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1 **The exploitation of rabbits for food and fur by late MIS 5 Neandertals**

2

3 Maxime PELLETIER<sup>1, 2,\*</sup>, Emmanuel DESCLAUX<sup>3, 4</sup>, Jean-Philip BRUGAL<sup>2</sup>, Pierre-Jean TEXIER<sup>2</sup>

4

5 <sup>1</sup>Department of Archaeology, History, Culture and Communication Studies, Faculty of Humanities, University of  
6 Oulu, Oulu, Finland

7

8 <sup>2</sup>Aix Marseille Univ, CNRS, Minist Culture, LAMPEA, Aix-en-Provence, France

9

10 <sup>3</sup>Laboratoire départemental de Préhistoire du Lazaret, Nice, France

11

12 <sup>4</sup>Université Côte d'Azur, CNRS, CEPAM, Nice, France

13

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

15

16

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21

22 **Highlights:**

23

24 • The largest known assemblage of rabbit remains consumed by Middle Palaeolithic  
25 humans

26

27 • Pié Lombard represents a unique case of the intense exploitation of rabbits by  
28 Neandertals

29

30 • Late MIS 5 appears as a period where small game was regularly exploited

31

32 **Abstract**

33

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

55

56

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

59

## 60 1. Introduction

61

62 The behavioural complexity and flexibility of the Neandertals, as well as their cognitive  
63 capacities compared with anatomically modern humans, continues to attract significant  
64 attention from paleoanthropologists and prehistorians. Changes in subsistence strategies or  
65 the development of symbolic practices amongst Neandertal societies are commonly  
66 considered as evidence for the emergence so-called "modern" behaviours. Increasing  
67 evidence of the behavioral, social and cultural "modernity" of Neandertals is in no small part  
68 due to new fieldwork at previously excavated sites and the re-evaluation of old collections  
69 using new analytical approaches. We now know that these groups developed remarkably  
70 similar behaviours to anatomically modern humans, including the burial of their dead (Pettitt,  
71 2002, 2011; Rendu et al., 2014), personal ornaments (Zilhão et al., 2010; Finlayson et al.,  
72 2012; Radovčić et al., 2015), pigment processing (Soressi and d'Errico, 2007; Roebroeks et  
73 al., 2012; Hoffmann et al., 2018a; Dayet et al., 2019, Pitarch Martí et al., 2019), the  
74 manufacture of bone tools (d'Errico et al., 2012; Soressi et al., 2013), rock art (Rodríguez-  
75 Vidal et al., 2014; Hoffmann et al., 2018b), frequent aquatic resource exploitation (Trinkaus  
76 et al., 2019), and the construction of complex structures deep within karstic cave systems  
77 (Jaubert et al., 2016). In terms of subsistence practices, although the majority of evidence  
78 suggest Neandertals primarily focused on ungulates (e.g., Richards and Trinkaus, 2009;  
79 Discamps et al., 2011; Rendu and Morin, 2018), recent research indicates a more substantial  
80 contribution of small game to the diet, including leporids (e.g., Gerber, 1973 = ne mentionne  
81 pas la chasse au lapin !!; Brown et al., 2011; Cochard et al., 2012; Hardy et al., 2013), birds  
82 (Blasco et al., 2014, 2016; Romero et al., 2017; Gómez-Olivencia et al., 2018), small  
83 terrestrial carnivores (Soulie and Mallye, 2012; Gabucio et al., 2014; Gómez-Olivencia et al.,  
84 2018), tortoises (Blasco, 2008; Nabais and Zilhão, 2019), and marine resources (Stringer et  
85 al., 2008; Brown et al., 2011; Gutiérrez-Zugasti et al., 2018).

86

87 Amongst these small preys, the European rabbit (*Oryctolagus cuniculus*) is of particular  
88 interest, as they sometimes occupied a major role in Palaeolithic socio-economic systems in  
89 Western Europe. The remains of leporids are frequently found in archaeological sites where  
90 in some cases they constitute the most abundant species (e.g., Pelletier, 2018). The first  
91 European evidence for the exploitation of these small mammals dates to the Middle  
92 Pleistocene, around 400-350 kyr BP (Desclaux, 1992; El Guennouni, 2001; Sanchis and  
93 Fernández Peris, 2008; Blasco and Fernández Peris, 2012). However, whether Middle  
94 Palaeolithic hunter-gatherers regularly exploited rabbits remains an open question. Several  
95 studies have highlighted the systematic acquisition (hunting and / or trapping) and  
96 consumption of rabbits to be uniquely associated with Upper Paleolithic anatomically modern  
97 humans (Stiner, 1994; Villaverde et al., 1996; Stiner et al., 1999, 2000; Aura et al., 2002;  
98 Hockett and Haws, 2002; Cochard and Brugal, 2004; Pérez Ripoll, 2004; Lloveras et al.,  
99 2011; Fa et al., 2013). For example, Stiner et al. (1999) argue that the significant increase of  
100 leporids in the human diet at the end of the Upper Paleolithic is related to the demographic  
101 growth of human groups. The gradual increase in the density of rabbit remains in different  
102 Upper Paleolithic techno-complexes would equally reflect profound cultural changes in the  
103 socio-economic organization of human groups (Cochard and Brugal, 2004). In fact, despite  
104 the typically low return rates compared to ungulates (Speth and Spielmann, 1983; Ugan,  
105 2005), the socio-economic potential of leporids is also reflected by the fact that both their  
106 bones and pelts can be exploited (e.g., Hockett, 1994; d'Errico and Laroulandie, 2000;  
107 Fontana, 2003; Cochard, 2005).ref Fontana ?

108

109 The regular incorporation of small game during earlier periods, particularly the Middle  
110 Paleolithic, has been questioned by some researchers who argue that Neandertals, unlike  
111 modern humans, lacked the cognitive capacity and / or a sufficiently well-developed  
112 technology for regularly exploiting small game (Stiner et al., 1999; Fa et al., 2013). While it is  
113 now clear that Neandertal groups did consume rabbits (Gerber, 1973 ??; Blasco, 1995;  
114 Sanchis and Fernández Peris, 2008; Brown et al., 2011; Blasco and Fernández Peris, 2012;

115 Cochard et al., 2012; Hardy et al., 2013; Rufà et al., 2014; Pérez et al., 2017; Carvalho et al.,  
116 2018; Morin et al., 2019), in many cases a significant portion of the rabbit remains can be tied  
117 to carnivores or raptors (El Guennouni, 2001; Lloveras et al., 2010, 2011; Sanchis Serra,  
118 2012; Rufà et al., 2014). Understanding the agent(s) responsible for the leporid accumulation  
119 in Middle Paleolithic contexts is thus essential for providing insights on this aspect of  
120 Neandertal subsistence behavior.

121

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

135

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

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

144

## 145 **2. Material and Methods**

146

### 147 *2.1. Pié Lombard rock-shelter*

148

149 The site of Pié Lombard is located near the small town of Tournettes-sur-Loup (Alpes-  
150 Maritimes, France), on the east bank of the Loup River, 9 km from the Mediterranean Sea  
151 and 15 km south of the Alpine foothills (Fig. 1). Situated 250 meters a.s.l, this small  
152 rockshelter in Bajocian-Bathonian (Middle Jurassic) limestone was exposed following karstic  
153 erosion. Discovered in 1962 by an amateur prospector (A. Mellira), the site yielded  
154 Mousterian lithics and Upper Pleistocene faunal remains (Lumley-Woodyear, 1969).  
155 Excavations at the site were directed by one of us (P.-J.T.) as part of a larger analysis of the  
156 region's Middle Palaeolithic archaeological record (Texier, 1972, 1974). The exhaustive  
157 excavation of the rockshelter's archaeostratigraphic sequence, which included the systematic  
158 wet-sieving of sediments (using 5, 2 and 0.4 mm sieve meshes), was carried out mainly  
159 between 1971 and 1975, accompanied by fieldwork in 1983 and 1985, and a final excavation  
160 season in 1996. This work recovered a significant amount of lithic and bone remains  
161 accumulated in a diacalse at the front of the rock-shelter. The three-meter deep  
162 archaeological sequence was documented in a four meter long and less than one metre wide  
163 trench (Fig. 2).

164

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

169

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

177

178 • A rich Mousterian complex (ensemble II) (1,000 lithics and fauna per m<sup>2</sup>) subdivided  
179 into 5 lithological layers (*d*, *e*, *e1*, *f*, *g*) and attributed to the MIS 5 to 4 transition based on a  
180 thermoluminescence (TL) date of  $70 \pm 8$  kyr BP (Valladas et al., 1987). Stalagmites  
181 supporting Mousterian sediments returned ?! two ESR dates of  $147 \pm 10$  kyr and  $130 \pm 20$   
182 kyr BP (Yokoyama et al., 1983). The Mousterian lithic industry comprises 902 pieces, most of  
183 which are retouched and attributable to the Levallois method. Semi-local and allochthonous  
184 raw materials are most common, with transfer distances not exceeding 40 km. However,  
185 several microquartzite and jasper pieces derive from sources found respectively to 60 and  
186 240 km (Porraz, 2005). In terms of faunal remains, 16 species of large mammals have been  
187 identified (Table 1) from around 2,500 identifiable elements and several thousand bone  
188 splinters (Texier et al., 2011; Romero et al., 2017). Among herbivores, Alpine ibex (*Capra*  
189 *ibex*) and red deer (*Cervus elaphus*) dominate the Mousterian complex, representing 63%  
190 and 30% (NISP) of the assemblage, respectively, and are accompanied by a limited number  
191 of chamois remains (*Rupicapra rupicapra*; 4%). The carnivore assemblage is dominated by  
192 panther (*Panthera pardus*), wolf (*Canis lupus*) and lynx (*Lynx spelaea*) and includes juvenile  
193 remains of panther and brown bear (*Ursus arctos*). Preliminary zooarchaeological data  
194 indicate that, while Neandertal groups are clearly responsible for the introduction of several  
195 deer and ibex carcasses, it is impossible to exclude a contribution from other predators (e.g.  
196 wolf, leopard, and lynx) to the ungulate assemblage. Except for the lagomorphs, which are  
197 represented by a single species, the European rabbit *O. cuniculus*, the Mousterian deposits



198 yielded a relatively diversified small vertebrates collection comprising 45 species (Table 1; 1  
199 lagomorph, 2 reptiles, 1 amphibian, 2 insectivores, 5 bats, 10 rodents, and 24 birds). A  
200 combination of malacological, palynological and faunal data is consistent with cooler climatic  
201 conditions than experience today in the region and typified by wooded and open areas with a  
202 marked Mediterranean influence. Finally, the site produced two deciduous incisors attributed  
203 to a Neandertal individual of between 2 and 4 years of age (Texier et al., 2011).

204  
205 The site of Pié Lombard was initially hypothesized as a possible place in carnivore's fur  
206 exploitation activities (Brugal and Jaubert, 1996) but no clear evidence support it ; carnivores  
207 used the rocks-shleter as natural location (natural death, reproductive place) and occupied  
208 the site for long and different periods of time (Texier et al., 2011; Romero et al., 2017).  
209 Despite the difficult access to the site during the Pleistocene, Neandertals nevertheless  
210 imported deer or ibex carcasses for immediate consumption in the rock-shelter. It is likely  
211 that Pié Lombard functioned as a seasonal basecamp incorporated within a well-developed  
212 territorial system rather than as short stay hunting camp (Texier et al., 2011). In addition, it  
213 has been recently demonstrated that Neandertals were equally responsible for part of the  
214 bird remains from Pié Lombard primarily as a food source and potentially for the use of their  
215 feathers (Romero et al., 2017).

216

## 217 *2.2. The rabbit assemblage*

218

219 The rabbit assemblage from the Mousterian complex consists of more than 16,000 bones,  
220 which were conditioned and stored by anatomical part during the exhaustive sorting of the  
221 small vertebrate remains. During our study, we paid particular attention to the identification of  
222 coxal bones, noting only a limited number of coxal bone fragments (NISP=50) mixed with the  
223 other previously sorted anatomical elements. This pattern suggests that coxal bones were  
224 present during excavations and the subsequent conditioning of the material, meaning that  
225 the limited number of specimens is highly unlikely to reflect a taphonomic bias. We assume

226 that the box containing the missing coxal bones was lost during the relocation of the  
227 collections. In order to avoid biases when comparing the Pie Lombard assemblage with other  
228 studies, we excluded this element from all analyzes.

229

230 As multiple taphonomical criteria are shared by several accumulating agents (e.g., Cochard,  
231 2007, 2008; Lloveras et al., 2010; Pelletier et al., 2016), it remains difficult to reliably identify  
232 the origin of rabbit assemblages recovered from archaeological sites. This being the case,  
233 we integrated four different data sources to investigate the nature of the accumulation:  
234 mortality profiles, skeletal-part representation, bone breakage and bone surface  
235 modifications.

236

#### 237 *2.2.1. Mortality profile of rabbits*

238

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

243

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

247

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

250

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

253

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

255

256 It has recently been shown that age structure models of rabbit populations can help to  
257 identify acquisition strategies, predator behaviors or the type of accumulation (Pelletier et al.,  
258 2016, 2017). Although age distributions may depend on the type of the predator, the season  
259 of capture and / or geography (e.g., Cochard 2004b, 2008; Lloveras et al., 2012a; Arriaza et  
260 al., 2017), and that several accumulator agents (e.g., foxes and eagle-owls) produce very  
261 similar mortality profiles; they nevertheless rule out certain predators that prey almost  
262 exclusively on adult individuals, such as medium-to-large sized carnivores (i.e., badgers,  
263 dholes, lynx), large birds of prey (i.e., eagles, vultures), and humans (Hockett, 1991;  
264 Cochard, 2004a, 2007; Mallye et al., 2008; Lloveras et al., 2011, 2014a, 2016, 2017;  
265 Cochard et al., 2012; Pelletier et al., 2016, 2017). Age structure can also be useful for  
266 identifying or excluding several potential species known to prey on rabbits. For this study, we  
267 used ternary diagrams (Stiner, 1990) modified after Discamps and Costamagno (2015) and  
268 specifically adapted for rabbit populations by Pelletier et al. (2016).

269

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

276

### 277 *2.2.2. Anatomical representation of rabbits*

278

279 The number of identified specimens (NISP), minimum number of skeletal elements (MNE)  
280 and the minimum number of individuals (MNI) were calculated for each skeletal element

281 (Reitz and Wing, 1999; Lyman, 2008). Relative abundance (RA) was calculated using the  
282 formula proposed by Dodson and Wexlar (1979):

283

284 • 
$$\%RA = [MNE/(MNI * E)] * 100$$

285

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

290

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

295

296 • 
$$PCRT/CR\% = [(PCRT * 32) / ((PCRT * 32) + (CR * 182))] * 100$$

297

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

300

301 • 
$$PCRAP/CR\% = [(PCRAP * 32) / ((PCRAP * 32) + (CR * 112))] * 100$$

302

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

305

306 • 
$$PCRLB/CR\% = [(PCRLB * 32) / ((PCRLB * 32) + (CR * 10))] * 100$$

307

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

310

311 • 
$$\mathbf{AUT/ZE\%} = [(AUT * 12) / ((AUT * 12) + (ZE * 98))] * 100$$

312

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

315

316 • 
$$\mathbf{AN/PO\%} = [(AN * 12) / ((AN * 12) + (PO * 16))] * 100$$

317

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

320

321 • 
$$\mathbf{Z/E\%} = [(Z * 4) / ((Z * 4) + (E * 6))] * 100$$

322

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

324

### 325 *2.2.3. Bone breakage and surface modifications*

326

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

335

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

338

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

341

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

345

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

348

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

352

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

355

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

358

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

363

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

368

### 369 **3. Results**

370

#### 371 *3.1. Mortality profile*

372

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

380

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

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

392

### 393 *3.2. Anatomical representation*

394

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

403

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



417 phrase...Balanced between the anterior and posterior elements allows a clear link with the  
418 anthropogenic accumulations.

419

### 420 *3.3. Bone breakage: frequency and type*

421

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

427

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

438

439 In terms of long bones, all breakage categories were found among which fragments of  
440 diaphysis are most abundant. Humerus and tibia are most often represented by distal  
441 epiphyses, while proximal epiphyses of radius, ulna and femur fragments are more frequent  
442 (Table 4). Thirty-five percent of all long bones are represented by shaft cylinder fragments,  
443 with nearly 20% representing the humerus, femur and tibia (Fig. 5). Most long bone fractures  
444 concern green bone (Table 5) and are characterized by an oblique fracture angle (68%) and

445 a V-shaped profile (70%). Dry bone breaks with a right fracture angle (17%) and a transverse  
446 fracture profile (15%) are less common, and result from post-depositional processes.  
447 Approximately 15% of bone breakage is modern, probably occurring during excavation  
448 and/or cleaning.

449

#### 450 *3.4. Bone surface modifications*

451

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

460

461 Most of the bone surface modifications can be attributed to human activity. A total of 481  
462 bony elements (3% of NISP), primarily long bones (n=219), display cut-marks (Fig. 6; Table  
463 6). Cut-marks are also frequent on metacarpals (n=43) and metatarsals (n=107), and  
464 concern mainly lateral metapods, such as the metacarpal II (n=10) and V (n=16), and  
465 metatarsal II (n=26) and V (n=31). A significant number of cutmarks were also recorded on  
466 the calcaneus (n = 54), talus (n = 12) and scapula (n = 14). On the long bones, most cut-  
467 marks were located on shafts and near the epiphyses and are almost always transverse to  
468 the principal axis of the bone. Traces of burning are evident on 9% of NISP and are not  
469 concentrated on any particular portion of the skeleton; 15% of cases concern the epiphyses,  
470 with long bones, the calcaneus, talus, metapodials and phalanges most commonly affected  
471 (Table 6).

472

## 473 **4. Discussion**

474

### 475 *4.1. The origin of the Pié Lombard rabbit assemblage*

476

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

491

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

501 representation of cranial elements. It can look like to accumulations produced by some  
502 raptors but these tend to focus essentially on immature individuals (Sanchis Serra, 2000;  
503 Cochard, 2004b; Lloveras et al., 2009a; Sanchis Serra et al., 2014) and **severe ???!** the limbs  
504 and / or head before transporting the most nutritious parts for consumption elsewhere  
505 (Donazar, 1988).

506

507 Can this particular skeletal-part representation of Pié Lombard be connected to the  
508 differential preservation of bone remains? According to Pavao and Stahl (1999) density  
509 differences between hindlimb (more dense) and forelimb (less dense) elements should be  
510 reflected in femur and tibia outnumbering humerus, radius and ulna. At Pié Lombard, all of  
511 these elements are present in similar proportions, which is consistent with an overall good  
512 preservation of the assemblage. The underrepresentation of the extremities of the paws  
513 (phalanges, carpals/tarsals, and metapodials) is generally due to their small size and that  
514 these elements are frequently overlooked during excavations or lost during sieving when  
515 using large mesh sizes (Shaffer and Sanchez, 1994; Cannon, 1999; Val and Mallye, 2011a).  
516 A systematic water sieving .. wet line 156-157 protocol using less than 5 mm meshes during  
517 excavations at Pié Lombard exclude recovery biases affecting skeletal-part profiles. The  
518 absence of the differential transportation or preservation of rabbit remains at Pié Lombard  
519 suggests a particular context. Sketetal representation of rabbit remains in the Pié Lombard  
520 strongly suggests a human origin. Its assemblage falls between the anthropogenic  
521 accumulations such as the Mousterian occupation of Les Canalettes (Cochard et al., 2012),  
522 the Late Aurignation (sic) Aurignacian at Arbreda cave (Lloveras et al., 2016) or the Late  
523 Magdalenian at La Faurélie II (Cochard, 2004a), where rabbits were exploited uniquely as a  
524 source of food, and the anthropogenic accumulation from culture ? Gazel Cave where  
525 leporids were captured both for their fur and meat (Fontana, 2003).

526

527 Bone breakage linked to marrow extraction produces numerous epiphyseal and shaft-  
528 cylinder fragments (e.g., Hockett, 1991; Cochard, 2004a; Pérez Ripoll, 2004). With few

529 exceptions, rabbit accumulations from Upper Paleolithic contexts generally yield less than  
530 15% (of NISP) of shaft cylinders (Hockett and Bicho, 2000; Cochard, 2004a; Cochard and  
531 Brugal, 2004; Brugal, 2006; Lloveras et al., 2011, 2016; Rillardon and Brugal, 2014; Rufà et  
532 al., 2017). In this regard, the proportion of shaft cylinders at Pié Lombard (35%) is more  
533 similar to the Middle Paleolithic assemblage of Les Canalettes (39%; Cochard et al., 2012),  
534 which dates to the same period (i.e., MIS 5-4). The percentage of complete long bones  
535 (0.2%) is equally consistent with anthropogenic accumulations (e.g., Cochard et al., 2012;  
536 Lloveras et al., 2016; Rufà et al., 2017) and is lower than that observed for modern predators  
537 (Sanchis Serra, 2000; Lloveras et al., 2008, 2009a, 2012b, 2014a, 2017; Mallye et al., 2008).  
538 Moreover, fauna accumulations generated by non-human predators are characterized by  
539 very high percentages of digested remains (>60%). At Pié Lombard, less than 3% of NISP  
540 show traces of digestion and only 33 elements bear carnivore teeth-marks (0.2%) reflecting  
541 an extremely limited impact of non-human predator. The skinning and defleshing of rabbit  
542 carcasses leaves clear evidence in the form of cut-marks and traces of burning on the distal  
543 ends of long bones (Vigne et al., 1981; Vigne and Marival-Vigne, 1983; Lloveras et al.,  
544 2009b). At Pié Lombard, 3% of bones are cut-marked and 9% show traces of burning, a  
545 pattern consistent with what is observed in anthropogenic accumulations (for a synthesis,  
546 see Lloveras et al., 2016).

547

548 Moreover, the accumulation of small vertebrates at Pié Lombard is characterized by a very  
549 high proportion of rabbits (Table 1). Such an overrepresentation has never, to our  
550 knowledge, been encountered in any Pleistocene natural death assemblage or mixed  
551 accumulation (rock shelter or cave sites; e.g., Andrews, 1990; Desclaux et al., 2011) or in any  
552 modern coprocoenosis (e.g., Géroutet, 1984; Bayle, 1992; Lloveras et al., 2014a, 2014b,  
553 2017; Sanchis Serra et al., 2014). This confirms the unique nature of the Pié Lombard  
554 Mousterian assemblage, which results from the acquisition and processing of small game,  
555 primarily rabbits as well as birds, by Neandertal groups. The presence of a limited number of

556 digested remains and carnivore-gnawed bones shows that another agent, probably a small  
557 terrestrial carnivore, contributed only marginally to the accumulation.

558

#### 559 *4.2. Function of the Pié Lombard site*

560

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

571

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

582

583 Although it is still difficult to definitely demonstrate the processing of leporid pelts by  
584 prehistoric hunter-gatherers (e.g., Cochard, 2004a; Mallye et al., 2018), numerous cut-marks  
585 potentially unrelated to meat consumption are present. Generally, skinning carcasses for  
586 pelts leaves abundant evidence on bone, primarily on the skull (Lloveras et al., 2009b; Val  
587 and Mallye, 2011b). Although rabbit skull elements are too heavily fragmented and poorly  
588 represented at Pié Lombard to observe traces clearly referable to skinning, other lines of  
589 evidence are suggestive of this process. Metapodials alone bear nearly 31% of all recorded  
590 cut-marks, which are concentrated on lateral sides of metacarpals (II and V) and metatarsals  
591 (II and V), suggesting the removal of the skin (Val and Mallye, 2011b). The under-  
592 representation of these elements, as well as the phalanges, compared to the numerous  
593 tarsals, including the calcaneus and talus, which also carry numerous cut-marks resulting  
594 from skinning and disarticulation processes, could also testify to the transport of furs for  
595 tanning beyond excavated area. In this scenario, a large portion of tarsal elements  
596 (calcaneus, talus) would remain in the area where carcasses were processed for food, while  
597 the metapodials and phalanges would be transported still attached to the skin. Such a  
598 hypothesis was previously proposed by Cochard (2004a) for the Middle Paleolithic site of Les  
599 Canalettes. Finally, the very limited number of caudal vertebrae (NISP=14) equally suggests  
600 the removal of the tail with the skin (Fontana, 2003).

601

602 The importance of leporid fur for Upper Paleolithic societies remains a subject of  
603 considerable debate (Jullien and Pillard, 1969; Soffer, 1985; Alhaique, 1994; Charles and  
604 Jacobi, 1994; Morel and Muller, 1997; West, 1997; Pokines, 1998; Fontana, 2003; García-  
605 Argüelles et al., 2004). This is in no small part due to difficulties in reliably inferring skinning  
606 processes and the fact that cut-marks alone are not sufficient evidence for the removal of  
607 skins (Cochard, 2004a). Other taphonomic characteristics, such as skeletal-part  
608 representation provide additional evidence for skin processing. For example, the under-  
609 representation of the autopodial and caudal vertebrae at a butchery or consumption site give  
610 indirect evidence for such activities . At Pié Lombard, the limited number of these small

611 elements does not reflect either differential preservation processes or biases connected to  
612 sieving (i.e., mesh sizes). Traces of digestion on the autopodial could suggest that a  
613 scavenger biased anatomical representation. However, although digested bones are present  
614 at Pié Lombard, the impact of a terrestrial carnivore, such as red fox, wildcats, or lynx (Table  
615 1), is extremely low (2.6% and 0.2 %, respectively, of bones bear evidence of digestion or  
616 tooth-marks). This indicates that, while these species may have scavenged remains left by  
617 humans, their presence could not be linked to the under-representation of the autopodial.

618

619 Whether rabbits were sought specifically for their fur or first and foremost as a source of food  
620 remain an open question. In any event, the working of skins leaves very little trace on bones  
621 themselves, and wear on non-perishable tools is often the only evidence of this activity  
622 (Beyries, 2008). While bone and stone tools from Middle Palaeolithic contexts have been  
623 linked to the processing of skins (e.g., Chase, 1990; Texier et al. 1996; d'Errico et al., 2012;  
624 Soressi et al., 2013), no such evidence was recovered from Pié Lombard. With this being the  
625 case, tanning may have occurred outside the excavated area or at another site, as indicated  
626 by the under-representation of the metapodials and phalanges (cf. *supra*). Likewise,  
627 demonstrating fur processing at Pié Lombard to have been related with the manufacturing of  
628 clothes, either for group members or as trade goods, is also impossible. Substantial  
629 ethnographic and archaeological evidence, however, attests to the importance of leporid fur  
630 for human societies (Teit, 1906; Emmons, 1911; Rogers, 1963, 1973; Oberg, 1973; Speck,  
631 1977; Rogers and Smith, 1994; Charles, 1997; Kennedy and Bouchard, 1998; Lahren, 1998;  
632 Beyries, 2008), whether utilitarian purposes, such as the use of long bones to produce  
633 needles (Soffer, 1985; McComb, 1989; Leesch, 1997; Cochard, 2005) or personal ornaments  
634 manufactured from long bone shaft cylinders (Hockett, 1994; d'Errico and Laroulandie,  
635 2000). There now exists robust evidence of personal ornament use by Neandertals, including  
636 raptor terminal phalanges (Morin and Laroulandie, 2012), bird feathers (Peresani et al., 2011;  
637 Finlayson et al., 2012; Fiore et al., 2016), small to medium carnivore teeth (Caron et al.  
638 2011; Soulier and Mallye, 2012), and shells (Stringer et al., 2008; Mellars, 2010; Zilhão et al.,



639 2010). In view of the high number of rabbit remains present at Pié Lombard, it is reasonable  
640 to assume that this small prey played an important role in the socio-economic practices of  
641 Neandertal groups in southern France during MIS 5-4.

642

643 Taken together, there is sufficient evidence from Pié Lombard demonstrating rabbits to have  
644 been roasted and consumed on the site, with their pelts subsequently processed and  
645 transported away. Moreover, the numerous cut-marks, burnt bones and shaft cylinders are  
646 all consistent with what is commonly found on Upper Paleolithic sites and is readily  
647 comparable with the Mousterian rabbit assemblage from Les Canalettes. The Neandertal  
648 groups who occupied Pié Lombard therefore exploited rabbits in the same way as Upper  
649 Paleolithic anatomically modern humans. Interestingly, while it is generally accepted that  
650 rabbits were of secondary importance in the Neandertal diet due to a significantly lower  
651 caloric return compared to ungulates (Table 7) , the large number of rabbits at Pié Lombard  
652 provided at least 226 kg of meat, representing more than 7% of the group's overall caloric  
653 intake (Table 8)...si on considère que tous les herbivores sont apportés par l'homme ce qui  
654 n'est pas le cas ?...moduler la phrase. This value is much higher than what is known on other  
655 Mousterian sites. Indeed, rabbit generally constituted less than 1% of the energy intake of  
656 the Mousterian groups, with its role in the human diet increasing significantly in the Upper  
657 Paleolithic, especially during the Magdalenian (Table 8) in France (Cochard and Brugal,  
658 2004). The exploitation of small game (rabbits and birds) at Pié Lombard departs markedly  
659 from this pattern. The large number of rabbits (Table 1) suggests they were the principal  
660 focus of Neandertal subsistence practices at Pié Lombard and **may reflect difficulties in**  
661 **accessing the rockshelter and hence an emphasis on more easily transported small game**  
662 **rather than large herbivores...**...mouais, mais lieu pas terrible pour warren d'une part, et  
663 Caprid apporté assez complet aussi...pas trop lourd  
664 Il faut revoir cette 'fin'

665

666 *4.3. The exploitation of rabbits by Neandertal societies: a regional and repetitive*  
667 *phenomenon?*

668

669 Prior to the Upper Paleolithic in southwestern Europe, it is generally assumed that small  
670 game was rarely exploited by humans (Stiner, 2013). Consequently, the place of rabbits in  
671 the Neandertal diet has been the subject of considerable debate. When present in Middle  
672 Paleolithic assemblages, taphonomic analyses have generally demonstrated rabbits to have  
673 been primarily accumulated by carnivores or raptors (Defleur et al., 1994; Blasco, 1995;  
674 Martínez-Valle, 1996; Fernández-Jalvo and Andrews, 2000; El Guennouni, 2001; Hockett,  
675 2006; Lloveras et al., 2011; Sanchis Serra, 2012). Evidence of human modifications on rabbit  
676 remains is uncommon, and Neandertals are often considered to have played very minor role  
677 in their accumulation. For example, while the Mousterian assemblages from Bolomor Cave  
678 (NISP=457, MNI=49; Blasco and Fernández-Peris, 2012), Arbreda Cave (NISP=1,317,  
679 MNI=43; Lloveras et al., 2010), Les Canalettes (NISP=1,627, MNI=58; Cochard et al., 2012),  
680 Columbeira Cave (NISP=1,784; Carvalho et al., 2018), El Salt (NISP=1,789; Pérez et al.,  
681 2017), or Teixoneres Cave (NISP=3,964, MNI=49; Rufà et al., 2014) contain a limited  
682 number of rabbit remains, only Bolomor Cave and Les Canalettes produced robust evidence  
683 for a rabbit accumulation linked to more long-term, repetitive Neandertal occupations. In this  
684 respect, the over 16,000 rabbit remains and the presence of least 225 individuals make the  
685 Pié Lombard assemblage not only unique for the Middle Palaeolithic but readily comparable  
686 to hominid accumulations found from Upper Paleolithic sites such as: Les Cendres Cave  
687 (NISP=14,976, MNI=337; Real, 2016), La Faurélie II (NISP=15,569, MNI=87; Cochard,  
688 2004a), Arbreda Cave (NISP=17,700, MNI=43; Lloveras et al., 2016) or Molí del Salt  
689 (NISP=22,627, MNI=445; Rufà et al., 2017). With this being the case, how best to interpret  
690 the exceptional number of rabbits in Middle Paleolithic assemblage from Pié Lombard? It is  
691 often argued that Upper Palaeolithic hunter-gatherers most likely adapted their subsistence  
692 strategies 1) depending on the availability of different preys in the landscape; 2) as response  
693 to increasing group size and social structure; or 3) following profound changes in socio-

694 economic organization in connection with settlement patterns and resource management  
695 (e.g., Stiner et al., 1999, 2000; Aura et al., 2002; Cochard and Brugal, 2004). Similar  
696 behaviours have partially been demonstrated for several Middle Paleolithic sites in  
697 southwestern Europe based on the zooarcheological analyses of large (e.g., Discamps et al.,  
698 2011; Morin et al., 2014; Rendu and Morin, 2018) and / or small mammals (e.g., Sanchis  
699 Serra and Fernández Peris, 2008; Blasco and Fernández Peris, 2012; Blasco et al., 2014).  
700 These research raise question on the idea that the diversification and intensification of  
701 subsistence strategies were coincident with Middle to Upper Palaeolithic transition (e.g.,  
702 Stiner et al., 2000; Hockett and Haws, 2002; Aura et al., 2002). Pié Lombard provides  
703 additional evidence for the regular exploitation of small prey around 70-75 kyr, almost 25-30  
704 kyr before the emergence of the Upper Palaeolithic.

705

706 In addition, rabbits were abundantly available in the Mediterranean region of Western Europe  
707 from MIS 5 until the beginning of MIS 4. During this period of temperate environmental  
708 conditions associated with substantial forest cover (Pelletier, 2018), rabbits only occasionally  
709 formed part of the Neandertal diet (Blasco and Fernández Peris, 2012; Cochard et al., 2012;  
710 Hardy et al., 2013; this study). During MIS 4 to 2, although environmental and climatic  
711 changes led to a decline in rabbit populations and their retreat into several refugia in the  
712 Iberian Peninsula (Branco et al., 2002; Pelletier, 2018), rabbits were continuously exploited in  
713 these areas (Blasco, 1995; Sanchis Serra and Fernández Peris, 2008; Lloveras et al., 2010;  
714 Brown et al., 2011; Rufà et al., 2014; Pérez et al., 2017; Carvalho et al., 2018). During MIS 3  
715 (around 45 kyr BP), Europe witnessed a genuine “cultural revolution” (Mellars, 1996; Bar-  
716 Yosef, 1998, 2002), as Middle Palaeolithic cultural traditions gave way to Upper Palaeolithic  
717 technological and symbolic innovations (McBrearty and Brooks, 2000; d’Errico, 2003;  
718 Henshilwood and Marean, 2003; Zilhão, 2011). This transition equally coincided with  
719 substantial biological change, where Neandertals were gradually replaced by dispersing  
720 anatomically modern humans (Trinkaus, 1986, 2007; Stringer and Andrews, 1988; Stringer,  
721 2002). Despite these profound cultural and biological changes, rabbits continued to be

722 exploited at the beginning of the Upper Paleolithic in the Iberian Peninsula by Aurignacian  
723 (between 40 and 30 kyr BP; Rosado-Méndez et al., 2015; Lloveras et al., 2016; Sanchis et  
724 al., 2016), Gravettian / Solutrean (Brugal, 2006; Hockett and Haws, 2009; Lloveras et al.,  
725 2011; Aura et al., 2012; Manne et al., 2012; Sanchis et al., 2016), and Magdalenian societies  
726 (Aura et al., 2002; Sarrión et al., 2008; Rufà et al., 2017; Yravedra et al., 2018). On the other  
727 hand, no clear evidence for the exploitation of rabbits is currently available for southern  
728 France during the early Upper Paleolithic (Cochard and Brugal, 2004). This is likely  
729 explained by the absence of this species in this region until the end of the Late Glacial  
730 (Pelletier, 2018). The reincorporation of rabbit in post-Late Glacial subsistence strategies  
731 accompanied the return of more temperate climatic conditions in the region (Séronie-Vivien,  
732 1994; Cochard, 2004a; Jones, 2006; Rillardon and Brugal, 2014).

733

734 The distribution and density of rabbit populations in southwestern Europe during the Middle  
735 and Late Pleistocene was therefore relatively discontinuous and largely dependent on  
736 climatic conditions (Pelletier, 2018). When rabbits were available, they were consumed by  
737 both Neandertals and anatomically modern humans. Thus, the diversification of the human  
738 diet towards end of the Upper Paleolithic, notably the inclusion of leporids, cannot be tied  
739 uniquely to cognitive, cultural or economic changes but better tracks palaeobiogeographic  
740 factors modifying the range of this species. If the exploitation of small prey during the Middle  
741 Paleolithic now appears uncontested, several authors nevertheless maintain that changes  
742 in the importance of rabbit in human subsistence strategies was not due to prey availability  
743 and / or ecological or climatic variations but reflects a clear cultural choice (Lloveras et al.,  
744 2010, 2016; Sanchis et al., 2016). Although we acknowledge the continuous presence of this  
745 species on the eastern coast of the Iberian peninsula, significant differences are evident in  
746 the exploitation of rabbits between Mousterian and Aurignacian groups at Arbreda Cave  
747 (Lloveras et al., 2010, 2016) or between Aurignacian and Gravettian groups of **Malladetes** =  
748 verifier orthographe de ce site Cave (Sanchis et al., 2016), differences potentially due to the  
749 socio-economic organization of these human groups. Finally, the integration of leporids in the

750 diet, especially at the Middle-Upper Paleolithic transition, could be the result of multiple  
751 factors integrating both prey availability and human choice, whose relative impact would  
752 have varied between regions (i.e., the eastern coast of Spain versus southern France).

753

754 In addition to Romero et al.'s (2017) recent demonstration of the exploitation of birds at Pié  
755 Lombard, our data, combined with evidence from Les Canalettes (Cochard et al., 2012),  
756 demonstrates that around 70-75 kyr Neandertal groups in southern France had a diversified  
757 subsistence strategy that sometimes incorporated a significant proportion of small game.  
758 This pattern suggests that these groups had both a clear knowledge of their ecosystem and  
759 paleobiodiversity and implement specific acquisition strategies. Two modes of acquisition are  
760 generally cited to explain the presence of high numbers of rabbits in Paleolithic assemblages  
761 (Jones, 2006): 1) a mass collection near burrows or warrens, where immature individuals are  
762 often abundant; or 2) an opportunistic capture of solitary individuals in the landscape, which  
763 is reflected in the prevalence of adult individuals. Although these arguments (Jones, 2006)  
764 have recently been questioned (Pelletier et al., 2015; Pelletier, 2018, 2019), the large  
765 number of rabbits at Pié Lombard suggests the use of specific acquisition methods to  
766 capture multiple individuals. The near-absence of immature individuals can probably be  
767 explained by their low energy return or that rabbits were procured outside the birthing season  
768 (Cochard et al., 2012). Ethnographic and historical sources report the use of several  
769 techniques to hunt large numbers of small prey, such as leporids, including bows and arrows,  
770 throwing weapons, nets, snares, or individual or collective traps (Nelson, 1973; Bean, 1974;  
771 Oswalt, 1976; Callou, 2003; Lupo and Schmitt, 2005). Although the perishable nature of  
772 these technologies makes it difficult to identify them archaeologically, their use is regularly  
773 attributed to Upper Paleolithic hunter-gatherers (e.g., Stiner et al., 1999; Hoffecker, 2005;  
774 Rufà et al., 2017) as well as the Middle Stone Age of South Africa (Wadley, 2010). **It would**  
775 **come of no surprise** !! aie..trouver autre chose ! that some of these techniques were used at  
776 Pié Lombard. The pattern of Middle Palaeolithic rabbit exploitation documented at Pié  
777 Lombard currently finds no equivalent in Europe for this period and provides indirect

778 evidence for the development of advanced hunting strategies by Neandertals during MIS 5-4  
779 as well as their advanced cognitive capacities.

780

## 781 **5. Conclusion**

782

783 Given the current state of debate concerning the diet and cognitive capacities of  
784 Neandertals, demonstrating the primary accumulation agent responsible for faunal  
785 assemblages, especially those dominated by small mammals, as at Pié Lombard, is  
786 fundamental. Our taphonomic analysis shows the rabbit remains at the site to have primarily  
787 accumulated by Neandertals, who sought both the meat and pelts of these small mammals.  
788 The intense exploitation of rabbit at Pié Lombard reveals Neandertals were not only able to  
789 exploit their environment but also maximize the return of available resources. Moreover, the  
790 high numbers of rabbits potentially suggests that a variety of trapping techniques were  
791 developed during the Middle Paleolithic, well before the arrival of modern humans in Western  
792 Europe.

793

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

801

802 Finally, the intense and regular use of small game, potentially requiring sophisticated  
803 acquisition techniques, is no longer limited to the end of Upper Paleolithic. The exploitation of  
804 small animals seems to have been above all influenced by environmental conditions and

805 social factors, rather than by biological and cultural differences between Neandertals and  
806 modern humans.

807

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809

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811

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825

#### 826 **Author contributions**

827

828 **Maxime Pelletier:** Conceptualization, Methodology, Formal Analysis, Investigation, Writing –  
829 Original Draft. **Emmanuel Desclaux:** Conceptualization, Formal Analysis, Investigation,  
830 Writing – Original Draft. **Jean-Philip Brugal:** Writing – Original Draft, Supervision. **Pierre-**  
831 **Jean Texier:** Resources, Writing – Original Draft, Supervision, Project Administration.

832

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1590

1591 **Figure captions (color online only)**

1592

1593 **Figure 1** (2 columns). Location of the Pié Lombard rock-shelter.

1594

1595 **Figure 2** (2 columns). Stratigraphy of Pié Lombard (after Texier et al., 2011). A. Plan of the site and  
1596 location of the Paleolithic deposits (excavation 1971-1986); B. View of the excavation in 1974; C.  
1597 sagittal profile in squares C/D 3-5.

1598

1599 **Figure 3** (1 or 1,5 column). Mortality profiles for the Pié Lombard Mousterian complex (**PL**) and other  
1600 reference collections. BI = Bettant I, BVIII = Bettant VIII (Mallye et al., 2008), FA = fox accumulation  
1601 (outside the den), FD = fox den (inside the den), ABI = Aigües de Busot I, ABII = Aigües de Busot II,  
1602 PZ = Peña la Zafra (Sanchis Serra, 2000), BC = Benaxuai Caves (Sanchis Serra et al., 2014), CV3 =  
1603 El Conjunto de Coveta 3 (Sanchis Serra and Pascual Benito, 2011), LSC = Les Six Chemins (Pelletier  
1604 et al., 2016), VAU = Vaufrey (Cochard, 2007), CAN = Les Canalettes (Cochard et al., 2012), AN =  
1605 Anecrial (Brugal, 2006), LFII = La Faurélie II (Cochard, 2004a). Diagram divisions correspond to those  
1606 proposed by Discamps and Costamagno (2015): JOP = Juveniles-Old-Prime, JPO = Juveniles-Prime-  
1607 Old, P = Prime, O = Old. Confidence intervals have been omitted for clarity.

1608

1609 **Figure 4** (2 columns). Pié Lombard Mousterian skeletal-part representation (**PL**), as well as those of  
1610 the other reference collections. Attritional death in a rabbit-warren (Pelletier et al., 2016);  
1611 accumulations by terrestrial carnivores as the red fox (Sanchis Serra and Pascual Benito, 2011), the  
1612 European badger (Mallye et al., 2008) and the dhole (Cochard, 2007); accumulations by birds of prey  
1613 (golden eagle from Lloveras et al., 2017) and the eagle-owl (nest **2** and nest **1** from Lloveras et al.,  
1614 2009); and anthropogenic accumulation from Les Canalettes (**C**, Cochard et al., 2012), Arbreda cave  
1615 (**A**, Lloveras et al., 2016), La Faurélie II (**F**, Cochard, 2004a), and Gazel cave (**G**, Fontana, 2003).  
1616 Rectangles represent 95% confidence intervals.

1617

1618 **Figure 5** (2 columns). Examples of rabbit shaft cylinders from the Pié Lombard Mousterian complex.

1619

1620 **Figure 6** (2 columns). Cut-marks from Pié Lombard resulting from different processing activities, such  
1621 as skinning, defleshing and disarticulation. Numbers between brackets indicates number of cut-marks  
1622 per bones. %RA: percentage of relative abundance of the rabbit elements.

1623

1624 **Table captions**

1625

1626 **Table 1** (2 columns). The Pié Lombard Mousterian faunal assemblage. MNI: Minimum number of  
1627 individuals.

1628

1629 **Table 2** (1 column). Rabbit skeletal elements identified in the Mousterian complex from Pié Lombard.  
1630 NISP = number of identified skeletal parts, MNE = minimum number of elements, RA = relative  
1631 abundance.

1632

1633 **Table 3** (1 column). Proportions of different parts of the skeleton in the Mousterian complex from Pié  
1634 Lombard, along with 95% confidence intervals. For the definition of the indices see the section  
1635 concerning the "Anatomical representation of rabbits".

1636

1637 **Table 4** (2 column). Numbers and percentages of rabbit skeletal elements from the Pié Lombard  
1638 Mousterian complex included in each breakage category. Cranium as complete (C), incisive bone (IB),  
1639 incisive bone + maxilla (IBM), maxilla (M), zygomatic arch (ZA) and neurocranium (NC). Mandibles as  
1640 complete (C), incisive part (IP), mandible body + incisive part (MBI), mandible body (MB), mandible  
1641 body + branch (MBB) and condylar process (CP). Scapula as complete (C), glenoid cavity (GC),  
1642 glenoid cavity + neck (GCN), glenoid cavity + neck + fossa (GCNF), neck + fossa (NF) and fossa (F).  
1643 Long bones (humerus, radius, ulna, femur, tibia), metacarpal and metatarsal bones were classified as  
1644 complete (C), proximal epiphysis (PE), proximal epiphysis + shaft (PES), shaft (S), shaft + distal  
1645 epiphysis (SDE) and distal epiphysis (DE). Vertebrae as complete (C), vertebral body (VB), vertebral  
1646 epiphysis (VE) and spinous process (SP). Phalanges as complete (C), proximal fragment, (P), distal  
1647 fragment (D) and fragment (F). Patella, carpals, tarsals (calcaneus, talus, cuboid, cuneiform,  
1648 navicular), ribs and teeth as complete (C) and fragment (F).

1649

1650 **Table 5** (2 column). Fracture angle and fracture outline frequencies for rabbit long bones from the Pié  
1651 Lombard Mousterian complex. N = effective, NISP = number of identified specimens.

1652

1653 **Table 6** (1 column). Distribution of cut-marks, burnt bones, digestion damage and tooth marks on  
1654 rabbit bones by anatomical part in Mousterian complex from Pié Lombard. N = effective, NISP =  
1655 number of identified specimens.

1656

1657 **Table 7** (1 column). Average total weight values, average meat weight and average calorie values for  
1658 meat weight for several faunal species present during the Paleolithic of southwestern Europe (from  
1659 Brugal, 2005 and Cole, 2017).

1660

1661 **Table 8** (2 columns). Caloric intake of rabbits compared to large herbivores from different Paleolithic  
1662 deposits in Western Europe. MNI fauna for Terra Amata (from Valensi and El Guennouni, 2004),  
1663 Bolomor cave (from Blasco and Fernández Peris, 2012), Lazaret cave (from Lumley et al., 2004),  
1664 Arbreda cave (from Lloveras et al. 2016), La Peña de Estebanvela (from Yravedra et al. 2018), Molí  
1665 del Salt (from Rufà et al., 2017). Raw data available in Table 7.