ann. Paléontol.* 94, 89-101. <https://doi.org/10.1016/j.annpal.2008.03.001>
- Cochard, D., Brugal, J.-P., 2004. Importance des fonctions de sites dans les accumulations paléolithiques de léporidés. In: Brugal, J.-P., Desse, J. (Eds.), *Petits animaux et sociétés humaines. Du complément alimentaire aux ressources utilitaires*, Actes Des XXIV^{ème} Rencontres Internationales D'archéologie et D'histoire d'Antibes. APDCA, Antibes, pp. 217-230.
- Cochard, D., Brugal, J.-P., Morin, E., Meignen, L., 2012. Evidence of small fast game exploitation in the Middle Paleolithic of Les Canelettes, Aveyron, France. *Quatern. Int.* 264, 32-51. <https://doi.org/10.1016/j.quaint.2012.02.014>
- Cole, J., 2017. Assessing the calorific significance of episodes of human cannibalism in the Palaeolithic. *Scientific Reports* 7, 44707. <https://doi.org/10.1038/srep44707>

984

985 Dayet, L., Faivre, J.-P., Le Bourdonnec, F.-X., Discamps, E., Royer, A., Claud, E., Lahaye, C., Cantin,
986 N., Tartar, E., Queffelec, A., Gravina, B., Turq, A., d'Errico, F., 2019. Manganese and iron oxide
987 use at Combe-Grenal (Dordogne, France): A proxy for cultural change in Neanderthal
988 communities. *J. Archaeol. Sci. Rep.* 25, 239-256. <https://doi.org/10.1016/j.jasrep.2019.03.027>

989

990 d'Errico, F., 2003. The invisible frontier. A multiple species model for the origin of behavioral
991 modernity. *Evol Anthropol.* 12, 188-202. <https://doi.org/10.1002/evan.10113>

992

993 d'Errico, F., Laroulandie, V., 2000. Bone technology at the Middle-Upper Palaeolithic transition. The
994 case of the worked bones from Buran-Kaya III level C (Crimea, Ukraine). In: Orschiedt, J.,
995 Weniger, G.-C., (Eds.), *Neanderthals and Modern humans - Discussing the transition: Central and*
996 *Eastern Europe from 50.000-30.000 B.P.* Neanderthal Museum, Mettmann, pp. 227-242.

997

998 d'Errico, F., Borgia, V., Ronchitelli, A., 2012. Uluzzian bone technology and its implications for the
999 origin of behavioural modernity. *Quatern. Int.* 259, 59-71.
1000 <https://doi.org/10.1016/j.quaint.2011.03.039>

1001

1002 Defleur, A., Bez, J.-F., Cregut-Bonnoure, E., Desclaux, E., Onoratini, G., Radulescu, C., Thinon, M.,
1003 Vilette, P., 1994. Le niveau moustérien de la grotte de l'Adaouste (Jouques, Bouches-du-Rhône):
1004 approche culturelle et paléoenvironnements. *Bull. Mus. Anthropol. Préhist. Monaco* 37, 11-48.

1005

1006 Delibes, M., Hiraldo, F., 1981. The rabbit as a prey in the Iberian Mediterranean ecosystem. In: Myers,
1007 K., MacInnes, C.D., (Eds.), *Proceedings of the World Lagomorph Conference.* University of
1008 Guelph, Guelph, pp. 614-622.

1009

1010 Desclaux, E., 1992. Les petits vertébrés de la Caune de l'Arago (Tautavel, Pyrénées-orientales):
1011 paléontologie, paléoécologie, taphonomie. Ph.D. Dissertation, National Museum of Natural History,
1012 Paris.

1013

1014 Desclaux, E., Hanquet, C., El Guennouni, K., 2011. Origine(s) des accumulations de
 1015 micromammifères dans quelques sites préhistoriques du Pléistocène moyen et supérieur d'Europe
 1016 méridionale. In: Laroulandie, V., Mallye, J.-B., Denys, C. (Eds.), Taphonomie des Petits Vertébrés:
 1017 Référentiels et Transferts aux Fossiles. Actes de la Table Ronde du RTP Taphonomie, BAR
 1018 International Series, pp. 110-118.
 1019
 1020 Discamps, E., Costamagno, S., 2015. Improving mortality profile analysis in zooarchaeology: a revised
 1021 zoning for ternary diagrams. J. Archaeol. Sci. 58, 62-76. <https://doi.org/10.1016/j.jas.2015.03.021>
 1022
 1023 Discamps, E., Jaubert, J., Bachellerie, F., 2011. Human choices and environmental constraints:
 1024 deciphering the variability of large game procurement from Mousterian to Aurignacian times (MIS
 1025 5-3) in southwestern France. Quat. Sci. Rev. 30, 2755-2775.
 1026 <https://doi.org/10.1016/j.quascirev.2011.06.009>
 1027
 1028 Dodson, P., Wexlar, D., 1979. Taphonomic Investigations of Owl Pellets. Paleobiology 5, 275-284.
 1029
 1030 Donazar, J.A., 1988. Variaciones en la alimentación entre adultos reproductores y pollos en el Búho
 1031 Real (*Bubo bubo*). Ardeola 35, 278-284.
 1032
 1033 El Guennouni, K., 2001. Les lapins du Pléistocène moyen et supérieur de quelques sites
 1034 préhistoriques de l'Europe méditerranéenne : Terra-Amata, Orgnac 3, Baume Bonne, grotte du
 1035 Lazaret, grotte du Boquete de Zafarraya, Arma delle Manie : étude paléontologique, taphonomique
 1036 et archéozoologique. Ph.D. Dissertation, National Museum of Natural History, Paris.
 1037
 1038 Emmons, G.T., 1911. The Tahltan Indians. The University Museum Anthropological Publications,
 1039 Philadelphia.
 1040
 1041 Fa, J.E., Stewart, J.R., Lloveras, L., Vargas, J.M., 2013. Rabbits and hominin survival in Iberia. J.
 1042 Hum. Evol. 64, 233-241. <https://doi.org/10.1016/j.jhevol.2013.01.002>
 1043

1044 Fernández-Jalvo, Y., Andrews, P., 1992. Small mammal taphonomy of Gran Dolina, Atapuerca
 1045 (Burgos), Spain. J. Archaeol. Sci. 19, 407-428. [https://doi.org/10.1016/0305-4403\(92\)90058-B](https://doi.org/10.1016/0305-4403(92)90058-B)
 1046
 1047 Fernández-Jalvo, Y., Andrews, P., 2000. The taphonomy of Pleistocene caves with particular
 1048 reference to Gibraltar. In: Stringer, C.B., Barton, R.N.E., Finlayson, C. (Eds.), Neanderthals on the
 1049 Edge. Oxbow Books, Oxford, pp. 171-182.
 1050
 1051 Finlayson, C., Brown, K., Blasco, R., Rosell, J., Negro, J.J., Bortolotti, G.R., Finlayson, G., Sánchez
 1052 Marco, A., Giles Pacheco, F., Rodríguez Vidal, J., Carrión, J.S., Fa, D.A., Rodríguez Llanes, J.M.,
 1053 2012. Birds of a Feather: Neanderthal Exploitation of Raptors and Corvids. PLoS ONE 7, e45927.
 1054 <https://doi.org/10.1371/journal.pone.0045927>
 1055
 1056 Finlayson, S., Finlayson, G., Giles Guzmán, F., Finlayson, C., 2019. Neanderthals and the cult of the
 1057 Sun Bird. Quat. Sci. Rev. 217, 217-224. <https://doi.org/10.1016/j.quascirev.2019.04.010>
 1058
 1059 Fiore, I., Gala, M., Romandini, M., Cocca, E., Tagliacozzo, A., Peresani, M., 2016. From feathers to
 1060 food: Reconstructing the complete exploitation of avifaunal resources by Neanderthals at Fumane
 1061 cave, unit A9. Quatern. Int. 421, 134-153. <https://doi.org/10.1016/j.quaint.2015.11.142>
 1062
 1063 Fontana, L., 2003. Characterization and exploitation of the arctic hare (*Lepus timidus*) during the
 1064 Magdalenian: surprising data from Gazel Cave (Aude, France). In: Costamagno, S., Laroulandie,
 1065 V. (Eds.), Mode de vie au Magdalénien : Apports de l'archéozoologie, Actes du XIV^e Congrès
 1066 UISPP. BAR International Serie 1144, Oxford, pp. 101–118.
 1067
 1068 Gabucio, M.J., Cáceres, I., Rodríguez-Hidalgo, A., Rosell, J., Saladié, P., 2014. A wildcat (*Felis*
 1069 *silvestris*) butchered by Neanderthals in Level O of the Abric Romaní site (Capellades, Barcelona,
 1070 Spain). Quatern. Int. 326-327, 307-318. <https://doi.org/10.1016/j.quaint.2013.10.051>
 1071

1072 García-Argüelles, P., Nadal, J., Estrada, A., 2004. Balma del Gai rock shelter: an Epipaleolithic rabbit
1073 skinning factory. In: Combré, P., Vermeersch, P., (Eds.), *Le Mésolithique, Actes du XIVème*
1074 *Congrès UISPP. BAR International Series 1302*, Oxford, pp. 115-120.

1075

1076 Gerber, J.-P., 1973. *La Faune de grands mammifères du Würm ancien dans le Sud-Est de la France.*
1077 Ph.D. Dissertation, University of Provence, Marseille.

1078

1079 Géroudet, P., 1984. *Les rapaces diurnes et nocturnes d'Europe.* Delachaux et Niestlé, Lausanne.

1080

1081 Gómez-Olivencia, A., Sala, N., Núñez-Lahuerta, C., Sanchis, A., Arlegi, M., Rios-Garaizar, J., 2018.
1082 First data of Neandertal bird and carnivore exploitation in the Cantabrian Region (Axlor;
1083 Barandiaran excavations; Dima, Biscay, Northern Iberian Peninsula). *Scientific Reports* 8, 10551.
1084 <https://doi.org/10.1038/s41598-018-28377-y>

1085

1086 Gutiérrez-Zugasti, I., Rios-Garaizar, J., Marín-Arroyo, A.B., Rasines del Río, P., Maroto, J., Jones,
1087 J.R., Bailey, G.N., Richards, M.P., 2018. A chrono-cultural reassessment of the levels VI–XIV from
1088 El Cuco rock-shelter: A new sequence for the Late Middle Paleolithic in the Cantabrian region
1089 (northern Iberia). *Quatern. Int.* 747, 44-55. <https://doi.org/10.1016/j.quaint.2017.06.059>

1090

1091 Hassani, M., 2016. *La grande faune de la couche 4 de l'abri des Canalettes (Aveyron). Modalités*
1092 *d'acquisition du gibier à partir des restes dentaires.* Master 2 Dissertation, University of Nice
1093 Sophia-Antipolis, Nice. (unpublished)

1094

1095 Hardy, B.L., Moncel, M.-H., Daujeard, C., Fernandes, P., Béarez, P., Desclaux, E., Chacon Navarro,
1096 M.G., Puaud, S., Gallotti, R., 2013. Impossible Neanderthals? Making string, throwing projectiles
1097 and catching small game during Marine Isotope Stage 4 (Abri du Maras, France). *Quat. Sci. Rev.*
1098 82, 23-40. <https://doi.org/10.1016/j.quascirev.2013.09.028>

1099

1100 Henshilwood, C.S., Marean, C.W., 2003. The Origin of Modern Human Behavior: Critique of the
1101 Models and Their Test Implications. *Curr. Anthropol.* 44, 627-651. <https://doi.org/10.1086/377665>

1102

1103 Hockett, B.S., 1991. Toward distinguishing human and raptor patterning on leporid bones. *Am.*
1104 *Antiquity* 56, 667-679. <https://doi.org/10.2307/281544>

1105

1106 Hockett, B.S., 1994. A descriptive reanalysis of the leporid bones from Hogup cave, Utah. *J. Calif. Gt.*
1107 *Basin Anthropol.* 16, 106-117.

1108

1109 Hockett, B.S., 1996. Corroded, thinned and polished bones created by golden eagles (*Aquila*
1110 *chrysaetos*): Taphonomic implications for Archaeological Interpretations. *J. Archaeol. Sci.* 23, 587-
1111 591. <https://doi.org/10.1006/jasc.1996.0055>

1112

1113 Hockett, B.S., Bicho, N.F., 2000. The rabbits of Picareiro Cave: small mammal hunting during the Late
1114 Upper Palaeolithic in the Portuguese Estremadura. *J. Archaeol. Sci.* 27, 715-723.
1115 <https://doi.org/10.1006/jasc.1999.0496>

1116

1117 Hockett, B.S., Haws, J.A., 2002. Taphonomic and Methodological Perspectives of Leporid Hunting
1118 During the Upper Paleolithic of the Western Mediterranean Basin. *J. Archaeol. Method Th.* 9, 269-
1119 302. <https://doi.org/10.1023/A:1019503030246>

1120

1121 Hockett, B.S., Haws, J.A., 2009. Continuity in animal resource diversity in the Late Pleistocene human
1122 diet of Central Portugal. *Before Farming* 2009, 1-14. <https://doi.org/10.3828/bfarm.2009.2.2>

1123

1124 Hoffeecker, J.F., 2005. Innovation and technological knowledge in the Upper Paleolithic of Northern
1125 Eurasia. *Evol Anthropol.* 14, 186-198. <https://doi.org/10.1002/evan.20066>

1126

1127 Hoffmann, D.L., Angelucci, D.E., Villaverde, V., Zapata, J., Zilhão, J., 2018a. Symbolic use of marine
1128 shells and mineral pigments by Iberian Neandertals 115,000 years ago. *Sci. Adv.* 4, eaar5255.
1129 <https://doi.org/10.1126/sciadv.aar5255>

1130

1131 Hoffmann, D.L., Standish, C.D., García-Diez, M., Pettitt, P.B., Milton, J.A., Zilhão, J., Alcolea-
 1132 González, J.J., Cantalejo-Duarte, P., Collado, H., Balbín, R. de, Lorblanchet, M., Ramos-Muñoz, J.,
 1133 Weniger, G.-Ch., Pike, A.W.G., 2018b. U-Th dating of carbonate crusts reveals Neandertal origin of
 1134 Iberian cave art. *Science* 359, 912-915. <https://doi.org/10.1126/science.aap7778>
 1135
 1136 Jaubert, J., Verheyden, S., Genty, D., Soulier, M., Cheng, H., Blamart, D., Burlet, C., Camus, H.,
 1137 Delaby, S., Deldicque, D., Edwards, R.L., Ferrier, C., Lacrampe-Cuyaubère, F., Lévêque, F.,
 1138 Maksud, F., Mora, P., Muth, X., Régnier, E., Rouzaud, J.-N., Santos, F., 2016. Early Neanderthal
 1139 constructions deep in Bruniquel Cave in southwestern France. *Nature* 534, 111-114.
 1140 <https://doi.org/10.1038/nature18291>
 1141
 1142 Jones, E.L., 2004. The European rabbit (*Oryctolagus cuniculus*) and the development of broad
 1143 spectrum diets in south-western France: data from the Dordogne valley. In: Brugal, J.-P., Desse, J.
 1144 (Eds.), *Petits animaux et sociétés humaines. Du complément alimentaire aux ressources utilitaires*,
 1145 *Actes Des XXIVème Rencontres Internationales D'archéologie et D'histoire d'Antibes*. APDCA,
 1146 Antibes, pp. 273-284.
 1147
 1148 Jones, E.L., 2006. Prey choice, mass collecting, and the wild European rabbit (*Oryctolagus cuniculus*).
 1149 *J. Anthropol. Archaeol.* 25, 275-289. <https://doi.org/10.1016/j.jaa.2005.11.002>
 1150
 1151 Jullien, R., Pillard, B., 1969. Les lagomorphes découverts sur le sol de la cabane acheuléenne du
 1152 Lazaret. *Mémoire de la Société Préhistorique Française* 7, 75-83.
 1153
 1154 Kennedy, D., Bouchard, R.T., 1998. Lillooet. In: Walker, D.E. (Eds.), *Handbook of North American*
 1155 *Indians, Volume 12: Plateau*. Smithsonian Institution, Washington DC, pp. 174-190.
 1156
 1157 Lahren, S.L., 1998. Kalispel. In: Walker, D.E. (Eds.), *Handbook of North American Indians, Volume 12:*
 1158 *Plateau*. Smithsonian Institution, Washington DC, pp. 283-288.
 1159

1160 Leesch, D., 1997. Hauterive-Champréveyres, 10. Un campement magdalénien au bord du lac de
1161 Neuchâtel : cadre chronologique et culturel, mobilier et structures, analyse spatiale (secteur 1).
1162 Archéologie neuchâteloise, 19, Musée cantonal d'Archéologie, Neuchâtel.
1163
1164 Lloveras, L., Moreno-García, M., Nadal, J., 2008. Taphonomic analysis of leporid remains obtained
1165 from modern Iberian lynx (*Lynx pardinus*) scats. J. Archaeol. Sci. 35, 1-13.
1166 <https://doi.org/10.1016/j.jas.2007.02.005>
1167
1168 Lloveras, L., Moreno-García, M., Nadal, J., 2009a. The eagle owl (*Bubo bubo*) as a leporid remains
1169 accumulator: taphonomic analysis of modern rabbit remains recovered from nests of this predator.
1170 International J. Osteoarchaeol. 19, 573-592. <https://doi.org/10.1002/oa.995>
1171
1172 Lloveras, L., Moreno-García, M., Nadal, J., 2009b. Butchery, cooking and human consumption marks
1173 on rabbit (*Oryctolagus cuniculus*) bones: an experimental study. Journal of Taphonomy 7, 179-201.
1174
1175 Lloveras, L., Moreno García, M., Soler, N., 2010. The application of actualistic studies to assess the
1176 taphonomic origin of Musterian rabbit accumulations from Arbreda Cave (North-East Iberia).
1177 Archaeofauna 19, 99-119.
1178
1179 Lloveras, L., Moreno-García, M., Nadal, J., Zilhão, J., 2011. Who brought in the rabbits?
1180 Taphonomical analysis of Mousterian and Solutrean leporid accumulations from Gruta do
1181 Caldeirão (Tomar, Portugal). J. Archaeol. Sci. 38, 2434-2449.
1182 <https://doi.org/10.1016/j.jas.2011.05.012>
1183
1184 Lloveras, L., Moreno-García, M., Nadal, J., 2012a. Assessing the variability in taphonomic studies of
1185 modern leporid remains from Eagle Owl (*Bubo bubo*) nest assemblages: the importance of age of
1186 prey. J. Archaeol. Sci. 39, 3754-3764. <https://doi.org/10.1016/j.jas.2012.06.033>
1187

1188 Lloveras, L., Moreno-García, M., Nadal, J., 2012b. Feeding the foxes: an experimental study to assess
 1189 their taphonomic signature on leporid remains. *International J. Osteoarchaeol.* 22, 577-590.
 1190 <https://doi.org/10.1002/oa.1280>
 1191
 1192 Lloveras, L., Nadal, J., Moreno-García, M., Thomas, R., Anglada, J., Baucells, J., Martorell, C., Vilasís,
 1193 D., 2014a. The role of the Egyptian vulture (*Neophron percnopterus*) as a bone accumulator in cliff
 1194 rock shelters: an analysis of modern bone nest assemblages from North-Eastern Iberia. *J.*
 1195 *Archaeol. Sci.* 44, 76-90. <https://doi.org/10.1016/j.jas.2014.01.018>
 1196
 1197 Lloveras, L., Thomas, R., Lourenço, R., Caro, J., Dias, A., 2014b. Understanding the taphonomic
 1198 signature of Bonelli's Eagle (*Aquila fasciata*). *J. Archaeol. Sci.* 49, 455-471.
 1199 <https://doi.org/10.1016/j.jas.2014.06.005>
 1200
 1201 Lloveras, L., Maroto, J., Soler, J., Thomas, R., Moreno-García, M., Nadal, J., Soler, N., 2016. The role
 1202 of small prey in human subsistence strategies from Early Upper Palaeolithic sites in Iberia: the
 1203 rabbits from the Evolved Aurignacian level of Arbreda Cave. *J. Quat. Sci.* 31, 458-471.
 1204 <https://doi.org/10.1002/jqs.2869>
 1205
 1206 Lloveras, L., Cosso, A., Solé, J., Claramunt-López, B., Nadal, J., 2017. Taphonomic signature of
 1207 golden eagles (*Aquila chrysaetos*) on bone prey remains. *Hist. Biol.* 30, 835-854.
 1208 <https://doi.org/10.1080/08912963.2017.1319830>
 1209
 1210 Lumley-Woodyear, H. de, 1969. Le Paléolithique inférieur et moyen du Midi méditerranéen dans son
 1211 cadre géologique. Tome 1. Gallia Préhistoire, Paris.
 1212
 1213 Lumley, H. de, Echassoux, A., Bailon, S., Cauche, D., De Marchi, M.-P., Desclaux, E., El Guennouni,
 1214 K., Khatib, S., Lacombe, F., Roger, T., Valensi, P., 2004. Le sol d'occupation acheuléen de l'unité
 1215 archéostratigraphique UA 25 de la grotte du Lazaret (Nice, Alpes-Maritimes). EDISUD, Aix-en-
 1216 Provence.
 1217

1218 Lupo, K.D., Schmitt, D.N., 2002. Upper paleolithic net-hunting, small prey exploitation, and women's
 1219 work effort: a view from the ethnographic and ethnoarchaeological record of the Congo Basin. *J*
 1220 *Archaeol. Method. Theory.* 9, 147-179. <https://doi.org/10.1023/A:1016578224794>
 1221

1222 Lyman, R.L., 2008. *Quantitative Paleozoology*. Cambridge University Press, Cambridge.
 1223

1224 Mallye, J.-B., Cochard, D., Laroulandie, V., 2008. Accumulations osseuses en périphérie de terriers de
 1225 petits carnivores : les stigmates de prédation et de fréquentation. *Ann. Paléontol.* 94, 187-208.
 1226 <https://doi.org/10.1016/j.annpal.2008.06.002>
 1227

1228 Mallye, J.-B., Laroulandie, V., Bonnet-Jacquement, P., Boudadi-Maligne, M., Langlais, M., Man-Estier,
 1229 E., Vercoutère, C., Paillet P., 2018. L'utilisation des petits gibiers au Tardiglaciaire : Le cas de
 1230 Rochereil (collection Jude, Dordogne). In: Costamagno, S., Gourichon, L., Dupont, C., Dutour, O.,
 1231 Vialou, D. (Eds.), *Animal symbolisé - Animal exploité. Du Paléolithique à la Protohistoire*, Actes du
 1232 141eme Congrès du CTHS. CTHS Collection, Paris, pp. 89-111.
 1233

1234 Manne, T., Cascalheira, J., Évora, M., Marreiros, J., Bicho, N., 2012. Intensive subsistence practices
 1235 at Vale Boi, an Upper Paleolithic site in southwestern Portugal. *Quatern. Int.* 264, 83-99.
 1236 <https://doi.org/10.1016/j.quaint.2012.02.026>
 1237

1238 Martínez-Polanco, M.F., Blasco, R., Rosell, J., Ibañez, N., Vaquero, M., 2017. Rabbits as Food at the
 1239 end of the Upper Palaeolithic at Molí del Salt (Catalonia, Spain). *Int. J. Osteoarchaeol.* 27, 342-
 1240 355. <https://doi.org/10.1002/oa.2541>
 1241

1242 Martínez-Valle, R., 1996. *Fauna del Pleistoceno superior en el País Valenciano: aspectos*
 1243 *económicos, huella de manipulación y valoración paleoambiental*. Ph.D. Dissertation, University of
 1244 Valencia, Valencia.
 1245

1246 Mcbrearty, S., Brooks, A.S., 2000. The revolution that wasn't: a new interpretation of the origin of
 1247 modern human behavior. *J. Hum. Evol.* 39, 453-563. <https://doi.org/10.1006/jhev.2000.0435>

1248

1249 McComb, P., 1989. Upper Palaeolithic osseous artifacts from Britain and Belgium. BAR International
1250 Series 481, Oxford.

1251

1252 Mellars, P., 1996. The Neanderthal Legacy: An Archaeological Perspective from Western Europe.
1253 Princeton University Press, Princeton.

1254

1255 Mellars, P., 2010. Neanderthal symbolism and ornament manufacture: The bursting of a bubble? Proc.
1256 Nat. Acad. Sci 107, 20147-20148. <https://doi.org/10.1073/pnas.1014588107>

1257

1258 Morel, P., Müller, W., 1997. Hauterives-Champréveyres, 11. Un campement Magdalénien au bord du
1259 lac de Neuchatel : étude archéozoologique (secteur 1). Archéologie neuchâteloise, 23, Musée
1260 cantonal d'Archéologie, Neuchâtel.

1261

1262 Morin, E., Laroulandie, V., 2012. Presumed Symbolic Use of Diurnal Raptors by Neanderthals. PLoS
1263 ONE 7, e32856. <https://doi.org/10.1371/journal.pone.0032856>

1264

1265 Morin, E., Delagnes, A., Armand, D., Castel, J.-C., Hodgkins, J., 2014. Millennial-scale change in
1266 archaeofaunas and their implications for Mousterian lithic variability in southwest France. J.
1267 Anthropol. Archaeol. 36, 158-180. <https://doi.org/10.1016/j.jaa.2014.09.013>

1268

1269 Nabais, M., Zilhão, J., 2019. The consumption of tortoise among Last Interglacial Iberian
1270 Neanderthals. Quat. Sci. Rev. <https://doi.org/10.1016/j.quascirev.2019.03.024>

1271

1272 Nelson, R.K., 1973. Hunters of the northern forest: designs for survival among Alaskan Kutchin.
1273 University of Chicago Press, Chicago.

1274

1275 Oberg, K., 1973. The Social Economy of the Tlingit Indians. University of Washington Press, Seattle.

1276

1277 Oswalt, W.H., 1976. An Anthropological Analysis of Food-Getting Technology. Wiley, New-York.

1278

1279 Pavao, B., Stahl, P.W., 1999. Structural density assays of leporid skeletal elements with implications
1280 for taphonomic, actualistic and archaeological research. *J. Archaeol. Sci.* 26, 53-66.
1281 <https://doi.org/10.1006/jasc.1998.0299>

1282

1283 Pelletier, M., 2018. Évolution morphométrique et Biogéographie des Léporidés dans les
1284 environnements méditerranéens au Pléistocène. Implications socio-économiques pour les sociétés
1285 humaines. Ph.D. Dissertation, Aix-Marseille University, Aix-en-Provence. [https://tel.archives-](https://tel.archives-ouvertes.fr/tel-01951363)
1286 [ouvertes.fr/tel-01951363](https://tel.archives-ouvertes.fr/tel-01951363)

1287

1288 Pelletier, M., 2019. Morphological diversity of wild rabbit populations: implications for archaeology and
1289 palaeontology. *Biol. J. Linn. Soc. Lond* 128, 211-224. <https://doi.org/10.1093/biolinnean/blz074>

1290

1291 Pelletier, M., Royer, A., Holliday, T., Maureille, B., 2015. Lièvre et lapin à Regourdou (Montignac-sur-
1292 Vézère, Dordogne, France): Études paléontologique et taphonomique de deux accumulations
1293 osseuses d'origine naturelle. *Paléo* 26, 161-183.

1294

1295 Pelletier, M., Brugal, J.-P., Cochard, D., Lenoble, A., Mallye, J.-B., Royer, A., 2016. Identifying fossil
1296 rabbit warrens: insights from a taphonomical analysis of a modern warren. *J. Archaeol. Sci. Rep.*
1297 10, 331-344. <https://doi.org/10.1016/j.jasrep.2016.10.016>

1298

1299 Pelletier, M., Royer, A., Holliday, T.W., Discamps, E., Madelaine, S., Maureille, B., 2017. Rabbits in
1300 the grave! Consequences of bioturbation on the Neandertal “burial” at Regourdou (Montignac-sur-
1301 Vézère, Dordogne). *J. Hum. Evol.* 110, 1-17. <https://doi.org/10.1016/j.jhevol.2017.04.001>

1302

1303 Peresani, M., Fiore, I., Gala, M., Romandini, M., Tagliacozzo, A., 2011. Late Neandertals and the
1304 intentional removal of feathers as evidenced from bird bone taphonomy at Fumane Cave 44 ky
1305 B.P., Italy. *Proc. Nat. Acad. Sci.* 108, 3888-3893. <https://doi.org/10.1073/pnas.1016212108>

1306

1307 Pérez, L.J., Sanchis Serra, A., Hernández, C.M., Galván, B., 2017. Paleoecología de macromamíferos
 1308 aplicada a los conjuntos zooarqueológicos de El Salt y el Abric del Pastor (Alcoy, Alicante). In:
 1309 Sanchis Serra, A., Pascual Benito, J.L., (Eds.), Interaccions entre felins i humans. III Jornades
 1310 d'arqueozoologia. Museu de Prehistòria de València, Valencia, pp. 327-353.
 1311

1312 Pérez Ripoll, M., 2004. La consommation humaine des lapins pendant le Paléolithique dans la région
 1313 de Valencia (Espagne) et l'étude des niveaux gravettiens de La Cova de les Cendres (Alicante). In:
 1314 Brugal, J.-P., Desse, J. (Eds.), Petits animaux et sociétés humaines. Du complément alimentaire
 1315 aux ressources utilitaires, Actes Des XXIVème Rencontres Internationales D'archéologie et
 1316 D'histoire d'Antibes. APDCA, Antibes, pp. 191-206.
 1317

1318 Pettitt, P.B., 2002. The Neanderthal dead: exploring mortuary variability in Middle Palaeolithic. *Before*
 1319 *Farming* 1, 1-26. <https://doi.org/10.3828/bfarm.2002.1.4>
 1320

1321 Pettitt, P.B., 2011. *The Palaeolithic Origins of Human Burial*. New Ed. Routledge, Milton Park.
 1322

1323 Pitarch Martí, A., d'Errico, F., Turq, A., Lebraud, E., Discamps, E., Gravina, B., 2019. Provenance,
 1324 modification and use of manganese-rich rocks at Le Moustier (Dordogne, France). *PLoS ONE* 14,
 1325 e0218568. <https://doi.org/10.1371/journal.pone.0218568>
 1326

1327 Pokines, J.P., 1998. *The Paeoecology of Lower Magdalenian Cantabrian Spain*. BAR Internationnal
 1328 Serie 713, Oxford.
 1329

1330 Porraz, G., 2005. *En marge du milieu alpin. Dynamiques de formation des ensembles lithiques et*
 1331 *modes d'occupation des territoires au Paléolithique moyen*. Ph.D. Dissertation, University of
 1332 Provence, Aix-en-Provence.
 1333

1334 Radovčić, D., Sršen, A.O., Radovčić, J., Frayer, D.W., 2015. Evidence for Neandertal jewelry:
 1335 Modified white-tailed eagle claws at Krapina. *PLoS ONE* 10, e0119802.
 1336 <https://doi.org/10.1371/journal.pone.0119802>

1337

1338 Real, C., 2016. Estudio arqueozoológico y tafonómico del Magdalenense de la Cova de les Cendres
1339 (Teulada-Moraira, Alicante). Una visión desde la región centra del Mediterraneo ibérico. Ph.D.
1340 Dissertation, University of Valencia, Valencia.

1341

1342 Reitz, E.J., Wing, E.S., 1999. Zooarchaeology. Cambridge University Press, Cambridge.

1343

1344 Rendu, W., Morin, E., 2018. Les comportements de subsistence au Paléolithique moyen dans le Sud-
1345 Ouest de la France. In: Djindjian, F., (Ed.), La Préhistoire de la France. Hermann, Paris, pp. 132-
1346 135.

1347

1348 Rendu, W., Beauval, C., Crevecoeur, I., Bayle, P., Balzeau, A., Bismuth, T., Bourguignon, L., Delfour,
1349 G., Faivre, J.-P., Lacrampe-Cuyaubère, F., Tavormina, C., Todisco, D., Turq, A., Maureille, B.,
1350 2014. Evidence supporting an intentional Neandertal burial at La Chapelle-aux-Saints. Proc. Natl.
1351 Acad. Sci. 111, 81-86. <https://doi.org/10.1073/pnas.1316780110>

1352

1353 Richards, M.P., Trinkaus, E., 2009. Isotopic evidence for the diets of European Neanderthals and early
1354 modern humans. Proc. Natl. Acad. Sci.v106, 16034-16039.
1355 <https://doi.org/10.1073/pnas.0903821106>

1356

1357 Rillardon, M., Brugal, J.-P., 2014. What about the Broad Spectrum Revolution? Subsistence strategy
1358 of huntergatherers in Southeast France between 20 and 8 ka BP. Quatern. Int. 337, 129-153.
1359 <https://doi.org/10.1016/j.quaint.2014.01.020>

1360

1361 Rodríguez-Vidal, J., d'Errico, F., Giles Pacheco, F., Blasco, R., Rosell, J., Jennings, R.P., Queffelec,
1362 A., Finlayson, G., Fa, D.A., Gutiérrez López, J.M., Carrión, J.S., Negro, J.J., Finlayson, S.,
1363 Cáceres, L.M., Bernal, M.A., Fernández Jiménez, S., Finlayson, C., 2014. A rock engraving made
1364 by Neanderthals in Gibraltar. Proc. Natl. Acad. Sci. 111, 13301-13306.
1365 <https://doi.org/10.1073/pnas.1411529111>

1366

1367 Roebroeks, W., Sier, M.J., Nielsen, T.K., De Loecker, D., Parés, J.M., Arps, C.E.S., Múcher, H.J.,
 1368 2012. Use of red ochre by early Neandertals. *Proc. Natl. Acad. Sci.* 109, 1889-1894.
 1369 <https://doi.org/10.1073/pnas.1112261109>
 1370
 1371 Rogers, E.S., 1963. The Hunting Group-Hunting Territory Complex among the Mistassini Indians.
 1372 National Museum of Canada Bulletin 195, Ottawa.
 1373
 1374 Rogers, E.S., 1973. The Quest for Food and Furs: The Mistassini Cree, 1953-1954. National
 1375 Museums of Canada, Ottawa.
 1376
 1377 Rogers, E.S., Smith, D.B., 1994. Aboriginal Ontario: historical perspectives on the First Nations.
 1378 Dundurn Press, Toronto.
 1379
 1380 Romero, A.J., Díez, J.C., Brugal, J.-P., 2017. Aves de caza. Estudio tafonómico y zooarqueológico de
 1381 los restos avianos de los niveles musterienses de Pié Lombard (Alpes-Maritimes, Francia). *Munibe*
 1382 *Antropologia-Arkeologia* 68, 73-84. <https://doi.org/10.21630/maa.2017.68.14>
 1383
 1384 Rosado-Méndez, N.Y., Lloveras, L., Daura, J., Nadal, J., Sanz, M., 2015. Predator agents and leporid
 1385 accumulations: the case of Terrasses de la Riera dels Canyars (Gavà, Barcelona, Spain). *J.*
 1386 *Archaeol. Method Th.* 22, 980-1005. <https://doi.org/10.1007/s10816-014-9214-y>
 1387
 1388 Rufà, A., Blasco, R., Rivals, F., Rosell, J., 2014. Leporids as a potential resource for predators
 1389 (hominins, mammalian carnivores, raptors): An example of mixed contribution from level III of
 1390 Teixoneres Cave (MIS 3, Barcelona, Spain). *CR Palevol* 13, 665-680.
 1391 <https://doi.org/10.1016/j.crpv.2014.06.001>
 1392
 1393 Rufà, A., Blasco, R., Rosell, J., Vaquero, M., 2017. What is going on at the Molí del Salt site? A
 1394 zooarchaeological approach to the last huntergatherers from South Catalonia. *Hist. Biol.* 30, 786-
 1395 806. <https://doi.org/10.1080/08912963.2017.1315685>
 1396

1397 Sanchis Serra, A., 2000. Los restos de *Oryctolagus cuniculus* en las tafocenosis de *Bubo bubo* y
 1398 *Vulpes vulpes* y su aplicación a la caracterización del registro faunístico arqueológico. *Saguntum*
 1399 32, 31-50.
 1400
 1401 Sanchis Serra, A., 2012. Los lagomorfos del Paleolítico medio en la vertiente mediterránea ibérica :
 1402 Humanos y otros predadores como agentes de aporte y alteración de los restos óseos en
 1403 yacimientos arqueológicos, Serie de Trabajos Varios 115. Servicio de Investigación prehistórica -
 1404 Museo de Prehistoria de Valencia, Valencia.
 1405
 1406 Sanchis Serra, A., Fernández Peris, J., 2008. Procesado y consume antrópico de conejo en la Cova
 1407 del Bolomor (Tavernes de la Valldigna, Valencia). *El nivel XVIIc* (ca 350 ka). *Complutum* 19, 25-46.
 1408
 1409 Sanchis Serra, A., Pascual Benito, J.L., 2011. Análisis de las acumulaciones óseas de una guarida de
 1410 pequeños mamíferos carnívoros (Sitjar Baix, Onda, Castellón): implicaciones arqueológicas.
 1411 *Archaeofauna* 20, 47-71.
 1412
 1413 Sanchis Serra, A., Real Margalef, C., Morales Pérez, J.V., Pérez Ripoll, M., Tormo Cuñat, C., Carrión
 1414 Marco, Y., Pérez Jordá, G., Ribera Gómez, A., Bolufer Marqués, J., Villaverde, V., 2014. Towards
 1415 the identification of a new taphonomic agent: An analysis of bone accumulations obtained from
 1416 modern Egyptian vulture (*Neophron percnopterus*) nests. *Quatern. Int.* 330, 136-149.
 1417 <https://doi.org/10.1016/j.quaint.2013.10.047>
 1418
 1419 Sanchis, A., Real, C., Pérez Ripoll, M., Villaverde, V., 2016. El conejo en la subsistencia humana del
 1420 Paleolítico superior inicial en la zona central del Mediterráneo ibérico. In: Lloveras, L., Rissech, C.,
 1421 Nadal, J., Fullola, J.M. (Eds.), *What bones tell us / El que ens expliquen els ossos*. Universitat de
 1422 Barcelona, Barcelona, pp. 145-156.
 1423
 1424 Sarrión, I., Aura, J.E., Pascual Benito, J.L., Tiffagom, M., Sanchís Serra, A., 2008. Primeros datos
 1425 acerca de la ocupación prehistórica de la cueva de los Murciélagos. In: Sendra, A., Ballester, A.

1426 (Eds.), *Les Rodanes, un paraje de cuevas y simas* (Vilamarxant, València). Generalitat Valenciana.
 1427 Federació d'Espeleologia de la Comunitat Valenciana, Valencia, pp. 139-141.
 1428
 1429 Séronie-Vivien, M.-R., 1994. Données sur le lapin azilien. Le matériel du gisement de Pégourié,
 1430 Caniac-du-Causse (Lot). *Bull. Soc. préhist. Française* 91, 378-384.
 1431
 1432 Shaffer, B.S., Sanchez, J.L.J., 1994. Comparison of 1/8"- and 1/4"- mesh recovery of controlled
 1433 samples of small-to-medium-sized mammals. *Am. Antiq.* 59, 525-530.
 1434 <https://doi.org/10.2307/282464>
 1435
 1436 Soffer, O., 1985. *The upper Paleolithic of the Central Russian plain*. Academic Press, London.
 1437
 1438 Soressi, M., d'Errico, F., 2007. Pigments, Gravures, Parures: les comportements symboliques
 1439 controversés des Néandertaliens. In: Vandermeersch, B., Maureille, B., (Eds.), *Les Néandertaliens.*
 1440 *Biologie et cultures, Documents préhistoriques 23*. Éditions du CTHS, Paris, pp. 297-309.
 1441
 1442 Soressi, M., McPherron, S.P., Lenoir, M., Dogandžić, T., Goldberg, P., Jacobs, Z., Maigrot, Y.,
 1443 Martisius, N.L., Miller, C.E., Rendu, W., Richards, M., Skinner, M.M., Steele, T.E., Talamo, S.,
 1444 Texier, J.-P., 2013. Neandertals made the first specialized bone tools in Europe. *Proc. Nat. Acad.*
 1445 *Sci.* 110, 14186-14190. <https://doi.org/10.1073/pnas.1302730110>
 1446
 1447 Soulier, M.-C., Mallye, J.-B., 2012. Hominid subsistence strategies in the South-West of France: A
 1448 new look at the early Upper Palaeolithic faunal material from Roc-de-Combe (Lot, France).
 1449 *Quatern. Int.* 252, 99-108. <https://doi.org/10.1016/j.quaint.2011.03.053>
 1450
 1451 Speck, F.G., 1977. *Naskapi: The Savage Hunters of the Labrador Peninsula*. University of Oklahoma
 1452 Press, Norman.
 1453

1454 Speth, J.D., Spielmann, K.A., 1983. Energy source, protein metabolism, and hunter-gatherer
1455 subsistence strategies. *J. Anthropol. Archaeol.* 2, 1-31. [https://doi.org/10.1016/0278-](https://doi.org/10.1016/0278-4165(83)90006-5)
1456 [4165\(83\)90006-5](https://doi.org/10.1016/0278-4165(83)90006-5)
1457
1458 Stiner, M.C., 1990. The use of mortality patterns in archaeological studies of Hominid predatory
1459 adaptations. *J. Anthropol. Archaeol.* 9, 305-351. [https://doi.org/10.1016/0278-4165\(90\)90010-B](https://doi.org/10.1016/0278-4165(90)90010-B)
1460
1461 Stiner, M.C., 1994. Honor among thieves: a zooarchaeological study of neandertal ecology. Princeton
1462 University Press, Princeton.
1463
1464 Stiner, M.C., 2013. An unshakable Middle Paleolithic? Trends versus conservatism in the predatory
1465 niche and their social ramifications. *Curr. Anthropol.* 54, S288-S304.
1466 <https://doi.org/10.1086/673285>
1467
1468 Stiner, M.C., Munro, N.D., Surovell, T.A., Tchernov, E., Bar-Yosef, O., 1999. Paleolithic population
1469 growth pulses evidenced by small animal exploitation. *Science* 283, 190-194.
1470 <https://doi.org/10.1126/science.283.5399.190>
1471
1472 Stiner, M.C., Munro, N.D., Surovell, T., 2000. The Tortoise and the Hare. Small-Game Use, the Broad-
1473 Spectrum Revolution, and Paleolithic Demography. *Curr. Anthropol.* 41, 39-79.
1474 <https://doi.org/10.1086/300102>
1475
1476 Stringer, C.B., 2002. Modern human origins: progress and prospects. *Phil. Trans. R. Soc. B* 357, 563-
1477 579. <https://doi.org/10.1098/rstb.2001.1057>
1478
1479 Stringer, C.B., Andrews, P., 1988. Genetic and fossil evidence for the origin of modern humans.
1480 *Science* 239, 1263-1268. <https://doi.org/10.1126/science.3125610>
1481
1482 Stringer, C.B., Finlayson, J.C., Barton, R.N.E., Fernández-Jalvo, Y., Cáceres, I., Sabin, R.C., Rhodes,
1483 E.J., Currant, A.P., Rodríguez Vidal, J., Giles Pacheco, F., Riquelme-Cantal, J. A., 2008.

1484 Neanderthal exploitation of marine mammals in Gibraltar. *Proc. Nat. Acad. Sci.* 105, 14319-14324.
 1485 <https://doi.org/10.1073/pnas.0805474105>
 1486
 1487 Teit, J.A., 1906. The Lillooet Indians. *Memoir of the American Museum of Natural History*, New York.
 1488
 1489 Texier, P.-J., 1972. Industries du Paléolithique inférieur et moyen du Var et des Alpes-Maritimes dans
 1490 leur cadre géologique. Ph.D. Dissertation, University of Paris VI, Paris.
 1491
 1492 Texier, P.-J., 1974. L'industrie moustérienne de l'abri Pié Lombard (Tourrettes-sur-Loup, Alpes-
 1493 Maritimes). *Bull. Soc. préhist. Française* 71, 429-448. <https://doi.org/10.3406/bspf.1974.8277>
 1494
 1495 Texier, P.-J., Lemorini, C., Brugal, J.-P., Wilson, L., 1996. Une activité de proto-tannage des peaux
 1496 dans l'habitat moustérien de La Combette (Bonnieux, Vaucluse, France). In: Bietti, A., Grimaldi, S.
 1497 (Eds.), *Reduction processes (« Chaînes opératoires ») for the European Mousterian*. *Quaternaria*
 1498 *Nova VI*, pp. 369-392.
 1499
 1500 Texier, P.-J., Renault-Miskovsky, J., Desclaux, E., de Lumley, M.-A., Porraz, G., Tomasso, A., 2011.
 1501 L'abri Pié Lombard à Tourrettes-sur-Loup (Alpes-Maritimes) : anciennes fouilles (1971-1985),
 1502 nouvelles données. *Bull. Mus. Anthropol. Préhist. Monaco* 51, 19-49.
 1503
 1504 Tomasso, A., 2014. Territoires, systèmes de mobilité et systèmes de production : La fin du
 1505 Paléolithique supérieur dans l'arc liguro-provençal. Ph.D. Dissertation, University of Nice Sophia
 1506 Antipolis, Nice, and University of Pisa, Pisa.
 1507
 1508 Trinkaus, E., 1986. The Neandertals and Modern Human Origins. *Annu. Rev. Anthropol.* 15, 193-218.
 1509 <https://doi.org/10.1146/annurev.an.15.100186.001205>
 1510
 1511 Trinkaus, E., 2007. European early modern humans and the fate of the Neandertals. *Proc. Nat. Acad.*
 1512 *Sci.* 104, 7367-7372. <https://doi.org/10.1073/pnas.0702214104>
 1513

1514 Trinkaus, E., Samsel, M., Villotte, S., 2019. External auditory exostoses among western Eurasian late
 1515 Middle and Late Pleistocene humans. PLoS ONE 14, e0220464.
 1516 <https://doi.org/10.1371/journal.pone.0220464>
 1517
 1518 Ugan, A., 2005. Does size matter? Body size, mass collecting, and their implications for understanding
 1519 prehistoric foraging behavior. *Am. Antiq.* 70, 75-89. <https://doi.org/10.2307/40035269>
 1520
 1521 Val, A., Mallye, J.-B., 2011a. Taphonomie du fouilleur: influence de la maille de tamis sur la
 1522 représentation anatomique des petits animaux à fourrure. In: Laroulandie, V., Mallye, J.-B., Denys,
 1523 C. (Eds.), *Taphonomie des Petits Vertébrés: Référentiels et Transferts aux Fossiles. Actes de la*
 1524 *Table Ronde du RTP Taphonomie, BAR International Series*, pp. 93-100.
 1525
 1526 Val, A., Mallye, J.-B., 2011b. Small Carnivore Skinning by Professionals: Skeletal Modifications and
 1527 Implications for the European Upper Palaeolithic. *Journal of Taphonomy* 9, 221-243.
 1528
 1529 Valensi, P., El Guennouni, K., 2004. Comportements de subsistance et structures d'habitat sur le site
 1530 de plein air de Terra Amata (Paléolithique inférieur, France). In: *Le secrétariat du Congrès (Ed.)*
 1531 *Premiers hommes et Paléolithique Inférieur / Human Origins and the Lower Palaeolithic, General*
 1532 *sessions and posters. BAR International Series, Oxford*, pp. 75-85.
 1533
 1534 Valladas, H., Chadelle, J.-P., Geneste, J.-M., Joron, J.-L., Meignen, L., Texier, P.-J., 1987. Datations
 1535 par la thermoluminescence de gisements moustériens du Sud de la France. *L'Anthropologie* 91,
 1536 211-226.
 1537
 1538 Vigne, J.-D., Marinval-Vigne, M.-C., 1983. Méthode pour la mise en évidence de la consommation du
 1539 petit gibier. In: Clutton-Brock, J., Grigson, C. (Eds.), *Animals and Archaeology: Hunters and their*
 1540 *Prey. BAR International Series, Oxford*, pp. 239-242.
 1541

1542 Vigne, J.-D., Marival-Vigne, M.-C., Lanfranchi, F.d., Weiss, M.-C., 1981. Consommation du Lapin-rat
 1543 (*Prolagus sardus* Wagner) au Néolithique ancien méditerranéen Abri d'Araguina-Sennola
 1544 (Bonifacio, Corse). Bull. Soc. préhist. Française 78, 222-224.
 1545
 1546 Villa, P., Mahieu, E., 1991. Breakage patterns of human long bones. J. Hum. Evol. 21, 27-48.
 1547 [https://doi.org/10.1016/0047-2484\(91\)90034-S](https://doi.org/10.1016/0047-2484(91)90034-S)
 1548
 1549 Villaverde, V., Martínez-Valle, R., Guillem, P.M., Fumanal, M.P., 1996. Mobility and the role of small
 1550 game in the Middle Paleolithic of the central region of the spanish mediterranean: a comparison of
 1551 Cova Negra with other Paleolithic deposits. In: Carbonell, E., Vaquero, M., (Eds.), The Last
 1552 Neandertals, The First Anatomically Modern Humans: A Tale About The Human Diversity.
 1553 Universitat Rovira i Virgili, Tarragona, pp. 267-288.
 1554
 1555 Wadley, L., 2010. Were snares and traps used in the Middle Stone Age and does it matter? A review
 1556 and a case study from Sibudu, South Africa. J. Hum. Evol. 58, 179-192.
 1557 <https://doi.org/10.1016/j.jhevol.2009.10.004>
 1558
 1559 West, D., 1997. Hunting strategie in Central Europe during the last glacial maximum. BAR
 1560 International Serie 672, Oxford.
 1561
 1562 Yokoyama, Y., Quaegebeu, J.-P., Bibron, R., Léger, C., Chappaz, N., Michelot, C., Shen, G.-J.,
 1563 Nguyen, H.-V., 1983. ESR dating of stalagmites of the Caune de l'Arago, the Grotte du Lazaret, the
 1564 Grotte du Vallonnet and the abri Pié Lombard : a comparison with the U-Th method. In: Hackens,
 1565 T., Mejdahl, V., Bowman, S.G.E., Wintle, A.G., Aitken, M.J. (Eds.), Third specialist seminar on TL
 1566 and ESR dating. PACT 9, Strasbourg, pp. 381-389.
 1567
 1568 Yravedra, J., Andrés-Chaín, M., Cacho, C., Martos, J.A., Marquer, L., Avezuela, B., Jordá-Pardo, J.,
 1569 Martín-Lerma, I., Sesé, C., Valdivia, J., 2018. Recurrent Magdalenian occupation in the interior of
 1570 the Iberian Peninsula: new insights from the archaeological site of La Peña de Estebanvela
 1571 (Segovia, Spain). Archaeol. Anthropol. Sci., 1-13. <https://doi.org/10.1007/s12520-018-0620-z>

1572

1573 Zilhão, J., 2011. Aliens from Outer Time? Why the “Human Revolution” Is Wrong, and Where Do We
1574 Go from Here?. In: Condemi, S., Weniger, G.-C. (Eds.), Continuity and Discontinuity in the
1575 Peopling of Europe, Vertebrate Paleobiology and Paleoanthropology. Springer, Dordrecht, pp. 331-
1576 366.

1577

1578 Zilhão, J., Angelucci, D.E., Badal-García, E., d’Errico, F., Daniel, F., Dayet, L., Douka, K., Higham,
1579 T.F.G., Martínez-Sánchez, M.J., Montes-Bernárdez, R., Murcia-Mascarós, S., Pérez-Sirvent, C.,
1580 Roldán-García, C., Vanhaeren, M., Villaverde, V., Wood, R., Zapata, J., 2010. Symbolic use of
1581 marine shells and mineral pigments by Iberian Neanderthals. Proc. Nat. Acad. Sci. 107, 1023-
1582 1028. <https://doi.org/10.1073/pnas.0914088107>

1583

1584 **Figure captions (color online only)**

1585

1586 **Figure 1 (2 columns).** Location of the Pié Lombard rock-shelter.

1587

1588 **Figure 2 (2 columns).** Stratigraphy of Pié Lombard (after Texier et al., 2011). A. Plan of the site and
1589 location of the Paleolithic deposits (excavation 1971-1986); B. View of the excavation in 1974; C.
1590 sagittal profile in squares C/D 3-5.

1591

1592 **Figure 3 (1 or 1,5 column).** Mortality profiles for the Pié Lombard Mousterian complex (**PL**) and other
1593 reference collections. BI = Bettant I, BVIII = Bettant VIII (Mallye et al., 2008), FA = fox accumulation
1594 (outside the den), FD = fox den (inside the den), ABI = Aigües de Busot I, ABII = Aigües de Busot II,
1595 PZ = Penya la Zafra (Sanchis Serra, 2000), BC = Benaxuai Caves (Sanchis Serra et al., 2014), CV3 =
1596 El Conjunto de Coveta 3 (Sanchis Serra and Pascual Benito, 2011), LSC = Les Six Chemins (Pelletier
1597 et al., 2016), VAU = Vaufrey (Cochard, 2007), CAN = Les Canalettes (Cochard et al., 2012), AN =
1598 Anecrial (Brugal, 2006), LFII = La Faurélie II (Cochard, 2004a). Diagram divisions correspond to those
1599 proposed by Discamps and Costamagno (2015): JOP = Juveniles-Old-Prime, JPO = Juveniles-Prime-
1600 Old, P = Prime, O = Old. Confidence intervals have been omitted for clarity.

1601

Figure 4 (2 columns). Pié Lombard Mousterian skeletal-part representation (**PL**), as well as those of the other reference collections. Attritional death in a rabbit-warren (Pelletier et al., 2016); accumulations by terrestrial carnivores as the red fox (Sanchis Serra and Pascual Benito, 2011), the European badger (Mallye et al., 2008) and the dhole (Cochard, 2007); accumulations by birds of prey (golden eagle from Lloveras et al., 2017) and the eagle-owl (nest **2** and nest **1** from Lloveras et al., 2009); and anthropogenic accumulation from Les Canalettes (**C**, Cochard et al., 2012), Arbreda cave (**A**, Lloveras et al., 2016), La Faurélie II (**F**, Cochard, 2004a), and Gazel cave (**G**, Fontana, 2003). Rectangles represent 95% confidence intervals.

Figure 5 (2 columns). Examples of rabbit shaft cylinders from the Pié Lombard Mousterian complex.

Figure 6 (2 columns). Cut-marks from Pié Lombard resulting from different processing activities, such as skinning, defleshing and disarticulation. Numbers between brackets indicates number of cut-marks per bones. %RA: percentage of relative abundance of the rabbit elements. The coxal bone (dark grey), not taken into account in this study.

Table captions

Table 1 (2 columns). The Pié Lombard Mousterian faunal assemblage. MNI: Minimum number of individuals.

Table 2 (1 column). Rabbit skeletal elements identified in the Mousterian complex from Pié Lombard. NISP = number of identified skeletal parts, MNE = minimum number of elements, RA = relative abundance.

Table 3 (1 column). Proportions of different parts of the skeleton in the Mousterian complex from Pié Lombard, along with 95% confidence intervals. For the definition of the indices see the section concerning the "Anatomical representation of rabbits".

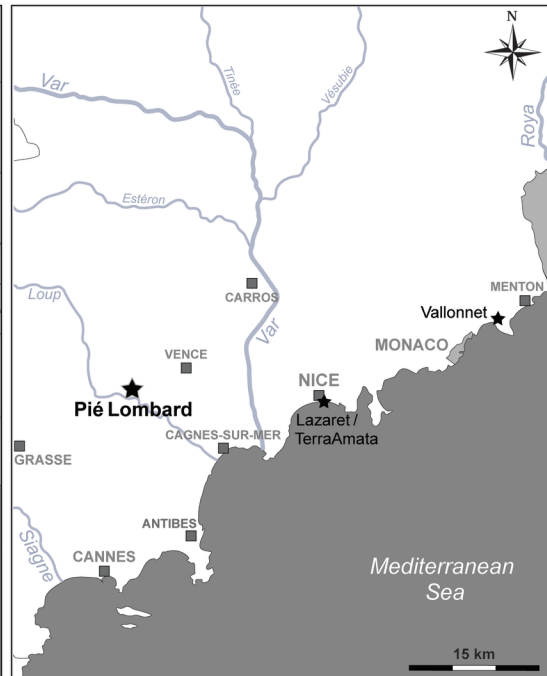
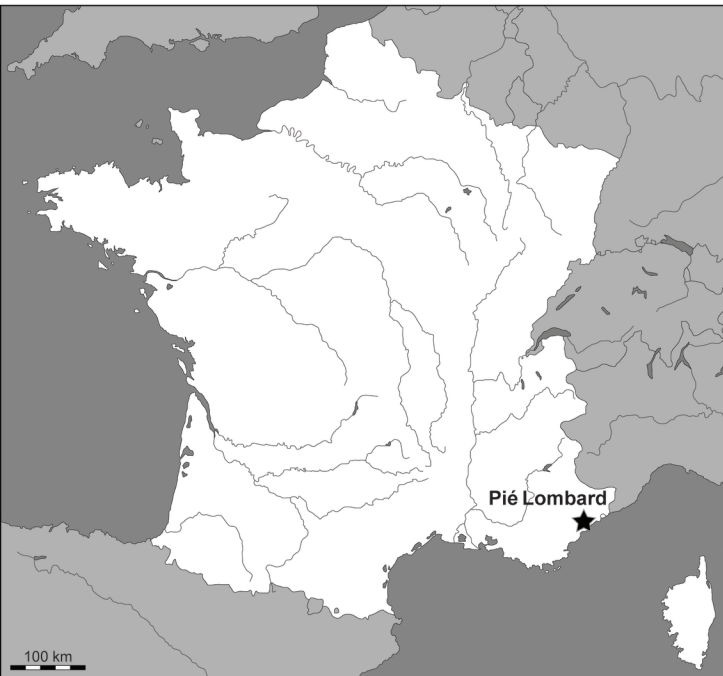
1631 **Table 4** (2 column). Numbers and percentages of rabbit skeletal elements from the Pié Lombard
1632 Mousterian complex included in each breakage category. Cranium as complete (C), incisive bone (IB),
1633 incisive bone + maxilla (IBM), maxilla (M), zygomatic arch (ZA) and neurocranium (NC). Mandibles as
1634 complete (C), incisive part (IP), mandible body + incisive part (MBI), mandible body (MB), mandible
1635 body + branch (MBB) and condylar process (CP). Scapula as complete (C), glenoid cavity (GC),
1636 glenoid cavity + neck (GCN), glenoid cavity + neck + fossa (GCNF), neck + fossa (NF) and fossa (F).
1637 Long bones (humerus, radius, ulna, femur, tibia), metacarpal and metatarsal bones were classified as
1638 complete (C), proximal epiphysis (PE), proximal epiphysis + shaft (PES), shaft (S), shaft + distal
1639 epiphysis (SDE) and distal epiphysis (DE). Vertebrae as complete (C), vertebral body (VB), vertebral
1640 epiphysis (VE) and spinous process (SP). Phalanges as complete (C), proximal fragment, (P), distal
1641 fragment (D) and fragment (F). Patella, carpals, tarsals (calcaneus, talus, cuboid, cuneiform,
1642 navicular), ribs and teeth as complete (C) and fragment (F).
1643

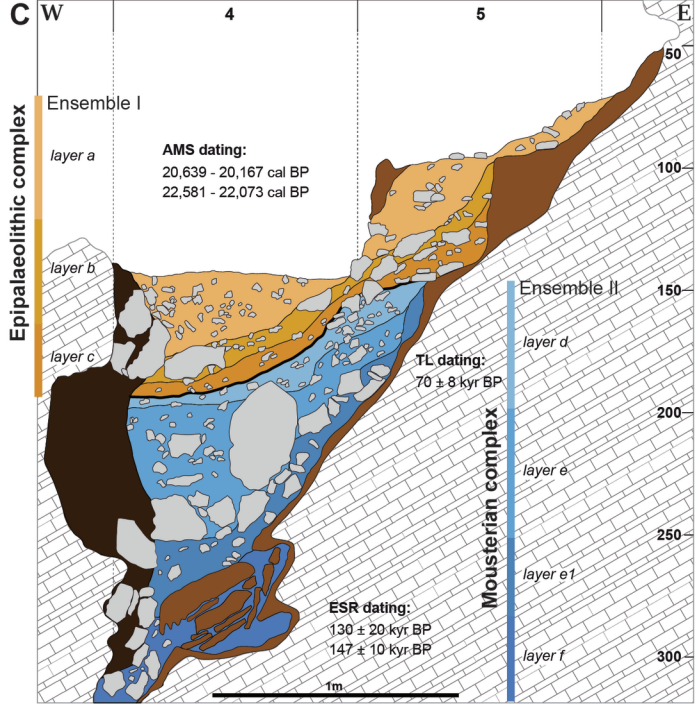
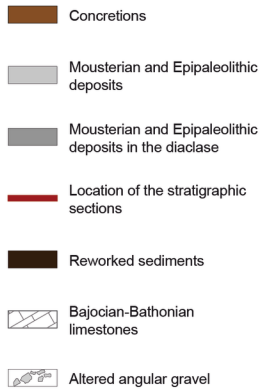
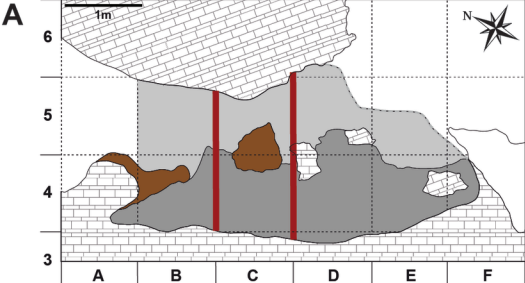
1644 **Table 5** (2 column). Fracture angle and fracture outline frequencies for rabbit long bones from the Pié
1645 Lombard Mousterian complex. N = effective, NISP = number of identified specimens.
1646

1647 **Table 6** (1 column). Distribution of cut-marks, burnt bones, digestion damage and tooth marks on
1648 rabbit bones by anatomical part in Mousterian complex from Pié Lombard. N = effective, NISP =
1649 number of identified specimens.
1650

1651 **Table 7** (1 column). Average total weight values, average meat weight and average calorie values for
1652 meat weight for several faunal species present during the Paleolithic of southwestern Europe (from
1653 Brugal, 2005 and Cole, 2017).
1654

1655 **Table 8** (2 columns). Caloric intake of rabbits compared to large herbivores from different Paleolithic
1656 deposits in Western Europe. MNI fauna for Terra Amata (from Valensi and El Guennouni, 2004),
1657 Bolomor cave (from Blasco and Fernández Peris, 2012), Lazaret cave (from Lumley et al., 2004),
1658 Arbreda cave (from Lloveras et al. 2016), La Peña de Estebanvela (from Yravedra et al. 2018), Molí
1659 del Salt (from Rufà et al., 2017). Raw data available in Table 7.





Accumulator agents :



Rabbit-Warren



Eagle-Owl



Red Fox



European Badger



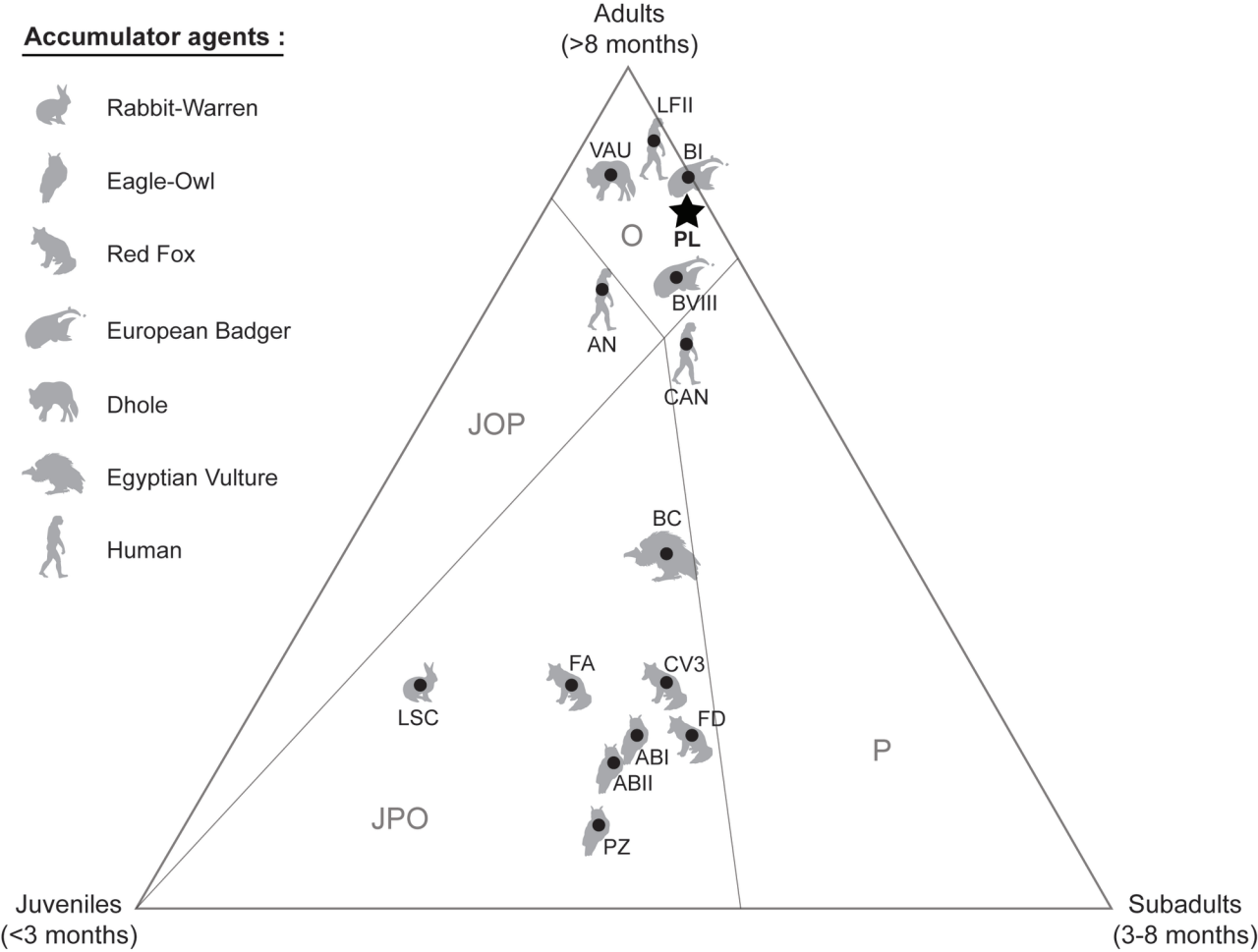
Dhole

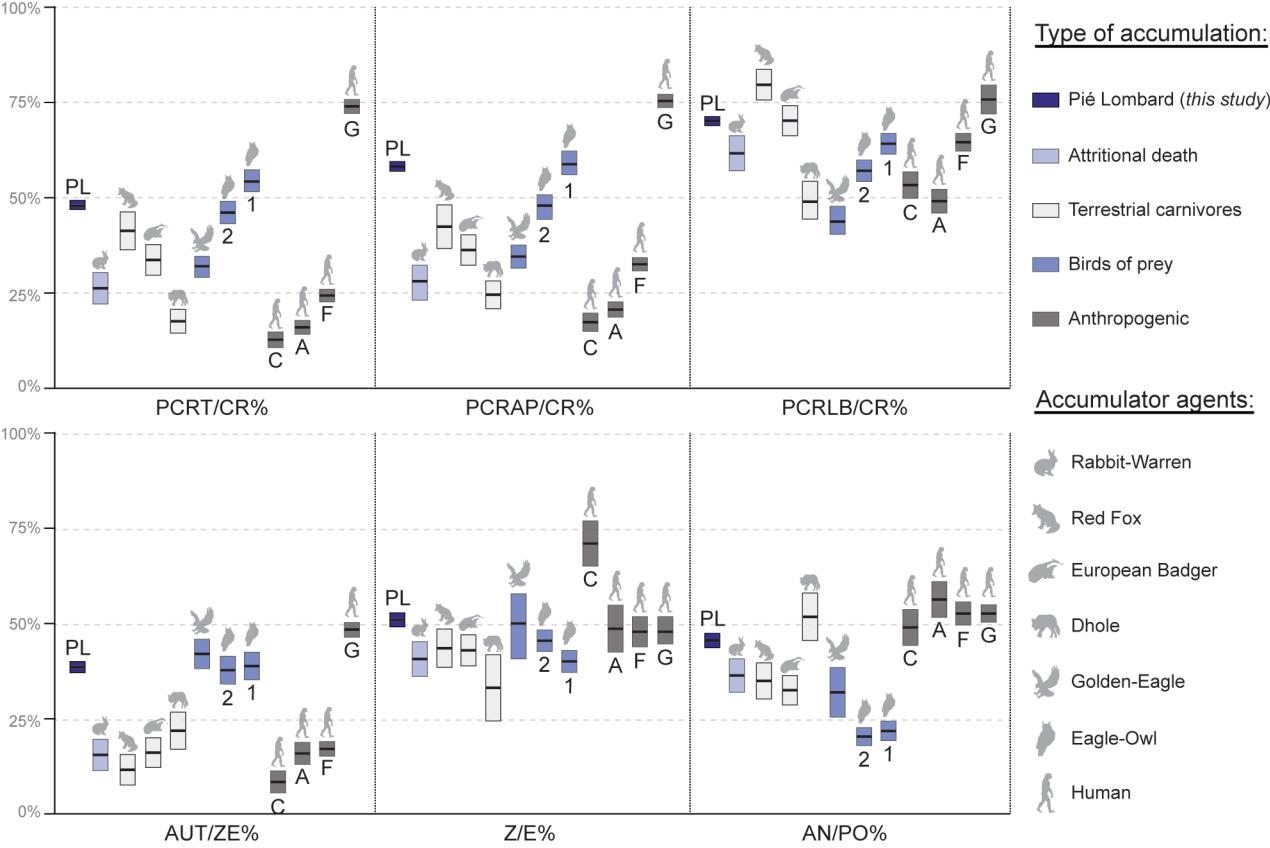


Egyptian Vulture



Human







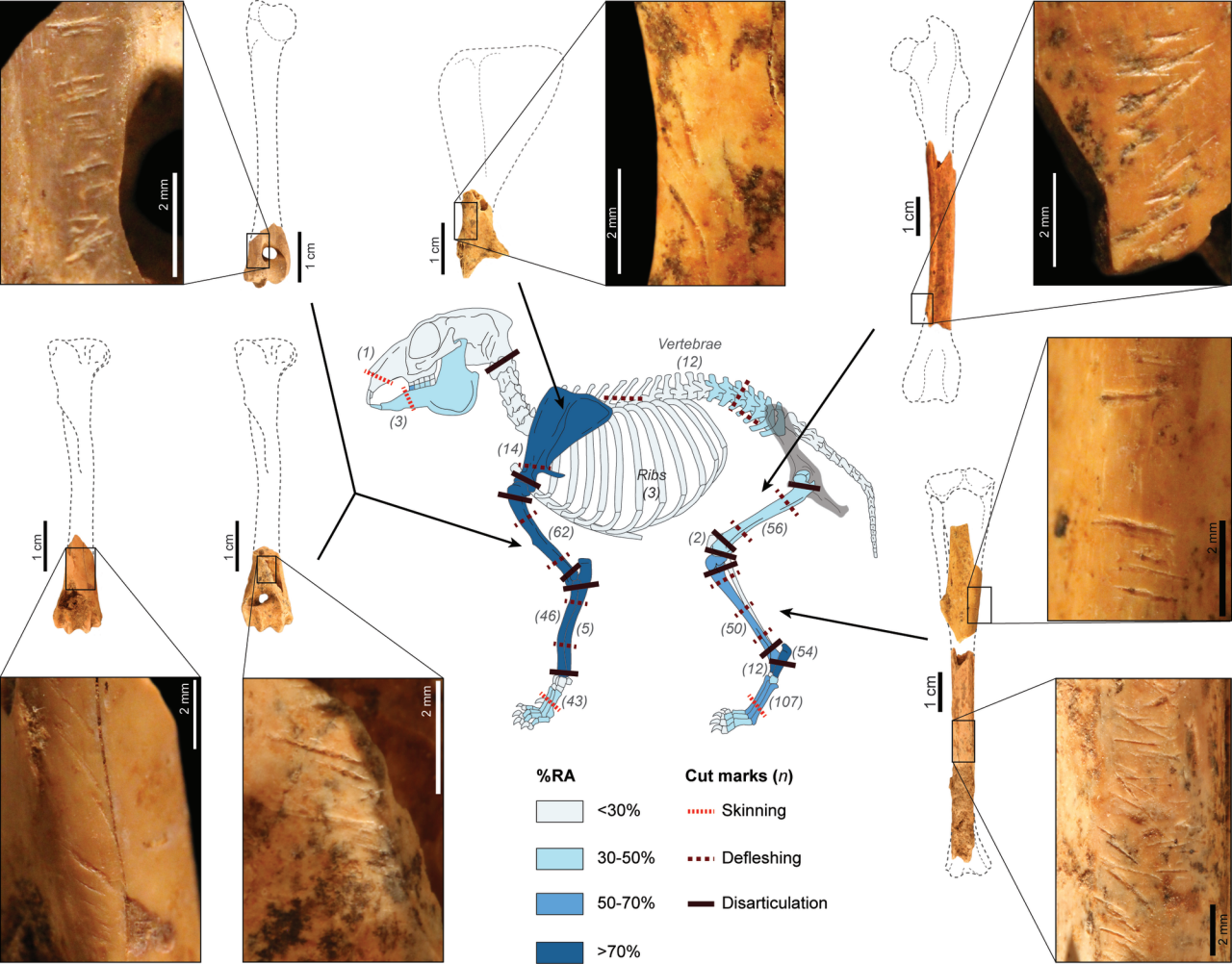


Table 1 (2 columns). The Pié Lombard Mousterian faunal assemblage. MNI: Minimum number of individuals.

Species	MNI	Species	MNI
CARNIVORA		INSECTIVORA	
<i>Felis silvestris</i>	2	<i>Talpa europaea</i>	2
<i>Lynx</i> sp.	2	<i>Crocidura</i> sp.	3
<i>Panthera pardus</i>	2		
<i>Vulpes vulpes</i>	1	AMPHIBIA	
<i>Canis lupus</i>	2	<i>Bufo bufo</i>	x
<i>Cuon</i> sp.	1		
<i>Ursus arctos</i>	4	REPTILIA	
		<i>Lacerta viridis</i>	x
PROBOSCIDEA		<i>Anguis fragilis</i>	x
<i>Elephas</i> sp.	(1)*		
ARTIODACTYLA		ANSERIFORMES	
<i>Bos primigenius</i>	1	<i>Anas platyrhynchos</i>	3
<i>Cervus elaphus</i>	15	<i>Mergus merganser</i>	X
<i>Sus scrofa</i>	1	<i>Tadorna tadorna</i>	X
<i>Capra ibex</i>	23		
<i>Dama dama</i>	1	ACCIPITRIFORMES	
<i>Rupicapra rupicapra</i>	3	<i>Aquila chrysaetos</i>	1
<i>Capreolus capreolus</i>	2	<i>Buteo buteo</i>	x
PERISSODACTYLA			
<i>Equus caballus</i>	2	COLUMBIFORMES	
		<i>Columba livia</i>	23
LAGOMORPHA		<i>Columba palumbus</i>	1
<i>Oryctolagus cuniculus</i> (this study)	225		
RODENTIA		GALLIFORMES	
<i>Apodemus sylvaticus</i>	22	<i>Alectoris graeca</i>	7
<i>Marmota marmota</i>	1	<i>Perdix perdix</i>	5
<i>Castor fiber</i>	3	<i>Lagopus</i> sp.	1
<i>Eliomys quercinus</i>	10		
<i>Glis glis</i>	1	PASSERIFORMES	
<i>Arvicola amphibius</i>	4	<i>Garrulus glandarius</i>	1
<i>Microtus arvalis</i>	2	<i>Pyrrhocorax graculus</i>	48
<i>Chionomys nivalis</i>	5	<i>Pyrrhocorax pyrrhocorax</i>	15
<i>Myodes glareolus</i>	2	<i>Corvus corax</i>	5
<i>Microtus duodecimcostatus</i>	5	<i>Corvus corone</i>	2
		<i>Hirundo rustica</i>	1
CHIROPTERA		<i>Ptyonoprogne rupestris</i>	5
<i>Rhinolophus ferrumequinum</i>	1	<i>Carduelis carduelis</i>	1
<i>Rhinolophus euryale</i>	1	<i>Coccothraustes coccothraustes</i>	2
<i>Miniopterus schreibersi</i>	1	<i>Anthus cf. campestris</i>	5
<i>Myotis myotis</i>	1	<i>Turdus merula</i>	1
<i>Myotis bechsteini</i>	1	<i>Turdus cf. viscivorus</i>	1
		STRIGIFORMES	
		<i>Athene noctua</i>	x
		<i>Aegolius funereus</i>	x

* one small fragment of tusk

Table 2 (1 column). Rabbit skeletal elements identified in the Mousterian complex from Pié Lombard. NISP = number of identified skeletal parts, MNE = minimum number of elements, RA = relative abundance.

	NISP	%NISP	MNE	%RA
Cranium	341	2.1	109	24.2
Mandible	269	1.7	146	32.4
Incisor	259	1.6	259	19.2
Upper molar	531	3.3	531	19.7
Lower molar	957	6.0	957	42.5
Scapula	434	2.7	354	78.7
Humerus	586	3.6	429	95.3
Radius	619	3.8	371	82.4
Ulna	433	2.7	316	70.2
Metacarpals	1,000	6.2	719	39.9
Carpals	120	0.7	120	6.7
Femur	438	2.7	186	41.3
Patella	70	0.4	70	15.6
Tibia	727	4.5	277	61.6
Metatarsals	1,763	11.0	1,021	56.7
Calcaneus	462	2.9	425	94.4
Talus	417	2.6	387	86.0
Cuboid	216	1.3	216	48.0
Cuneiform	109	0.7	109	8.1
Navicular	259	1.6	257	57.1
Proximal phalanx	2,123	13.2	1,886	46.6
Mesial phalanx	1,326	8.2	1,306	36.3
Distal phalanx	1,114	6.9	1,108	27.4
Vertebrae	1,057	6.6	675	7.5
Rib	420	2.6	314	5.9
Sternebrae	8	0.0	8	0.7
Sesamoids	9	0.1	9	-
Undetermined frag.	17	0.1	-	-
Total	16,084		12,568	

Table 3 (1 column). Proportions of different parts of the skeleton in the Mousterian complex from Pié Lombard, along with 95% confidence intervals. For the definition of the indices see the section concerning the "Anatomical representation of rabbits".

Index	
PCRT/CR%	48.1 \pm 0.8
PCRAP/CR%	57.9 \pm 0.9
PCRLB/CR%	70.1 \pm 0.8
AUT/ZE%	38.7 \pm 0.9
AN/PO%	45.8 \pm 1.4
Z/E%	51.1 \pm 2.5

Table 4 (2 column). Numbers and percentages of rabbit skeletal elements from the Pié Lombard Mousterian complex included in each breakage category. Cranium as complete (C), incisive bone (IB), incisive bone + maxilla (IBM), maxilla (M), zygomatic arch (ZA) and neurocranium (NC). Mandibles as complete (C), incisive part (IP), mandible body + incisive part (MBI), mandible body (MB), mandible body + branch (MBB) and condylar process (CP). Scapula as complete (C), glenoid cavity (GC), glenoid cavity + neck (GCN), glenoid cavity + neck + fossa (GCNF), neck + fossa (NF) and fossa (F). Long bones (humerus, radius, ulna, femur, tibia), metacarpal and metatarsal bones were classified as complete (C), proximal epiphysis (PE), proximal epiphysis + shaft (PES), shaft (S), shaft + distal epiphysis (SDE) and distal epiphysis (DE). Vertebrae as complete (C), vertebral body (VB), vertebral epiphysis (VE) and spinous process (SP). Phalanges as complete (C), proximal fragment, (P), distal fragment (D) and fragment (F). Patella, carpals, tarsals (calcaneus, talus, cuboid, cuneiform, navicular), ribs and teeth as complete (C) and fragment (F).

Breakage category											
Cranium	<i>n</i>	%	Mandible	<i>n</i>	%	Scapula	<i>n</i>	%	Humerus	<i>n</i>	%
C	0	0.0	C	0	0.0	C	1	0.2	C	2	0.3
IB	31	9.1	IP	46	17.1	GC	89	20.5	PE	40	6.8
IBM	0	0.0	MBI	87	32.3	GCN	189	43.5	PES	28	4.8
M	150	44.0	MB	79	29.4	GCNF	72	16.6	S	80	13.7
ZA	48	14.1	MBB	38	14.1	NF	53	12.2	SDE	298	50.9
NC	112	32.8	PC	19	7.1	F	30	6.9	DE	138	23.5
Radius	<i>n</i>	%	Ulna	<i>n</i>	%	Metacarpals	<i>n</i>	%	Femur	<i>n</i>	%
C	2	0.3	C	0	0.0	C	378	37.8	C	0	0.0
PE	33	5.3	PE	26	6.0	PE	8	0.8	PE	144	32.9
PES	337	54.4	PES	91	21.0	PES	297	29.7	PES	43	9.8
S	148	23.9	S	266	61.4	S	13	1.3	S	111	25.3
SDE	82	13.2	SDE	18	4.2	SDE	248	24.8	SDE	9	2.1
DE	17	2.7	DE	32	7.4	DE	56	5.6	DE	131	29.9
Tibia	<i>n</i>	%	Metatarsals	<i>n</i>	%	Vertebrae	<i>n</i>	%	Ribs	<i>n</i>	%
C	1	0.1	C	190	10.8	C	134	12.7	C	10	2.4
PE	40	5.5	PE	21	1.2	VB	696	65.8	F	410	97.6
PES	47	6.5	PES	733	41.6	VE	83	7.9			
S	362	49.8	S	74	4.2	SP	144	13.6			
SDE	151	20.8	SDE	541	30.7						
DE	126	17.3	DE	204	11.6						
Patella	<i>n</i>	%	Prox. Phal.	<i>n</i>	%	Mes. Phal.	<i>n</i>	%	Dist. Phal.	<i>n</i>	%
C	68	97.1	C	1495	70.4	C	1200	90.5	C	1101	98.8
F	2	2.9	P	391	18.4	P	106	8.0	F	13	1.2
			D	237	11.2	D	20	1.5			
Carpals	<i>n</i>	%	Calcaneus	<i>n</i>	%	Talus	<i>n</i>	%			
C	117	97.5	C	267	57.8	C	295	70.7			
F	3	2.5	F	195	42.2	F	122	29.3			
Cuboid	<i>n</i>	%	Cuneiform	<i>n</i>	%	Navicular	<i>n</i>	%			
C	198	91.7	C	108	99.1	C	217	83.8			
F	18	8.3	F	1	0.9	F	42	16.2			

Table 5 (2 column). Fracture angle and fracture outline frequencies for rabbit long bones from the Pié Lombard Mousterian complex. N = effective, NISP = number of identified specimens.

	Ancient break				Recent break	Total of long bone break	Total of long bones	NISP
	Fracture angles		Fracture outline					
	Oblique (green)	Right (dry)	V-shaped (green)	Transverse (dry)				
<i>N</i>	656	165	679	142	149	970	2803	16,084
% of breaks	67.6%	17.0%	70.0%	14.6%	15.4%	100%	-	-
%NISP	4.1%	1.0%	4.2%	0.9%	0.9%	34.6%	17.4%	100%

Table 6 (1 column). Distribution of cut-marks, burnt bones, digestion damage and tooth marks on rabbit bones by anatomical part in Mousterian complex from Pié Lombard. N = effective, NISP = number of identified specimens.

	<i>Cut marks</i>		<i>Burnt bones</i>		Digestion damage		Pits / Punctures	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Cranium	1	0.2	35	2.4	3	0.7	-	-
<i>Incisive bone</i>	1	0.2	6	0.4	-	-	-	-
<i>Petrous part</i>	-	-	3	0.2	1	0.2	-	-
<i>Maxillary</i>	-	-	19	1.3	-	-	-	-
<i>Neurocranium</i>	-	-	7	0.5	2	0.5	-	-
Mandible	3	0.6	21	1.4	3	0.7	2	6.1
Incisor	-	-	13	0.9	3	0.7	-	-
Upper molar	-	-	11	0.8	14	3.3	-	-
Lower molar	-	-	14	1.0	5	1.2	-	-
Scapula	14	2.9	56	3.8	23	5.4	8	24.2
Humerus	62	12.9	90	6.1	13	3.1	-	-
Radius	46	9.6	69	4.7	25	5.9	2	6.1
Ulna	5	1.0	47	3.2	17	4.0	1	3.0
Metacarpals	43	8.9	90	6.1	26	6.1	-	-
<i>Metacarpal II</i>	10	2.1	20	1.4	6	1.4	-	-
<i>Metacarpal III</i>	3	0.6	14	1.0	6	1.4	-	-
<i>Metacarpal IV</i>	7	1.5	14	1.0	2	0.5	-	-
<i>Metacarpal V</i>	16	3.3	9	0.6	6	1.4	-	-
<i>Metacarpal NS</i>	7	1.5	33	2.3	6	1.4	-	-
Carpals	-	-	3	0.2	1	0.2	-	-
Femur	56	11.6	65	4.4	24	5.7	6	18.2
Patella	2	0.4	8	0.5	7	1.7	-	-
Tibia	50	10.4	102	7.0	7	1.7	1	3.0
Metatarsals	107	22.2	149	10.2	25	5.9	3	9.1
<i>Metatarsal II</i>	26	5.4	27	1.8	4	0.9	1	3.0
<i>Metatarsal III</i>	10	2.1	31	2.1	1	0.2	-	-
<i>Metatarsal IV</i>	10	2.1	19	1.3	11	2.6	-	-
<i>Metatarsal V</i>	31	6.4	24	1.6	4	0.9	-	-
<i>Metatarsal NS</i>	30	6.2	48	3.3	5	1.2	2	6.1
Calcaneus	54	11.2	44	3.0	22	5.2	4	12.1
Talus	12	2.5	54	3.7	38	9.0	-	-
Cuboid	1	0.2	23	1.6	4	0.9	1	3.0
Cuneiform	-	-	8	0.5	4	0.9	-	-
Navicular	1	0.2	18	1.2	6	1.4	1	3.0
Proximal phalanx	-	-	194	13.2	51	12.0	1	3.0
Mesial phalanx	-	-	108	7.4	32	7.5	1	3.0
Distal phalanx	-	-	90	6.1	53	12.5	-	-
Vertebrae	12	2.5	107	7.3	14	3.3	2	6.1
<i>Atlas</i>	2	0.4	7	0.5	-	-	-	-
<i>Axis</i>	1	0.2	5	0.3	1	0.2	-	-
<i>Cervical vertebrae</i>	-	-	25	1.7	5	1.2	-	-
<i>Thoracic vertebrae</i>	4	0.8	25	1.7	1	0.2	1	3.0
<i>Lombar vertebrae</i>	5	1.0	37	2.5	5	1.2	1	3.0
<i>Sacrum</i>	-	-	3	0.2	-	-	-	-
<i>Caudal vertebrae</i>	-	-	4	0.3	-	-	-	-
<i>Vertebrae nd</i>	-	-	1	0.1	2	0.5	-	-
Rib	8	1.7	30	2.0	1	0.2	-	-
Sternebrae	-	-	1	0.1	-	-	-	-
Sesamoids	-	-	1	0.1	-	-	-	-
Undetermined frag.	4	0.8	14	1.0	3	0.4	-	-
Total	481	100	1,466	100	424	100	33	100
%NISP	3.0	-	9.1	-	2.6	-	0.2	-

Table 7 (1 column). Average total weight values, average meat weight and average calorie values for meat weight for several faunal species present during the Paleolithic of southwestern Europe (from Brugal, 2005 and Cole, 2017).

	Average total weight (kg)	Average meat weight (kg)	Kilocalorie value / Kg (meat)	Kilocalorie value / individual (meat)
<i>Bos primigenius</i>	687.5	412.5	2.04	841.50
<i>Capra ibex</i>	75.0	45.0	1.09	49.05
<i>Capreolus capreolus</i>	24.5	14.7	1.00	14.70
<i>Cervus elaphus</i>	165.0	99.0	1.24	122.76
<i>Dama dama</i>	71.3	42.8	1.24	53.01
<i>Equus caballus</i>	287.5	172.5	1.15	198.38
<i>Equus hydruntinus</i>	225.0	135.0	1.15	155.25
<i>Hemitragus bonali</i>	75.0	45.0	1.09	49.05
<i>Megaloceros giganteus</i>	480.0	288.0	1.24	357.12
<i>Rupicapra rupicapra</i>	41.3	24.8	1.05	25.99
<i>Sus scrofa</i>	102.5	61.5	4.00	246.00
<i>O. cuniculus</i>	1.8	1.5	1.07	1.61

Table 8 (2 columns). Caloric intake of rabbits compared to large herbivores from different Paleolithic deposits in Western Europe. MNI fauna for Terra Amata (from Valensi and El Guennouni, 2004), Bolomor cave (from Blasco and Fernández Peris, 2012), Lazaret cave (from Lumley et al., 2004), Arbreda cave (from Lloveras et al. 2016), La Peña de Estebanvela (from Yravedra et al. 2018), Molí del Salt (from Rufà et al., 2017). Raw data available in Table 7.

Period	Site (layer)	Date	Taxa (MNI)	Average meat weight (kg)	Kilocalorie value (meat)	Caloric intake of rabbits compared to large herbivores
Lower Paleolithic	Terra Amata (layer C1b)	MIS 11	Rabbit (19)	29	30	0.38%
			Total herbivores (33)	3599	7942	
Middle Paleolithic	Bolomor cave (layer XVIIc)	MIS 9	Rabbit (12)	18	19	0.94%
			Total herbivores (10)	1402	2039	
	Bolomor cave (layer XII)	MIS 7	Rabbit (10)	15	16	0.22%
			Total herbivores (30)	5043	7420	
	Lazaret cave (UA25)	MIS 6	Rabbit (25)	38	40	0.70%
			Total herbivores (34)	3824	5683	
	Bolomor cave (layer XI)	MIS 6	Rabbit (7)	10	11	0.55%
			Total herbivores (10)	1402	2039	
	Bolomor cave (layer IV)	MIS 5e	Rabbit (20)	30	32	0.44%
			Total herbivores (34)	4234	7324	
	Les Canalettes (layer 4)	MIS 5a	Rabbit (56)	84	90	0.60%
			Total herbivores (66)	10136	14881	
	Pié Lombard (ensemble II)	MIS 5a	Rabbit (225)	338	361	7.23%
			Total herbivores (48)	3486	4632	
Upper Paleolithic	Arbreda (layer G)	MIS 3	Rabbit (43)	65	69	1.64%
			Total herbivores (14)	2610	4145	
	Estebanvela (layer I)	MIS 2	Rabbit (210)	315	337	8.76%
			Total herbivores (32)	2904	3511	
	Molí del Salt (layer A)	MIS 2	Rabbit (455)	683	730	23.93%
			Total herbivores (16)	1238	2321	