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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-03017473
The exploitation of rabbits for food and fur by late MIS 5 Neandertals

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Abstract word count: 260; Main text word count: 8,191

Figures: 6; Tables: 8

Highlights:

- The largest known assemblage of rabbit remains consumed by Middle Palaeolithic humans

- Pié Lombard represents a unique case of the intense exploitation of rabbits by Neandertals

- Late MIS 5 appears as a period where small game was regularly exploited
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 (MIS 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 hitherto 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 the early Late Pleistocene.

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 so-called "modern" behaviours. Increasing evidence of the behavioral, social and cultural “modernity” of Neandertals is in no small part due to new fieldwork at previously excavated sites and the re-evaluation of old collections using new analytical approaches. 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., Gerber, 1973 = ne mentionne pas la chasse au lapin !!; Brown et al., 2011; 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 a major role in Palaeolithic socio-economic systems in Western Europe. The remains of leporids are frequently found in archaeological sites where in some cases they constitute 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 Palaeolithic 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 Palaeolithic is related to the demographic growth of human groups. The gradual increase in the density of rabbit remains in different Upper Palaeolithic 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).ref Fontana ?

The regular incorporation of small game during earlier periods, particularly the Middle Palaeolithic, 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; Morin et al., 2019), in many cases a significant portion of the rabbit remains can be tied
to 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 leporid accumulation
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 the preferential prey of more than 40
predators (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/context. 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 end of MIS 5, or transitional with MIS 4 (Texier et al., 2011). Here we present a
detailed taphonomical and zooarchaeological analysis of the large assemblage of rabbit
bones recovered from this important 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 small 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 250 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 diaclase 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 diaclase, 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 to 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 heavily-altered lithic material (n=81). 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 rich 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 ESR dates of 147 ± 10 kyr and 130 ± 20 kyr BP (Yokoyama et al., 1983). The Mousterian lithic industry comprises 902 pieces, most of which are retouched and attributable to the Levallois method. 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 respectively to 60 and 240 km (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 cooler 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).

The site of Pié Lombard was initially hypothesised as a possible place in carnivore’s fur exploitation activities (Brugal and Jaubert, 1996) but no clear evidence support it; carnivores used the rocks-shelter as natural location (natural death, reproductive place) and occupied the site for long and different periods of time (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. During our study, we paid particular attention to the identification of coxal bones, noting only a limited number of coxal bone fragments (NISP=50) mixed with the other previously sorted anatomical elements. This pattern suggests that coxal bones were 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 different data sources 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). Accord-
ing 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 type 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) does not accurately distinguish males from females in a reproducible manner (Pelletier et al., 2015). Indeed, 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
Relative abundance (RA) was calculated using the formula proposed by Dodson and Wexlar (1979):

\[
\%RA = \frac{\text{MNE}}{\text{MNI} \times \text{E}} \times 100
\]

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:

\[
\text{PCRT/CR\%} = \frac{(\text{PCRT} \times 32)}{(\text{PCRT} \times 32) + (\text{CR} \times 182)} \times 100
\]

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);

\[
\text{PCRAP/CR\%} = \frac{(\text{PCRAP} \times 32)}{(\text{PCRAP} \times 32) + (\text{CR} \times 112)} \times 100
\]

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

\[
\text{PCRLB/CR\%} = \frac{(\text{PCRLB} \times 32)}{(\text{PCRLB} \times 32) + (\text{CR} \times 10)} \times 100
\]
with PCRLB calculated as the total number of long bones (humerus, radius, ulna, femur, and tibia);

- \( \text{AUT/ZE}\% = \left( \frac{\text{AUT} \times 12}{\text{AUT} \times 12 + \text{ZE} \times 98} \right) \times 100 \)

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

- \( \text{AN/PO}\% = \left( \frac{\text{AN} \times 12}{\text{AN} \times 12 + \text{PO} \times 16} \right) \times 100 \)

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

- \( \text{Z/E}\% = \left( \frac{\text{Z} \times 4}{\text{Z} \times 4 + \text{E} \times 6} \right) \times 100 \)

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 in order to estimate their overall proportions and characterize and 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).
Break type was equally recorded for each bone element following Lloveras et al. (2008) and applied in several subsequent studies (e.g., Lloveras et al., 2009a, 2012b, 2014a, 2016):

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

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

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

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

- **Vertebrae** were recorded as complete (C), vertebral body (VB), vertebral epiphysis (VE) or spinous process (SP);

- **Phalanges** were recorded as complete (C), proximal fragment, (P), distal fragment (D) or fragment (F);

- **Patella, carpals, tarsals** (calcaneus, talus, cuboid, cuneiform, and navicular), ribs and teeth were classified as complete (C) or fragmentary (F). For teeth, breakage was recorded separately depending on whether teeth were found isolated or still set in the mandible (Fernández-Jalvo and Andrews, 1992).
All remains were observed under a light reflecting microscope (40x magnification) in order to systematically describe bone surface alterations. Evidences of non-human predation (i.e., digestion, tooth/beak marks) were counted for each element, as were traces of human modifications such as cut-marks or burning.

3. Results

3.1. Mortality profile

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

The Pié Lombard profile is distinct from those generated by solitary small-predators, such as foxes or eagle-owls, who preferentially prey upon juveniles with smaller body sizes (Fig. 3). It is also substantially different from modern warrens, which are characterised by higher numbers of both juvenile individuals and infants (Pelletier et al., 2016). Moreover, age profiles produced by solitary predators and typical of warrens are also characterized by greater proportions of immature individuals. This is not the case with the Pié Lombard profile, which is much more similar to those generated by larger predators such as badgers, dholes, or humans. In fact, the Pié Lombard mortality profile falls within the “old” (O) zone of the 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 Mousterian complex at Pié Lombard 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, 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 ribs, carpals, vertebrae and cuneiform are scarce (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 bones elements (i.e., PCRAP/CR% and PCRLB/CR%; Table 3). The AUT/ZE% index shows a deficit of the autopodia compared to the zygodia (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).
Balanced between the anterior and posterior elements allows a clear link with the anthropogenic accumulations.

3.3. Bone breakage: frequency and type

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

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

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

4.1. The origin of the Pié Lombard rabbit assemblage

Despite differences in the relative abundance of certain skeletal elements, the overall anatomical representation of rabbits at Pié Lombard suggests that whole carcasses were introduced to the site. Most potential rabbit predators transport whole carcasses and they can also mimic the pattern typically observed for warrens as an attritional mortality. However, infants are more present in warren and only leave the place 2 to 3 weeks after birth (Biadi and Le Gall, 1993). Their presence in a deposit could suggest a warren and a potential bioturbation of archaeological layers (Pelletier et al., 2016, 2017). Most predators, including humans, lynx, dholes, eagles or badgers, tend to focus primarily on adults which generally comprise at least 80% of an assemblage (Hockett, 1991; Hockett and Bicho, 2000; Jones, 2004; Cochard, 2004a, 2007; Brugal, 2006; Mallye et al., 2008; Lloveras et al., 2011, 2016, 2017; Cochard et al., 2012; Rillardon and Brugal, 2014; Rosado-Méndez et al., 2015; Arriaza et al., 2017; Rufà et al., 2017). Taken together, the absence of infant remains at Pié Lombard and an assemblage dominated by adult individuals (82%) is in good overall agreement with an accumulation produced by a large predator.

Anatomical profiles produced by terrestrial predators are generally similar, especially when complete carcasses are transported. In the anthropogenic assemblages, the best-represented elements are generally mandibles, long bones, scapula and coxal bones (Hockett, 1991; Hockett et Haws, 2002; Cochard, 2004a; Brugal, 2006; Lloveras et al., 2016) which is the case with the Pié Lombard assemblage (except for coxal bones, which were excluded from our study; see section 2.2). Accumulations generated by lynx, skeletal profiles tend to be characterised by a higher abundance of cranial remains and an over-representation of forelimb bones compared to those of the hindlimbs (Lloveras et al., 2008). The Pié Lombard profile is clearly distinct from this pattern, particularly in the under-
representation of cranial elements. It can look like accumulations produced by some raptors but these tend to focus essentially on immature individuals (Sanchis Serra, 2000; Cochard, 2004b; Lloveras et al., 2009a; Sanchis Serra et al., 2014) and severe ??!! 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) 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 .. wet line 156-157 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 suggests a particular context. Skeletal representation of rabbit remains in the Pié Lombard strongly suggests a human origin. Its assemblage falls between the anthropogenic accumulations such as the Mousterian occupation of Les Canalettes (Cochard et al., 2012), the Late Aurignian (sic) Aurignacian 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 culture ? 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 yield 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 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 is 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. 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 Marinval-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., Géroudet, 1984; Bayle, 1992; Lloveras et al., 2014a, 2014b, 2017; Sanchis Serra et al., 2014). This confirms 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.

4.2. Function of the Pié Lombard site

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

Unlike the mixed origin of the avian assemblage, the rabbit remains from Pié Lombard were primarily transported to the site by Neandertal groups. The Pié Lombard rabbit’s assemblage demonstrates that whole carcasses have been brought and butchered on-site and bones broken to access marrow. At Les Canalettes, the low rate of burned bones (<1%) led Cochard (2004a) to suggest that carcasses were boiled rather than roasted. At Pié Lombard, the relatively high rate of burned bones (9%) suggests that rabbit carcasses were roasted rather than boiled. Rabbits can be roasting directly after been skinned without having first dismembered the carcass (Rufà et al., 2017). Moreover, disarticulation and defleshing are in fact easier after roasting, and do not require the use of tools, which could explain the low number of cut-marks observed on the remains.
Although it is still difficult to definitely demonstrate the processing of leporid pelts by prehistoric hunter-gatherers (e.g., Cochard, 2004a; Mally et al., 2018), numerous cut-marks 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 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 furs for tanning beyond 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 metapodians 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 (Julien and Pillard, 1969; Soffer, 1985; Alhaïque, 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 give 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 biased 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 extremely 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 could not be linked to the under-representation of the autopodial.

Whether rabbits were sought specifically for their fur or first and foremost as a source of food remain 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 with the manufacturing of clothes, either for group members or as trade goods, is also impossible. Substantial ethnographic and archaeological evidence, however, attests to the importance of leporid fur 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), bird feathers (Peresani et al., 2011; Finlayson et al., 21012; Fiore et al., 2016), small to medium carnivore teeth (Caron et al. 2011; Soulier and Mallye, 2012), and shells (Stringer et al., 2008; Mellars, 2010; Zilhão et al.,
In view of the high number of rabbit remains present at Pié Lombard, it is reasonable to assume that this small prey played an important role in the socio-economic practices of Neandertal groups in southern France during MIS 5-4.

Taken together, there is sufficient evidence from Pié Lombard demonstrating rabbits to have been roasted and consumed on the site, with their pelts subsequently processed and transported away. Moreover, the numerous cut-marks, burnt bones and shaft cylinders are all consistent with what is commonly found on Upper Paleolithic sites and is readily comparable with the Mousterian rabbit assemblage from Les Canalettes. The Neandertal groups who occupied Pié Lombard therefore exploited rabbits in the same way as Upper Paleolithic anatomically modern humans. Interestingly, while it is generally accepted that rabbits were of secondary importance in the Neandertal diet due to a significantly lower caloric return compared to ungulates (Table 7), the large number of rabbits at Pié Lombard provided at least 226 kg of meat, representing more than 7% of the group's overall caloric intake (Table 8)…si on considère que tous les herbivores sont apportés par l'homme ce qui n'est pas le cas ?…moduler la phrase. This value is much higher than what is known on other Mousterian sites. Indeed, rabbit generally constituted less than 1% of the energy intake of the Mousterian groups, with its role in the human diet increasing significantly in the Upper Paleolithic, especially during the Magdalenian (Table 8) in France (Cochard and Brugal, 2004). The exploitation of small game (rabbits and birds) at Pié Lombard departs markedly from this pattern. The large number of rabbits (Table 1) suggests they were the principal focus of Neandertal subsistence practices at Pié Lombard and may reflect difficulties in accessing the rockshelter and hence an emphasis on more easily transported small game rather than large herbivores….mouais, mais lieu pas terrible pour warren d'une part, et Caprid apporté assez complété aussi…pas trop lourd Il faut revoir cette ‘fin’
4.3. The exploitation of rabbits by Neandertal societies: a regional and repetitive phenomenon?

Prior to the Upper Paleolithic in southwestern Europe, it is generally assumed that small game was rarely exploited by humans (Stiner, 2013). Consequently, the place of rabbits in the Neandertal diet has been the subject of considerable debate. When present in Middle Paleolithic assemblages, taphonomic analyses have generally demonstrated rabbits to have been primarily accumulated by carnivores or raptors (Defleur et al., 1994; Blasco, 1995; Martínez-Valle, 1996; Fernández-Jalvo and Andrews, 2000; El Guennouni, 2001; Hockett, 2006; Lloveras et al., 2011; Sanchis Serra, 2012). Evidence of human modifications on rabbit remains is uncommon, and Neandertals are often considered to have played very minor role in their accumulation. For example, while the Mousterian assemblages from Bolomor Cave (NISP=457, MNI=49; Blasco and Fernández-Peris, 2012), Arbreda Cave (NISP=1,317, MNI=43; Lloveras et al., 2010), Les Canalettes (NISP=1,627, MNI=58; Cochard et al., 2012), Columbeira Cave (NISP=1,784; Carvalho et al., 2018), El Salt (NISP=1,789; Pérez et al., 2017), or Teixoneres Cave (NISP=3,964, MNI=49; Rufà et al., 2014) contain a limited number of rabbit remains, only Bolomor Cave and Les Canalettes produced robust evidence for a rabbit accumulation linked to more long-term, repetitive Neandertal occupations. In this respect, the over 16,000 rabbit remains and the presence of least 225 individuals make the Pié Lombard assemblage not only unique for the Middle Palaeolithic but readily comparable to hominid accumulations found from Upper Paleolithic sites such as: Les Cendres Cave (NISP=14,976, MNI=337; Real, 2016), La Faurélie II (NISP=15,569, MNI=87; Cochard, 2004a), Arbreda Cave (NISP=17,700, MNI=43; Lloveras et al., 2016) or Molí del Salt (NISP=22,627, MNI=445; Rufà et al., 2017). With this being the case, how best to interpret the exceptional number of rabbits in Middle Paleolithic assemblage from Pié Lombard? It is often argued that Upper Palaeolithic hunter-gatherers most likely adapted their subsistence strategies 1) depending on the availability of different preys in the landscape; 2) as response to increasing group size and social structure; or 3) following profound changes in socio-
economic organization in connection with settlement patterns and resource management (e.g., Stiner et al., 1999, 2000; Aura et al., 2002; Cochard and Brugal, 2004). Similar behaviours have partially been demonstrated for several Middle Paleolithic sites in southwestern Europe based on the zooarchaeological analyses of large (e.g., Discamps et al., 2011; Morin et al., 2014; Rendu and Morin, 2018) and/or small mammals (e.g., Sanchis Serra and Fernández Peris, 2008; Blasco and Fernández Peris, 2012; Blasco et al., 2014). These research raise question on 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, almost 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 (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, where 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 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 uncontestable, 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). Although we acknowledge 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 = verifier orthographe de ce site 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 Paleolthic 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 knowledge of their ecosystem and paleobiodiversity and implement 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). It would come of no surprise that some of these techniques were used at Pié Lombard. 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 the current state of debate 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 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 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 (leporids, carnivores, birds,…) 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 small game, potentially requiring 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

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

Acknowledgments

We wish to thank Marie Matu and Patrice Courtaud for granting us access to the “Ostéothèque de Pessac” to study some of the material. We thank the LAMPEA for their help and support of this research. We are very grateful to Brad Gravina for his constructive comments. = je ne vois pas cela en coparant les deux versions, et trouve que la traduction n’est pas top…mais bien sur je ne suis pas Anglophone, mais…bof !

Author contributions

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Fontana, L., 2003. Characterization and exploitation of the arctic hare (Lepus timidus) during the Magdalenian: surprising data from Gazel Cave (Aude, France). In: Costamagno, S., Laroulandie,


Figure captions (color online only)

Figure 1 (2 columns). Location of the Pié Lombard rock-shelter.
Figure 2 (2 columns). Stratigraphy of Pié Lombard (after Texier et al., 2011). A. Plan of the site and location of the Paleolithic deposits (excavation 1971-1986); B. View of the excavation in 1974; C. sagittal profile in squares C/D 3-5.

Figure 3 (1 or 1.5 column). Mortality profiles for the Pié Lombard Mousterian complex (PL) and other reference collections. BI = Bettant I, BVIII = Bettant VIII (Mallye et al., 2008), FA = fox accumulation (outside the den), FD = fox den (inside the den), ABI = Aïguës de Busot I, ABII = Aïguës de Busot II, PZ = Penya la Zafra (Sanchis Serra, 2000), BC = Benaxuai Caves (Sanchis Serra et al., 2014), CV3 = El Conjunto de Coveta 3 (Sanchis Serra and Pascual Benito, 2011), LSC = Les Six Chemins (Pelletier et al., 2016), VAU = Vaufrey (Cochard, 2007), CAN = Les Canalettes (Cochard et al., 2012), AN = Anecrial (Brugal, 2006), LFII = La Faurélie II (Cochard, 2004a). Diagram divisions correspond to those proposed by Discamps and Costamagno (2015): JOP = Juveniles-Old-Prime, JPO = Juveniles-Prime-Old, P = Prime, O = Old. Confidence intervals have been omitted for clarity.

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 Lomabrd 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.
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".

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).

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.
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.

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).

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.