

Identifying the accidental-natural mortality of leporids in the archaeological record: insights from a taphonomical analysis of a pitfall without evidence of human presence

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ABSTRACT: Leporids (Lagomorpha, Mammalia), especially the mountain hare (*Lepus timidus*) and the European rabbit (*Oryctolagus cuniculus*), have been among the most abundant small game in western Europe since the Pleistocene. These animals are preferred prey for more than 40 predators, which increases the chances of finding their skeletal remains at archaeological or natural sites, and in particular karstic formations alternately occupied by Palaeolithic human societies and other predators. Moreover, specific eco-ethological characteristics for both species also offer the possibility to produce a substantial quantity of their bones accumulated by natural mortality without predation, making it more difficult to identify their origin in the fossil record. Despite this fact, the taphonomic signature of accidental-natural accumulations of leporids in karsts, such as pitfalls, has never been properly characterised. In order to address these issues, we carried out a detailed taphonomic study of leporid remains in a pitfall without any evidence of human activity, namely at Coulet des Roches (Monieux, Vaucluse, south-eastern France). At this site, leporids are the most abundant species throughout the Last Glacial Maximum sedimentary sequence. The bone accumulation was analysed in order to determine the most relevant criteria to identify a natural accumulation that results from the accidental fall of individuals in the pitfall. The relative proportions of each species are consistent with their current ethology, and their mortality profiles are compatible with the structure of a living natural population. The completeness rate of the different skeletal portions for both species is relatively high, bones are less fragmented and, unlike what might be expected, very few anatomical connections were preserved. The observed anatomical representation, breakage, and bone surface modification patterns are discussed and compared with available data concerning accumulations with predation. Taken together, the identified criteria contribute valuable help in the recognition of accidental mortality in the fossil record, as well as to evaluate the proportion of leporid bones accumulated naturally and those accumulated by predation, human or not, in a deposit.

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KEYWORDS: accidental accumulation; Coulet des Roches; *Lepus timidus*; natural trap cave; *Oryctolagus cuniculus*

Introduction

In the midst of faunal remains regularly found in the Quaternary fossil record, leporids (rabbits and hares) are among the dominant taxa in most palaeontological and archaeological deposits in western Europe. Indeed, these animals have occupied a significant position in trophic relationships since they constitute the preferential prey for a large number of predators (humans, terrestrial carnivores, diurnal and nocturnal birds of prey). Moreover, leporids are of particular interest, as they have sometimes occupied an important, if not central, role in humans' socio-economic systems since the Middle Palaeolithic (Hockett and Bicho, 2000; Fontana, 2003; Cochard, 2004a; Pérez Ripoll, 2004; Brugal, 2006; Fontana and Chauvière, 2007; Sanchís and Fernández Peris, 2008; Brown *et al.*, 2011; Blasco and Fernández Peris, 2012; Cochard *et al.*, 2012; Blasco *et al.*, 2013; Lloveras *et al.*, 2016; Sanchís *et al.*, 2016; Rufà *et al.*, 2017; Mallye *et al.*, 2018; Morin *et al.*, 2019; Pelletier

et al., 2019). During the Pleistocene, hunter-gatherers and other predators alternately used karstic formations, such as caves or rock-shelters, as living spaces and the evidence of their respective activities can thus be found mixed in the same areas (Binford, 1981; Brain, 1981; Payne, 1983; Stiner, 1994). Deciphering the taphonomic context of leporid bones recovered from the fossil record is therefore crucial in evaluating the integrity of palaeo-ethnographic, palaeo-ethologic, or palaeo-environmental interpretations (Hockett, 1991; Cochard, 2004a; Sanchís, 2010; Lloveras, 2011; Pelletier *et al.*, 2016).

In recent decades, leporids have been the subject of active research in neo-taphonomy designed to characterise and identify their origins in a deposit. Thus, numerous experimental reference collections have been created to attempt to distinguish leporid bones accumulated by humans (Hockett, 1991; Pérez Ripoll, 1993; Lloveras *et al.*, 2009a) from those accumulated by other predators like foxes (Sanchís, 2000; Lloveras *et al.*, 2012a), lynxes (Lloveras *et al.*, 2008a; Rodríguez-Hidalgo *et al.*, 2015), badgers (Mallye *et al.*, 2008; Arilla *et al.*, 2019), coyotes (Schmitt and Juell, 1994; Armstrong, 2016a), wildcats (Álvarez *et al.*, 2012; Cohen and

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Kibii, 2015; Lloveras *et al.*, 2018), eagle owls (Sanchís, 2000; Cochard, 2004b; Lloveras *et al.*, 2009b, 2012b), golden eagles (Hockett, 1995, 1996; Schmitt, 1995; Lloveras *et al.*, 2017), vultures (Lloveras *et al.*, 2014a; Sanchís *et al.*, 2014) and other birds of prey (Hockett, 1989, 1991, 1995; Cruz-Urbe and Klein, 1998; Lloveras *et al.*, 2008b, 2014b; Armstrong, 2016a). However, for western Europe, these reference collections focus on European rabbit (*Oryctolagus cuniculus*) bone accumulation, while very little work has been done on the bone accumulations of larger leporids such as European hares (i.e. *Lepus europaeus*, *Lepus timidus*, *Lepus granatensis*, *Lepus corsicanus* and *Lepus castroviejo*). This difference can be explained by the biological and eco-ethological characteristics of each leporid species (Pelletier, 2018). Indeed, hares are solitary animals with high mobility, and are larger and faster, which further reduces the number of potential predators: more than 40 predators consume rabbits mainly and/or regularly (Delibes and Hiraldo, 1981) while only a dozen predators consume hares, and they are rarely the main prey of the diet (Haglund, 1966; Sulkava, 1966; Rukovsky and Kupriyanov, 1972; Sulkava *et al.*, 1984; Lindström *et al.*, 1986; Marcström *et al.*, 1989). In addition, unlike hares, the European rabbit is a sedentary and burrowing animal, with the ability to produce complex and substantial underground warrens (Biadi and Le Gall, 1993), the taphonomic characteristics of which have been previously documented (Pelletier *et al.*, 2016). This particularity accentuates the possibilities of discovery of its remains in the fossil record, and poses questions for the contemporaneity of these remains with other assemblage components (Callou, 2000; Pelletier *et al.*, 2017). Indeed, digging by rabbits can strongly rework a site's stratigraphy, moving archaeological artefacts and skewing the spatial data, thus bringing into question the integrity of the archaeostratigraphy and the reliability of the studied material (Bocek, 1986; Balek, 2002; Mallye, 2007, 2011).

In comparison, accumulations of hare bones in the fossil record are less frequent. Furthermore, the fact that there are almost no taphonomic studies on hares makes it difficult to identify their origin in a deposit. The majority of substantial accumulations of Quaternary hares have an anthropogenic origin (Poplin, 1976; Pailhaugue, 1995, 1998; Morel and Müller, 1997; Fontana, 2003; Cochard, 2005; Fontana and Chauvière, 2007; Müller, 2013; Julien and Karlin, 2014; Maul, 2014) or natural origin as the consequence of dead-fall individuals in natural karstic traps. For instance, the hypothesis of an accidental-natural mortality of hares has been proposed by Cochard (2004a) for the Coudoulous II (Tour-de-Faure, Lot, France) and Igue des Rameaux (Saint-Antonin-Noble-Val, Tarn-et-Garonne, France) deposits. The same scheme was recognised in Regourdou (Montignac-sur-Vézère, Dordogne, France; Pelletier *et al.*, 2015) and Igue du Gral (Sauliac-sur-Célé, Lot, France; Castel *et al.*, 2014; Mallye and Pelletier, unpublished) pitfalls. However, these different sites have also all yielded lithic artefacts associated with faunal remains. For example, at Igue des Rameaux and Coudoulous II, the presence of stone tools indicates an *in situ* human occupation (Rouzaud *et al.*, 1990; Brugal and Jaubert, 1991); and at Igue du Gral and Regourdou, lithic artefacts are accidentally present, i.e. from the plateau towards the inside of the karstic network (Castel *et al.*, 2008; Turq in Maureille *et al.*, 2015). In the latter case, it was also demonstrated that the different stratigraphic levels were highly bioturbated during the Late Pleistocene by rabbit burrows, thus biasing any interpretations related to anthropic occupation or palaeoenvironments of the site (Pelletier *et al.*, 2017). Except for Igue du Gral ($n \approx 4000$ remains), the number of leporid remains at these deposits is on average less than 1500 vestiges.

The Late Pleistocene palaeontological assemblage at Coulet des Roches (Monieux, Vaucluse, France), consists of more than 14 000 leporid remains accumulated from a pitfall, making it the most abundant species throughout the stratigraphic sequence. This site offers the opportunity to better characterise an accidental-natural mortality of leporids at a site without any evidence of human activity. Here we present a detailed taphonomical and zooarchaeological analysis of the assemblage, with the goal of evaluating and discerning the accidental-natural mortality in archaeological deposits. This is important, since accumulated fossil remains in pitfalls could be associated with animals accidentally falling into them, evidence of human presence, or scavenging by carnivores (Coumont *et al.*, 2013).

Material and methods

The Coulet des Roches pitfall

The site of Coulet des Roches is a pitfall situated in the municipality of Monieux (Vaucluse, France), opening in the north-western part of the Vaucluse hills, on the western edge of the Albion plateau (Fig. 1) located at an altitude of 700 m. It is a vertical hole with an ellipsoidal opening of 4 m x 2 m in Lower Aptian (Bedoulian, Lower Cretaceous) limestone, which was exposed following karstic erosion. The entrance well widens up to its current depth of 14 m with access to a large chamber 10 m long and 3–4 m wide (Fig. 2), whose access is direct from the surface without any possibility for animals to descend or ascend intentionally. After clearance works by a group of cavers from Carpentras between 1971 and 1973, a survey operation was carried out in 2007. Since 2008, exhaustive excavations of the site using archaeological methods (i.e. use of a grid reference, spatial quotation of remains, and systematic wet sieving of sediments) were directed by one of the authors (EC-B.). This work recovered an abundant amount of modern, Holocene (Northgrippian and Meghalayan periods) and Upper Pleistocene faunal remains (Crégut-Bonnoure *et al.*, 2014; Rodríguez-Varela *et al.*, 2015; Crégut-Bonnoure *et al.*, 2018).

The excavation of the filling made it possible to identify five stratigraphic units (US; Crégut-Bonnoure *et al.*, 2017). Radiocarbon dating of numerous bones and charcoals date the Coulet des Roches infillings from the end of the Pleistocene to the middle of the Holocene (Crégut-Bonnoure *et al.*, 2014, 2017, 2018). All the dates were calibrated using the program OxCal, v.4.2.4 (Bronk Ramsey, 2009) based on the IntCal 13 calibration curve (Reimer *et al.*, 2013):

- Ensemble 1 is subdivided into two sedimentary units (US1 and US2) and consists of a black sediment rich in charcoal. Dating places these deposits between the beginning and the middle of the Holocene (10 577–10 278 cal BP and 3973–2872 cal BP).
- Ensemble 2, represented by US3, occupies most of the cavity and corresponds to the Last Glacial Maximum (LGM) and Last Glacial (LG) sequence. This unit, about 4 m thick, contains homogeneous cryoclastic sediment formed by the accumulation of small-sized graded limestone fragments. Dating obtained on large mammal bones locate this stratigraphic unit at between 12 514–11 984 cal BP and 27 783–27 441 cal BP.
- Ensemble 3 is scree.
- Ensemble 4 is represented by two sedimentary units (US4 and US5). US4 is composed of brown earthy sediment and is

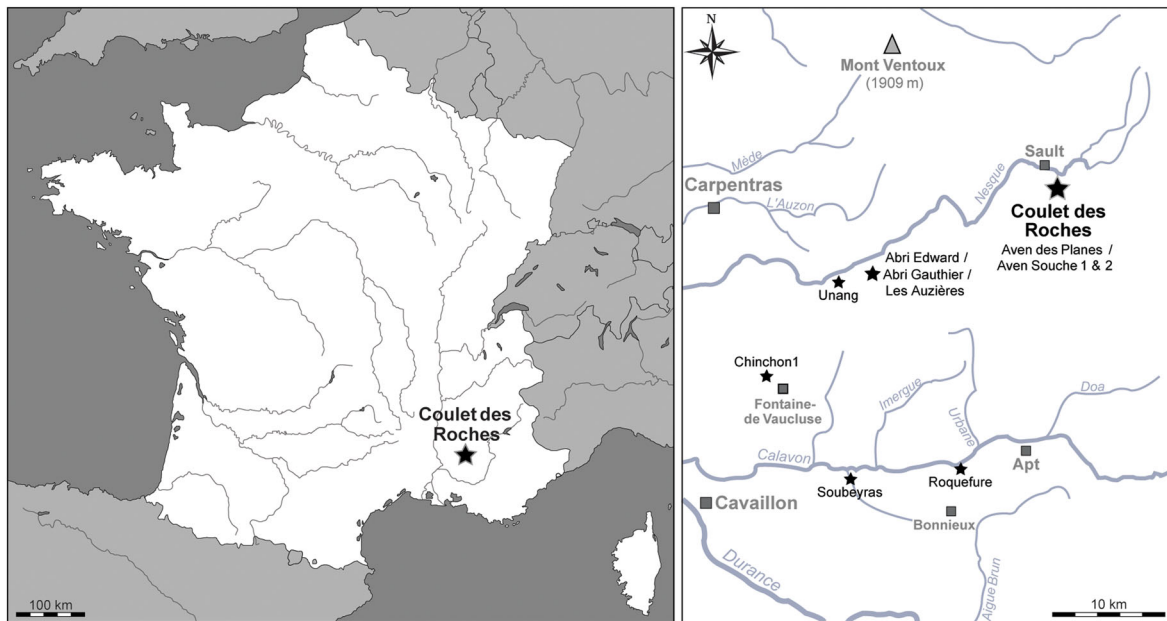


Figure 1. Location of Coulet des Roches pitfall. [Color figure can be viewed at wileyonlinelibrary.com]

located at the base of the south-western corner of the chamber. Its dating from a fragment of deer antler provided an age of 41 868–39 451 cal BP (Marine Isotopic Stage 3). Finally, US5, identified in the mid-eastern sector of the chamber, is composed of a cryoclastic limestone corroded by significant water circulation (the sediment is loaded with argil, laterally). It can be correlated to 'Tursac' episode (between 27 780 and 27 540 BP).

The LGM and LG fauna accumulation (US3) is represented by at least 48 species of large and small mammals and birds: five herbivores, five carnivores, two leporids, five insectivores,

13 rodents and 18 birds (Table 1). Among the herbivores, horse (*Equus ferus gallicus*) and Alpine ibex (*Capra ibex*) dominate the assemblage and are represented by complete skeletons, mostly found in anatomical connection. The carnivore assemblage is dominated by mustelids like the least weasel (*Mustela nivalis*), the stoat (*Mustela erminea*) and the polecat (*Mustela putorius*), whose bone remains were more dispersed. The state of preservation is noteworthy, with a large number of bones found complete, as well as intact skulls. The majority of the Coulet des Roches bone accumulation, in particular ungulate remains, suggests the accidental fall of animals into the pitfall. However, the presence of some isolated remains of reindeer (*Rangifer*

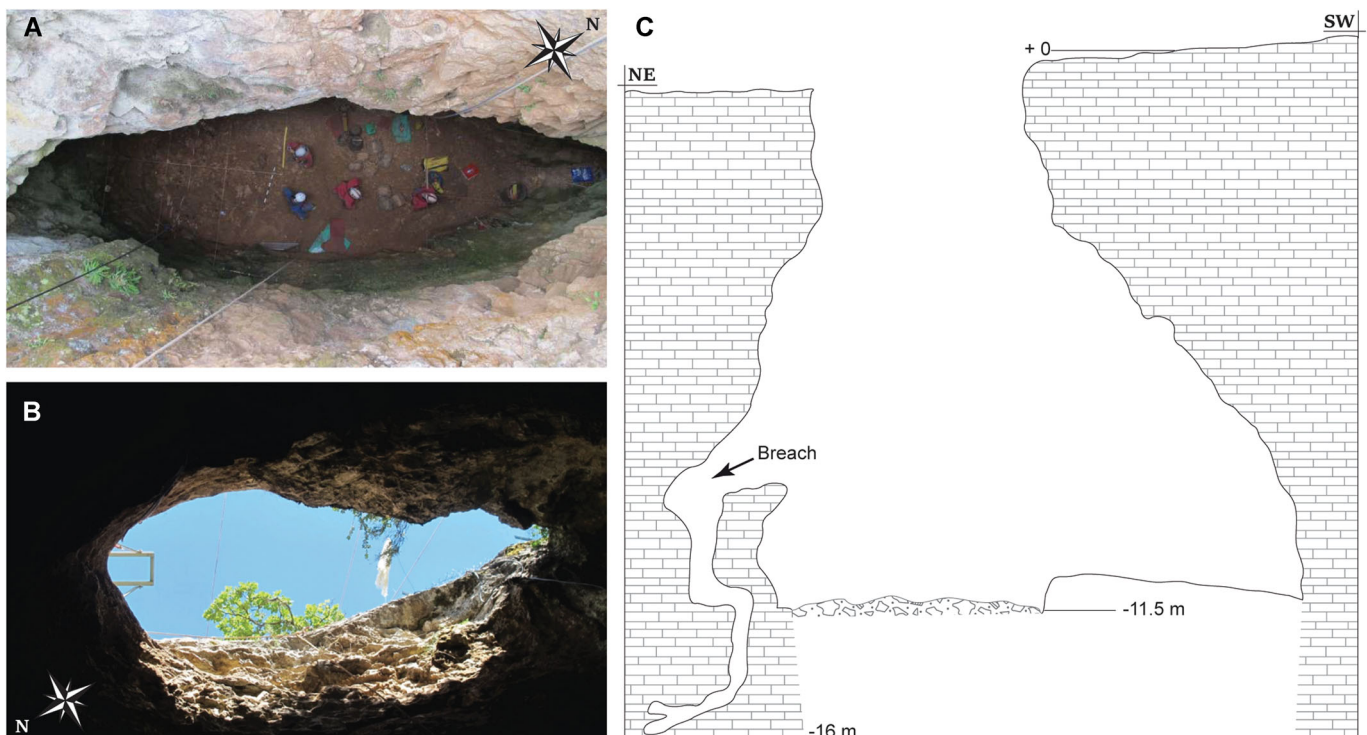


Figure 2. Configuration of Coulet des Roches pitfall (after Crégut-Bonnoure *et al.*, 2017). (A) Top view of the excavation in 2016. (B) Bottom view of the entrance well. (C) Cross section of the site. [Color figure can be viewed at wileyonlinelibrary.com]

Table 1. Taxonomic composition of Coulet des Roches faunal assemblage during Last Glacial Maximum. MNI: Minimum number of individuals.

Species	MNI	Species	MNI
CARNIVORA		LAGOMORPHA (this study)	
<i>Vulpes vulpes</i>	7	<i>Lepus timidus</i>	114
<i>Vulpes lagopus</i>	1	<i>Oryctolagus cuniculus</i>	19
<i>Mustela putorius</i>	4		
<i>Mustela erminea</i>	14		
<i>Mustela nivalis</i>	48	ACCIPITRIFORMES	
		<i>Aquila chrysaetos</i>	x
PERISSODACTYLA		<i>Circus</i> sp.	x
<i>Equus ferus gallicus</i>	17	FALCONIFORMES	
ARTIODACTYLA		<i>Falco</i> cf. <i>peregrinus</i>	x
<i>Rangifer tarandus</i>	1	<i>Falco tinnunculus</i>	x
<i>Capra ibex</i>	15	STRIGIFORMES	
<i>Rupicapra rupicapra</i>	1	<i>Bubo scandiacus</i>	x
<i>Rupicapra pyrenaica</i>	1	<i>Aegolius funereus</i>	x
INSECTIVORA		GALLIFORMES	
<i>Talpa europaea</i>	5	<i>Lagopus mutus</i>	x
<i>Crocidura leucodon/russula</i>	1		
<i>Sorex</i> sp.	1	COLUMBIFORMES	
<i>Sorex minutus</i>	1	<i>Columba oenas</i>	x
<i>Sorex gr. araneus/coronatus</i>	1	<i>Columba livia</i>	x
RODENTIA		<i>Columba livia-oenas</i>	x
<i>Marmota marmota primigenia</i>	6	PASSERIFORMES	
<i>Eliomys quercinus</i>	6	<i>Pyrhacorax pyrhacorax</i>	x
<i>Apodemus sylvaticus</i>	35	<i>Pyrhacorax graculus</i>	x
<i>Arvicola amphibius</i>	3	<i>Corvus monedula</i>	x
<i>Microtus (Stenocranius) gregalis</i>	2	<i>Pyrhacorax/Corvus</i>	x
<i>Microtus arvalis</i>	104	<i>Garrulus glandarius</i>	x
<i>Microtus arvalis/agrestis</i>	47	<i>Nucifraga caryocatactes</i>	x
<i>Chionomys nivalis</i>	264	<i>Hirundo</i> sp.	x
<i>Clethrionomys glareolus</i>	8		
<i>Microtus (Terricola) duodecimcostatus</i>	1	GRUIFORMES	
<i>Microtus (Terricola) cf. multiplex</i>	2	<i>Rallus aquaticus</i>	x
<i>Microtus oeconomus</i>	27		
<i>Dicrostonyx torquatus</i>	32		

Note: x, presence.

tarandus), chamois (*Rupicapra rupicapra*) and Arctic fox (*Vulpes lagopus*) could indicate that these specimens were brought to the pitfall with the sediment of the filling, most probably in connection with a phenomenon of solifluction outside the cavity. The accumulation of skeletons in the south-eastern part of the deposit reveals the presence of a névé at the bottom of the pitfall (Crégut-Bonnoure *et al.*, 2017).

Micromammals are abundant throughout the sequence both in terms of diversity and number of individuals. If we refer to both frequency and intensity of the digestion of the molars and incisors, on the basis of current observations (Andrews, 1990; Royer *et al.*, 2018), their accumulation probably corresponds to pellets of varied and opportunistic nocturnal raptors (Woodthorpe, 2017), possibly the snowy owl (*Bubo scandiacus*), many remains of which were identified at the site. Moreover, another predator, probably a carnivore, may also be responsible for part of the micromammal accumulation, as evidenced by traces of digestion on the bone material. Some

carnivores are likely to have participated in part of the accumulation, such as the least weasel (*Mustela nivalis*), which has a more specialised diet (Andrews and Nesbit-Evans, 1983; Cheylan and Bayle, 1988). Given the configuration of the pitfall, it is likely that carnivores were able to survive the fall and practice scavenging on the carcasses already present at the bottom. However, this possible predation would only account for a small proportion of the US3 assemblage at Coulet des Roches. In terms of the avian assemblage, the Alpine chough (*Pyrhacorax graculus*) is the dominant species. The presence of numerous remains of juveniles attributable to this species indicates *in situ* mortality, since this bird tends to nest in natural cavities such as pitfalls. Finally, no trace of human occupation or activity was found in the bone assemblage and/or at the site.

The leporid assemblage

Excavations conducted between 2008 and 2018 from Coulet des Roches recovered more than 14 000 leporid remains throughout the entire stratigraphic sequence of the LGM-LG (US3). The material is very well preserved, with 97% of the leporid bones identified anatomically, and 95% attributed specifically to either the European rabbit (*Oryctolagus cuniculus*) or the mountain hare (*Lepus timidus*).

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 leporid assemblages recovered from archaeological sites. This being the case, we integrated four types of data to investigate the nature of the accumulation: mortality profiles, skeletal-part representation, bone breakage and bone surface modifications.

Mortality profile of leporids

In zooarchaeological studies, the age structures of fossil populations generally contribute to defining the type of mortality, in order to identify acquisition strategies and behaviours of human or non-human predators (Klein and Cruz-Urbe, 1983; Steele and Weaver, 2002; Fernández, 2009; Discamps and Costamagno, 2015). It has recently been shown that age structure models of rabbit populations can help to identify acquisition strategies, predator behaviours or the type of accumulation (Pelletier *et al.*, 2016, 2017, 2019). Although age distributions may depend on the size of the predator, the season of capture and/or geography (e.g. Cochard 2004b, 2008; Lloveras *et al.*, 2012b; Arriaza *et al.*, 2017), and the fact 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 carnivores (e.g. badgers, dholes and lynx), large birds of prey (i.e. eagles and 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, 2019). Age structure can also be useful for identifying or excluding several potential species known to prey on rabbits, as well as attritional-natural mortality. For this study, we used ternary diagrams (Stiner, 1990), modified after Discamps and Costamagno (2015) specifically adapted for hare and rabbit populations.

Age at death was estimated from the degree of long bone (humerus, radius, ulna, femur and tibia) ossification. In rabbits, adult size is reached between three and five months (Biadi and Le Gall, 1993), while ossification is complete by eight months (Jones, 2006). In mountain hares, adult size is reached at

around four months, but all the epiphyses of the long bones are fused at around 11 months (Flux, 1970). Generally, three age classes can be distinguished:

- Juveniles: aged less than three months in rabbits and less than four months in mountain hares, with unfused epiphyses that have not yet reached their adult size.
- Subadults: aged between three and eight months in rabbits and between four and 11 months in mountain hares, which, although having reached their adult size, nevertheless display incompletely fused epiphyses.
- Adults: aged over eight months in rabbits and more than 11 months in mountain hares, with all epiphyses fused.

Anatomical representation of leporids

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

$$\%RA = [MNE/(MNI \times E)] \times 100 \quad (1)$$

where MNE is the minimum number of skeletal elements, MNI is 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.

The proportion of skeletal elements for all hare and rabbit age classes was calculated using adjusted ratios based on the work of Andrews (1990) and Lloveras *et al.* (2008a), and slightly modified by Pelletier *et al.* (2016):

$$PCRT/CR\% = [(PCRT \times 32)/((PCRT \times 32) + (CR \times 184))] \times 100 \quad (2)$$

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);

$$PCRAP/CR\% = [(PCRAP \times 32)/((PCRAP \times 32) + (CR \times 114))] \times 100 \quad (3)$$

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

$$PCRLB/CR\% = [(PCRLB \times 32)/((PCRLB \times 32) + (CR \times 10))] \times 100 \quad (4)$$

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

$$AUT/ZE\% = [(AUT \times 12)/((AUT \times 12) + (ZE \times 98))] \times 100 \quad (5)$$

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

$$AN/PO\% = [(AN \times 14)/((AN \times 14) + (PO \times 16))] \times 100 \quad (6)$$

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

$$Z/E\% = [(Z \times 4)/((Z \times 4) + (E \times 6))] \times 100 \quad (7)$$

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

To avoid any confusion, it is important to note that unlike the indices defined by Lloveras *et al.* (2008a), those presented by Pelletier *et al.* (2016) and used in this paper provide values of between 0 and 100%; values that are around 50% indicate a balance between the two compared portions and any results deviating from 50% indicate an imbalance in proportions, i.e. an over- or under-representation of a skeletal portion.

Bone breakage and surface modifications

To help discern leporid assemblages resulting from natural deaths from those produced by predators, the percentages of complete elements, isolated teeth, and articulated elements were calculated (Cochard, 2004a). 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.* (2008a) and applied in several subsequent studies (e.g. Lloveras *et al.*, 2009b, 2012a, 2014a, 2016; Pelletier *et al.*, 2019):

- Craniums 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).
- Coxal bones were recorded as complete (C), acetabulum (A), acetabulum and ischium (AIS), acetabulum, ischium and ilium (AISIL), acetabulum and ilium (AIL), ischium (IS) or ilium (IL).
- 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. Evidence of non-human predation (i.e. digestion, tooth/beak marks) was counted for each element, as were potential traces of human modifications such as cutmarks or burning.

Results

The leporid assemblage recovered from Coulet des Roches is well preserved and comprises 14 015 elements (NISP), the majority of which relate to the mountain hare (*L. timidus*; 85% of NISP), compared with about 10% of remains attributable to the European rabbit (*O. cuniculus*; Table 2). The remaining 5% correspond to undetermined leporid bone. Leporid remains are distributed over almost the entire area of the pitfall, although they are mostly concentrated in the south-southwestern part of the deposit (Fig. 3A). On the other hand, very few skeletons in strict anatomical connection were documented during the excavation. In general, individuals were found either dislocated or by forming bone concentrations in the sediment (Fig. 3B–C).

Mortality profile

Regarding mountain hare, the excavation yielded at least 114 individuals estimated from the total number of right tibias. The different stages of epiphysation of the long bones indicate the presence of 24 juveniles, 32 subadults and 58 adults. The mortality profile of hare in Coulet des Roches is very close to that of Igue du Gral, both located between the JPO and P zones (Fig. 4A), which corresponds to the theoretical structure of a living natural population (Discamps and Costamagno, 2015). It differs from the profiles obtained from anthropogenic accumulation, essentially composed of adult individuals ('Old' zone: LM, BR5, HC), as well as accumulations produced by the eagle owl, mainly dominated by subadults ('Prime' zone: JP8, JP9). However, this mortality

profile also differs from the profiles found in other pitfalls such as Regourdou and Coudoulous II.

Regarding the rabbit, the Coulet des Roches assemblage reveals at least 19 individuals: six juveniles, five subadults and eight adults located in the JPO zone (Fig. 4B). This type of profile is distinguishable from those produced by human predation or generated by badgers or dholes that preferentially hunt and/or catch adult individuals. On the other hand, it is closer to the profiles obtained for solitary carnivores (i.e. foxes and eagle owls) and differs from the accumulations found in rabbit warrens where juveniles and infants are very numerous (Pelletier *et al.*, 2016). Finally, this profile is similar to that encountered at the Igue du Gral.

Anatomical representation

At the Coulet des Roches, all skeletal parts of both species were identified (Table 2). This pattern is consistent with the introduction of complete skeletons at the site. In mountain hares, scapula, coxal, long bones (i.e. humerus, radius, ulna, femur and tibia), metatarsals and mandibles are the most represented elements in the assemblage (%RA > 70%; Table 2). In contrast, small bones and teeth, such as mesial and distal phalanges, carpals, small tarsals (i.e. cuneiform and cuboid), caudal vertebrae, upper second incisors and upper third molars are the least represented (%RA < 20%). Furthermore, postcranial elements are slightly under-represented in terms of cranial elements (PCRT/CR% = 44% and PCRAP/CR% = 41%; Table 3), although the latter are a little over-represented compared with long-bone limb elements (PCRLB/CR

Table 2. Leporid skeletal elements identified in Coulet des Roches assemblage. NISP = number of identified skeletal parts, MNE = minimum number of elements, RA = relative abundance.

	<i>Lepus timidus</i>			<i>Oryctolagus cuniculus</i>			Undetermined leporid	
	NISP	MNE	%RA	NISP	MNE	%RA	NISP	MNE
Cranium	1008	991	51.1	115	106	32.8	103	91
Mandible	220	163	71.5	35	31	81.6	5	2
Incisor	261	259	37.9	50	50	43.9	18	18
Upper molar	512	512	37.4	70	70	30.7	21	21
Lower molar	705	705	61.8	129	129	67.9	5	5
Scapula	213	167	73.2	27	27	71.1	4	2
Humerus	298	218	95.6	48	32	84.2	1	1
Radius	230	179	78.5	29	26	68.4	-	-
Ulna	234	164	71.9	43	35	92.1	2	2
Metacarpals	463	461	50.5	43	43	28.3	-	-
Carpals	134	134	14.7	7	7	4.6	-	-
Coxal	241	190	83.3	47	27	71.1	1	1
Femur	349	207	90.8	62	32	84.2	-	-
Patella	33	33	14.5	5	5	13.2	2	2
Tibia	340	222	97.4	55	36	94.7	-	-
Fibula	68	60	26.3	8	8	21.1	9	9
Metatarsals	749	730	80.0	93	93	61.2	19	16
Calcaneus	144	144	63.2	16	12	31.6	-	-
Talus	77	77	33.8	9	9	23.7	1	1
Cuboid	35	35	15.4	7	7	18.4	-	-
Cuneiform	23	23	3.4	4	4	3.5	-	-
Navicular	61	61	26.8	8	8	21.1	-	-
Proximal phalanx	630	622	30.3	59	52	15.2	72	72
Mesial phalanx	322	318	17.4	31	24	7.9	39	39
Distal phalanx	381	381	18.6	22	22	6.4	15	15
Vertebrae	1887	1784	39.1	194	194	25.5	43	33
Rib	1888	1402	51.2	131	116	25.4	106	88
Sternebrae	209	209	36.7	14	14	14.7	3	3
Sesamoids	63	63	-	5	5	-	-	-
Undetermined frag.	139	-	-	8	-	-	255	-
Total	11 917	10 514		1374	1224		724	421

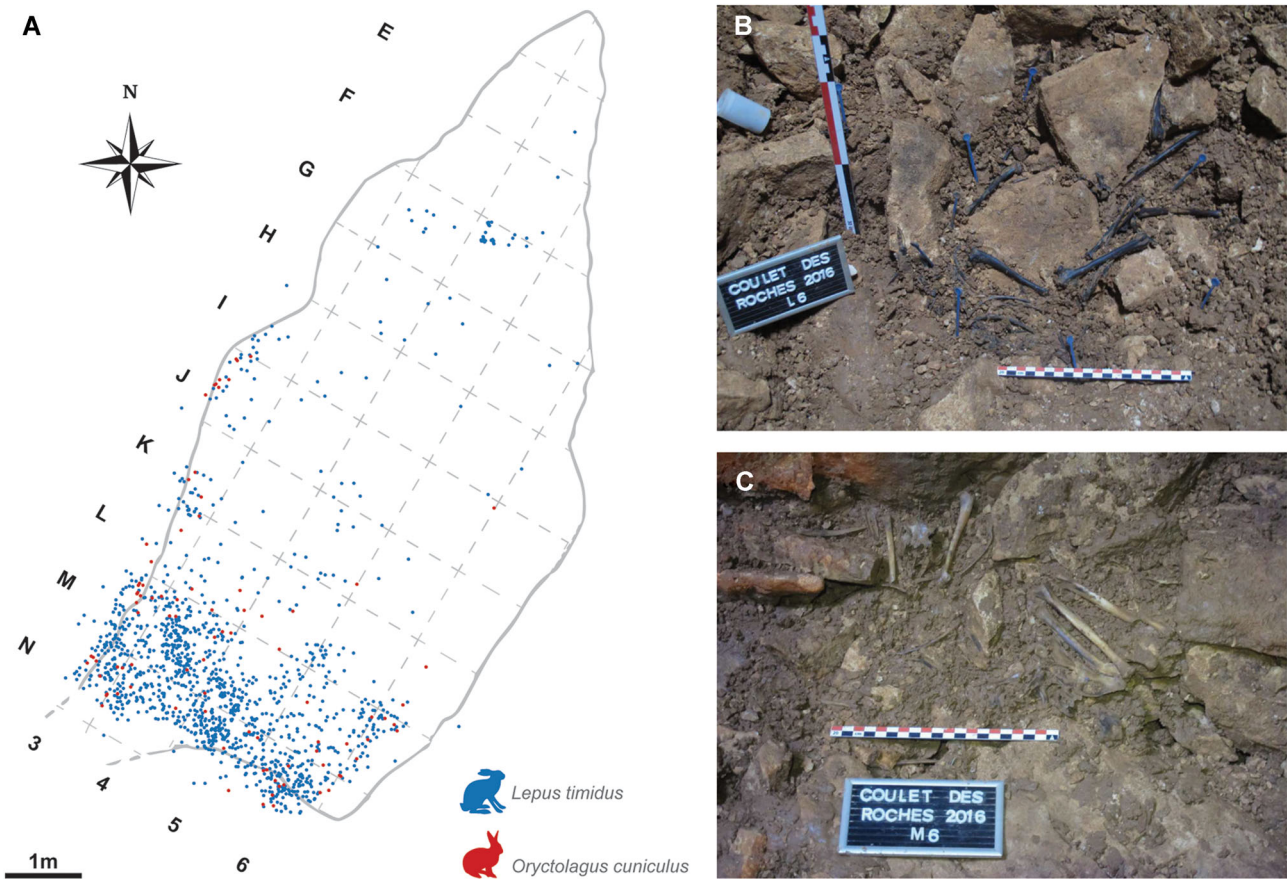


Figure 3. (A) Spatial distribution of coordinated leporid bones at Coulet des Roches, overhead view. (B) Bones of an individual mountain hare located in the L6 square in 2016. (C) Complete skeleton of a mountain hare located in the M6 square in 2016. [Color figure can be viewed at wileyonlinelibrary.com]

% = 64%). The AUT/ZE% index shows a deficit of autopodia compared with zygapodia (26%), and relatively equal proportions of lower- and upper-limb elements (Z/E% = 47%) as well as anterior and posterior members (AN/PO% = 45%). In

general, the skeletal-part representation of Coulet des Roches' hares is closer to natural accumulations (i.e. non-anthropogenic) such as in the natural trap caves of Igue du Gral, Coudoulous II or Regourdou (Fig. 5A). Regarding

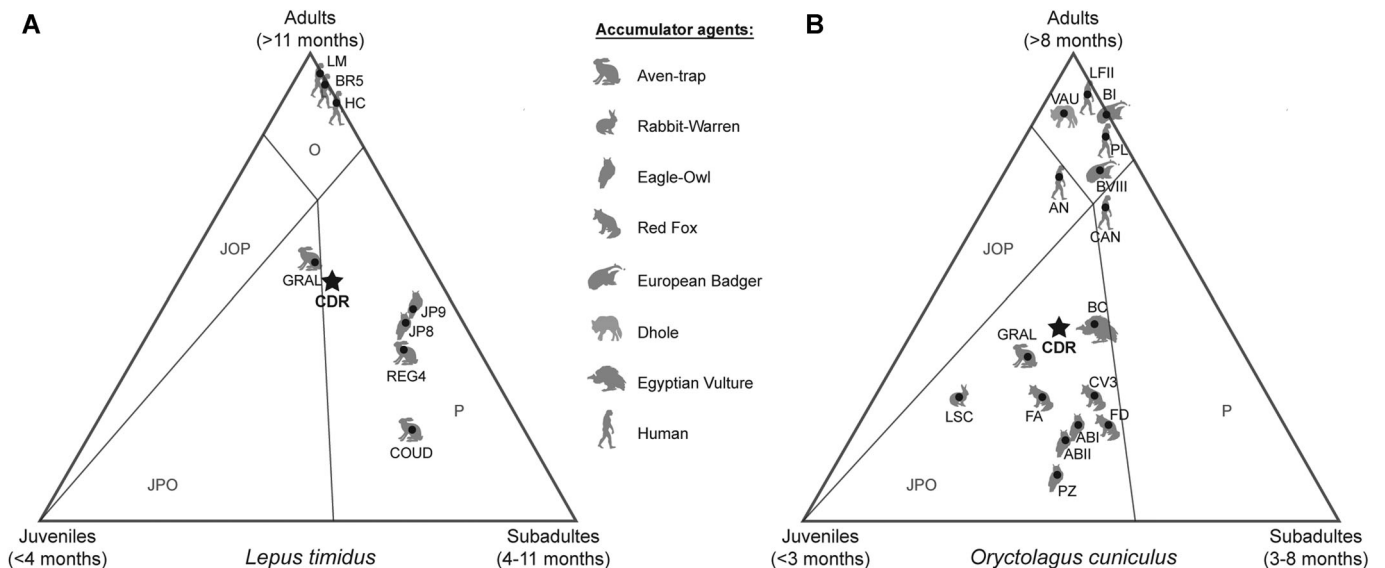


Figure 4. Mortality profiles for mountain hares, *Lepus timidus* (A) and rabbits, *Oryctolagus cuniculus* (B) at Coulet des Roches (CDR) and other reference collections. LM=La Madeleine (Fontana and Chauvière, 2007); BR5=Bois-Ragot (Cochard, 2005); HC=Hauterive-Champréveyres (Morel and Müller, 1997); JP8=Jean-Pierre 1 layer 8, JP9=Jean-Pierre 1 layer 9 (Gay, 2011); GRAL=Igue du Gral (Mallye and Pelletier, unpublished); REG4=Regourdou (Pelletier *et al.*, 2015); COUD=Coudoulous II (Cochard, 2004a); LFII=La Faurélie II (Cochard, 2004a); PL=Pié Lombard (Pelletier *et al.*, 2019); AN=Anecrial (Brugal, 2006); CAN=Les Canalettes (Cochard *et al.*, 2012); BI=Bettant I, BVIII=Bettant VIII (Mallye *et al.*, 2008); VAU=Vaufrey (Cochard, 2007); BC=Benaxuai Caves (Sanchís *et al.*, 2014); CV3=El Conjunto de Coveta 3 (Sanchís and Pascual, 2011); FA=fox accumulation (outside the den), FD=fox den (inside the den), ABI=Aigües de Busot I, ABII=Aigües de Busot II, PZ=Penya la Zafra (Sanchís, 2000); LSC=Les Six Chemins (Pelletier *et al.*, 2016). 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. [Color figure can be viewed at wileyonlinelibrary.com]

Table 3. Proportions of different parts of the skeleton in Coulet des Roches assemblage, along with 95% confidence intervals. For the definition of the indices see the section concerning the 'Anatomical representation of leporids'.

Index	<i>Lepus timidus</i>	<i>Oryctolagus cuniculus</i>
PCRT/CR%	43.8 ± 1.0	31.7 ± 2.8
PCRAP/CR%	41.1 ± 1.2	31.9 ± 3.3
PCRLB/CR%	64.3 ± 1.8	63.7 ± 4.4
AUT/ZE%	26.0 ± 1.4	16.4 ± 3.5
AN/PO%	44.5 ± 1.9	45.3 ± 5.3
Z/E%	47.0 ± 3.1	50.3 ± 7.7

postcranial elements, indices Z/E% and AN/PO% tend to bring the anatomical representation of Coulet des Roches closer to accidental and anthropogenic accumulations, generally explained by the fact that individuals are introduced whole into the deposit, unlike accumulations generated by birds of prey. The index AUT/ZE% brings Coulet des Roches closer to Igue du Gral and Bois-Ragot, which reveals a better representation of the ends of the legs than at Coudoulous II, Regourdou or Jean-Pierre 1.

In rabbits, long limb bones, girdles and mandibles are also the elements best represented in the assemblage (%RA > 70%), while small elements (e.g. phalanges, carpals, cuneiform and cuboid) are less abundant (%RA < 20%). According to all the indices used, the skeletal-part representation of Coulet des Roches is close to attritional (i.e. Les Six Chemins) or

anthropogenic (i.e. Arbreda cave and La Faurélie) accumulations, and tends to be close to the accumulations generated by terrestrial carnivores (Fig. 5B). This is because in these types of accumulation, the complete carcasses of rabbits are transported to or deposited at the site (e.g. Cochard, 2004a, 2008). Furthermore, Coulet des Roches is relatively well differentiated from accumulations generated by foxes (i.e. El Conjunto de Coveta 3) or eagle owls (i.e. Natural Park Massís del Garraf).

Bone breakage: frequency and type

The overall bone fragmentation is relatively moderate for both mountain hares and rabbits (with 66% and 70% complete bones, respectively), although it varies according to bone element, size, and species (Tables 4 and S1). The smallest elements (i.e. patella, carpals, tarsals and phalanges) are more frequently complete (> 95%), while long bones (i.e. humerus, radius, femur and tibia) display a higher breakage rate, with an average of complete bones between 59% and 61% (Table 4). The ulna is more affected by breakage with only 27% complete bones because of the fragility of the distal part of its diaphysis (Pavao and Stahl, 1999). The same can be said regarding the scapula and the coxal bone, with 32% and 52% complete elements, respectively. Metacarpals, which are smaller, are more complete (95%) than metatarsals (81%). In this case, hare metatarsals are more fragmented than those of rabbits (Table S1). This pattern is generally observed for each bone, where the hare elements are more fragmented than those of rabbits. Vertebrae are relatively complete (> 85% of cases),

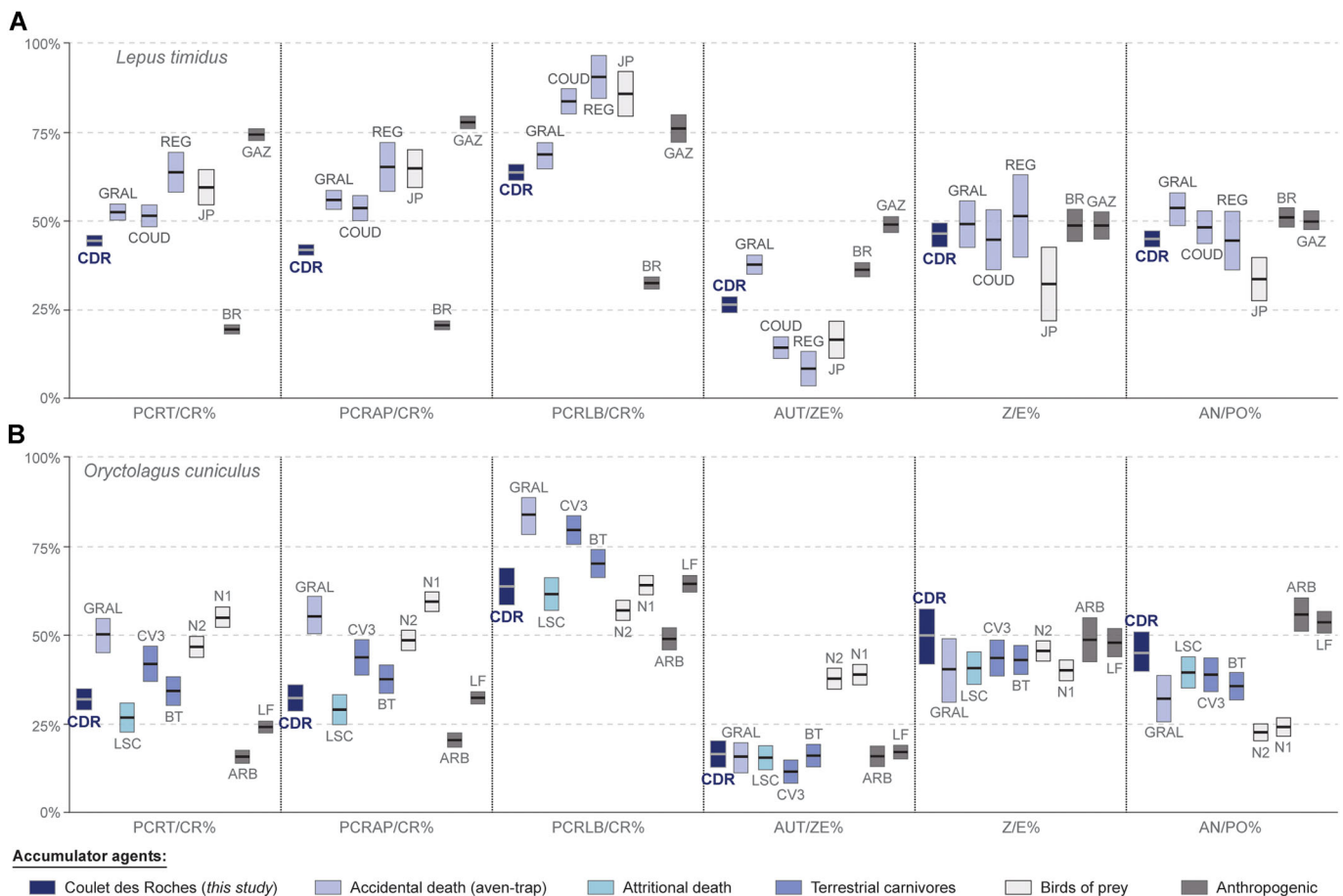


Figure 5. Skeletal-part representation for mountain hares, *Lepus timidus* (A) and rabbits, *Oryctolagus cuniculus* (B) of Coulet des Roches (CDR) and other reference collections. GRAL = Igue du Gral (Mallye and Pelletier, unpublished); COUD = Coudoulous II (Cochard, 2004a); REG = Regourdou (Pelletier *et al.*, 2015); JP = Jean-Pierre 1 (Gay, 2011); BR = Bois-Ragot (Cochard, 2005); GAZ = Gazel cave (Fontana, 2003); LSC = Les Six Chemins (Pelletier *et al.*, 2016); CV3 = El Conjunto de Coveta 3 (Sanchis and Pascual, 2011); BT = Bettant (Mallye *et al.*, 2008); N2 = Nest 2 and N1 = Nest 1 of the Natural Park Massís del Garraf in Barcelona (Lloveras *et al.*, 2009b); ARB = Arbreda cave (Lloveras *et al.*, 2016); LF = La Faurélie II (Cochard, 2004a). Rectangles represent 95% confidence intervals. [Color figure can be viewed at wileyonlinelibrary.com]



Figure 6. Mountain hare bones from Coulet des Roches. (A) Skull M6 121. (B) Skull N5 522. (C) Skull N4341-8. (D) Mandibles N4 341-8. (E) Left mandible M6 121. (F) Right mandible M6 121. (G) Left mandible N6284-1. (H) Right mandible N4 341-8. (I) Left scapula N6284-6. (J) Right scapula N4341-12. (K) Left humerus N4341-12. (L) Left humerus N6 284-2. (M) Left coxal N4341-9. (N) Left coxal N6284-34. (O) Right femur N4341-9. (P) Right femur N6284-30. (Q) Left tibia N4341-9. (R) Right tibia N6284-33. [Color figure can be viewed at wileyonlinelibrary.com]

Table 5. Fracture angle and fracture outline frequencies for leporid long bones from Coulet des Roches. N = effective, NISP = number of identified specimens.

	Ancient break				Recent break	Total of long bone break	Total of long bones	NISP
	Fracture angles		Fracture outline					
	Oblique (green)	Right (dry)	V-shaped (green)	Transverse (dry)				
N	40	553	44	549	174	767	1691	14 0154
% of breaks	5.2%	72.1%	5.7%	71.6%	22.7%	100%	-	-
%NISP	0.3%	3.9%	0.3%	3.9%	1.2%	45.4%	12.1%	100%

'punctures' that may refer to secondary scavenging by a small terrestrial predator in the cavity (Fig. 7D). Only four remains of hares show signs of digestion (two long-bone diaphysis splinters, one distal portion of a humerus and one metacarpal). Regarding abiotic traces, only 0.95% (NISP = 134) of remains bear fine parallel fissures, reflecting a weathering phenomenon on bones. Water is also responsible for some bone surface modifications: 41 remains (0.3%) present concretions, and traces of dissolution were found on 12.5% (NISP = 1752) of bones. In this case, different stages were reached, ranging from minor dissolution pits (Fig. 7A) to larger dissolving ranges that may remove some of the cortical bone (Fig. 7B–C).

Finally, parallel grooves perpendicular to the axis of the bone diaphysis were also found on 262 remains (1.9%). This is usually the result of dry bedload or following transport by water (Andrews and Cook, 1985; Behrensmeyer *et al.*, 1986; Olsen and Shipman, 1988), e.g. when the carcasses are

deposited at the bottom of the pitfall on a cone of scree. Although some traces of thrust can be confused with cutmarks of an anthropic origin (Fig. 7E–F), we report that no elements show traces that are attributable to intervention by humans (i.e. cutmarks, burnt bones and shaft cylinders) on the materials from Coulet des Roches.

Discussion

As a result of these analyses, several taphonomic and palaeoecological features have been identified. Despite differences in the relative abundance of some skeletal elements, the overall anatomical representation for both hares and rabbits confirms that carcasses have been introduced whole into the pitfall. Most potential predators of leporids can transport whole carcasses and produce similar taphonomic

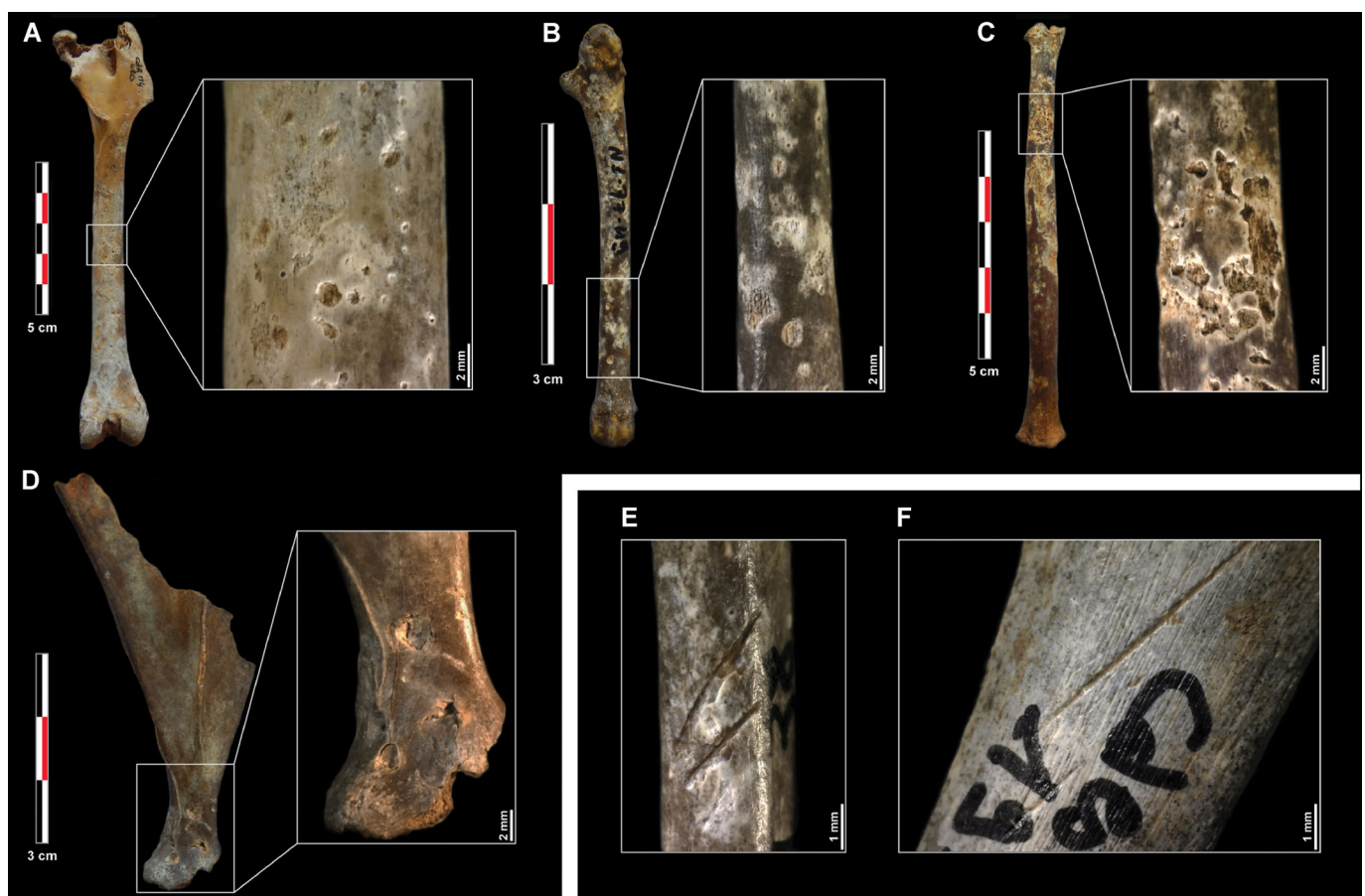


Figure 7. Bone surface modifications on leporid remains from Coulet des Roches. (A) Right femur M4 420 showing minor dissolution pits. (B) Fifth left metatarsal N3 77-49 showing moderate dissolution pits. (C) Left radius M4 991 showing larger dissolving ranges. (D) Right scapula M4 212-1 displaying gnawing damage caused by small terrestrial carnivores. (E–F) Grooves on leporid ribs (N3 81-38 and N4 192-6) as a result of bedload transport. [Color figure can be viewed at wileyonlinelibrary.com]

patterns, whether in terms of anatomical representation, mortality profile, breakage or bone surface modification. Taking each of these parameters for each species of leporids into account is therefore essential for a better reconstruction of the taphonomic history of an archaeological site, but also for a better understanding of the paleoecology of these animals during the LG.

Age of death distributions and palaeoecology

The mortality profiles show that this accidental-natural accumulation of hare is mainly constituted by adult individuals, whereas for rabbits the accumulation was characterised by more immature individuals. This is probably explained by a differential ethology between the two species. Mountain hares are solitary animals occupying very large areas and are capable of large seasonal migrations (Angerbjörn and Flux, 1995). To explain the prevalence of subadult hares in pitfalls at Coudoulous II and Igue des Rameaux, Cochard (2004a) previously hypothesised that these young individuals, which were more mobile and in search of new territories, were more likely to be trapped in pitfalls. However, at Coulet des Roches and Igue du Gral, the age structures correspond more to the theoretical structure of a living natural population. This theoretical model is consistent with population studies of modern mountain hares, including a ratio of adults slightly greater than the number of immature individuals (Walhovd, 1965; Flux, 1970; Hewson, 1976). At Coulet des Roches, hares would have accidentally fallen into the pitfall without a preferential 'selection' of age, but would rather reflect a living natural population, involving random trapping of individuals. These results showed an indicator of variability in the age structures of these fossil populations, which could be explained by the topography, history, duration, seasonality, and/or function of pitfalls. We cannot therefore really maintain that the accidental-natural mortality is characterised by a predominance of a particular age class, although the data from Coulet des Roches and Igue du Gral argue for a higher proportion of adults. The accidental mortality profile of the mountain hare from Coulet des Roches is, however, relatively different from accumulations generated by human groups or the Eurasian eagle owl. In the first case, hunter-gatherers tend to target adult individuals, while the eagle owl concentrates more on young individuals and subadults.

Rabbits, unlike hares, are sedentary animals, occupying much smaller areas, and they tend not to move very far away from their warrens (Biadi and Le Gall, 1993). Young non-breeding (or non-dominant) individuals that tend to look for new territories (or new warrens) exhibit greater mobility than adults and are therefore more likely to be trapped in pitfalls. This ethological characteristic may explain the fact that, compared with hares, fewer adult individuals were found at Coulet des Roches. The profile of the assemblage here is again similar to that at Igue du Gral, thus confirming the palaeoecological trend of rabbits from pitfalls. However, the accidental mortality of rabbits differs significantly from the accumulations generated by large predators such as humans, lynxes, dholes, eagles and badgers, which tend to focus mainly on adults (Hockett, 1991; Hockett and Bicho, 2000; 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; Pelletier *et al.*, 2019). It is also quite distinct from the profiles generated by small solitary predators, such as foxes and eagle owls, and from other natural mortality profiles without predation, specifically the attritional mortality in warrens. Rabbit warren accumulations are characterised by the predominance of infants

(Pelletier *et al.*, 2016), as they do not leave the warren until two weeks after birth (Biadi and Le Gall, 1993). However, no remains attributable to this age category were found at Coulet des Roches, and this excludes any potential bioturbation of the palaeontological levels at the deposit.

Thus, these characteristics in terms of population structure appear to be relatively different in both leporid species and are consistent with their distinct eco-ethology. The findings of differential age profiles according to the considered species seem to be a trend generally observed within pitfalls: in carnivores, most of them are adults, while in large herbivore communities, the profiles are characterised by an over-representation of the youngest individuals, which is ultimately similar to the structure of a living natural population (Coumont *et al.*, 2013). However, it seems that different taphonomic (i.e. differential preservation of skeletal elements), ethological (i.e. social segregation excluding certain individuals) or ecological (i.e. concept of time-averaging) factors can skew age models within pitfalls. Firstly, as mentioned before, it cannot be an impact of differential conservation, affecting more immature individuals that are well preserved and represented in Coulet des Roches. Then, unlike large mammals, ethological differences in leporid populations are hardly perceptible since these animals are either solitary, in the case of hares, or have an extremely complex and variable social organisation, as with rabbits. If we cannot exclude this bias, it seems unlikely that this could have had a significant impact on age models at the global scale of the site, knowing that each age group could be identified in relatively large proportions. Finally, the establishment of sedimentary filling and bone accumulations can correspond to long periods of time. At Coulet des Roches, the US3 was established between $10\ 360 \pm 60$ BP and $23\ 430 \pm 80$ BP (i.e. between $12\ 514$ – $11\ 984$ cal BP, laboratory reference BA 267376, and $27\ 783$ – $27\ 441$ cal BP, laboratory reference BA 476993), which could cause a significant bias on the proposed age structure. Indeed, a population is likely to grow or decrease, thereby altering the balance of age structures over time (Coumont, 2008). However, the model presented at Coulet des Roches is extremely close to that at Igue du Gral, which could be a repeated trend among hare and rabbit populations in pitfalls.

Taphonomical characteristics of Coulet des Roches leporid assemblage

Despite some variations in skeletal-part representation, the Coulet des Roches hare and rabbit skeletal profiles are relatively similar. These profiles are also very close to those produced by medium-sized carnivores (i.e. dholes, badgers and lynxes), large raptors (i.e. eagles and vultures) or humans (Cochard, 2004a, 2007; Mallye *et al.*, 2008; Lloveras *et al.*, 2008a, 2011, 2016, 2017; Cochard *et al.*, 2012; Rosado-Méndez *et al.*, 2015; Pelletier *et al.*, 2019), because these predators generally transport complete leporid carcasses to the consumption sites. In mountain hares, the skeletal representation of Coulet des Roches tends to be closer to the pitfall-like accumulations of Igue du Gral, Coudoulous II or Regourdou (Fig. 5A). In rabbits, this type of accidental-natural accumulation is also very close to the attritional-natural accumulation, where no predation impact was detected *in situ* (Pelletier *et al.*, 2016). This could then be a reliable taphonomic model for the interpretation of skeletal profiles in a natural context without predation.

In all cases, the bone representation is systematically distinct from the accumulations generated by the Eurasian eagle owl. This predator does not systematically transport complete carcasses to the consumption site, and therefore disarticulates

them in order to carry the most nutritious parts. In cases where it can transport the whole prey to its nest, it is unable to ingest the entire carcass as a terrestrial carnivore would. Generally, it segments the carcass into ingestible parts, which will impact the anatomical representation, in particular between the digested and undigested bones. Eagle owls preferentially consume the hindlimb elements (i.e. coxal, femur and tibia), compared with the forelimb parts. In hares, the Coulet des Roches assemblage revealed a better representation of the extremities of the paws than at Coudoulous II, Regourdou, or Jean-Pierre 1. This can be explained by a loss of small elements during sieving, as in Regourdou (Pelletier *et al.*, 2015, 2017), or when the limbs are cut up by the eagle owl, as was hypothesised at Jean-Pierre cave 1 (Gay, 2011). In addition, the under-representation of these small elements is also generally found at anthropogenic sites, and could be explained by the specific treatment of leporid carcasses; for example, in order to exploit their fur (Fontana, 2003; Cochard, 2004a; Cochard and Brugal, 2004; Pelletier *et al.*, 2019). At Coulet des Roches, the slight overall under-representation of small elements (teeth and extremities of the paws, such as the phalanges, carpals and tarsals) could therefore be explained by their small size and the fact that these elements are: 1) frequently overlooked during excavations; or 2) lost during sieving when using large mesh sizes (Shaffer and Sanchez, 1994; Cannon, 2003; Val and Mallye, 2011).

According to Pavao and Stahl (1999), in cases of differential preservation, density differences between hindlimb (denser) and forelimb (less dense) elements should be reflected in femurs and tibias, outnumbering the humerus, radius and ulna bones. With the same rate of fragmentation, long-bone shaft fragments will not be recognised in an equivalent manner. Thus, bones with well-marked muscle relief and other muscle insertions such as the tibia, humerus, radius and ulna will be more easily identified than femoral shaft fragments in which the shaft is very smooth. The AN/PO ratio will therefore be affected and will always be less than 50%. At Coulet des Roches, all of these elements are present in similar proportions, which is consistent with overall good preservation of the assemblage. In addition, this should further impact immature individuals since it is recognised that their bones are generally less well preserved. However, they are well represented and preserved at Coulet des Roches. Even though a significant impact of differential conservation on the bone assemblage cannot be totally ruled out, it must have been relatively limited.

Bone breakage patterns are regularly used to help identify the causative agent of an accumulation, usually related to the consumption or processing of carcasses by human or non-human predators. Significant breakage of green bones producing numerous epiphyseal and shaft-cylinder fragments, often accompanied by burning marks or cutmarks, are characteristic of anthropogenic accumulations (e.g. Hockett, 1991; Cochard, 2004a; Pérez Ripoll, 2004). However, at Coulet des Roches, these types of bone breakage and traces have never been observed. A high rate of breakage of green bones can also be generated by small terrestrial carnivores and birds of prey. However, at Coulet des Roches, only 45% of long bones are fragmented, which is a lower rate than the accumulations usually produced by these predators (Sanchís, 2000; Lloveras *et al.*, 2008a, 2008b, 2009b, 2012a, 2014a, 2017; Mallye *et al.*, 2008). In addition, this important fragmentation caused by the consumption of predators is usually accompanied by numerous tooth marks, beak marks or digestion marks on the bones. In our case, these traces are only anecdotal with only 17 remains bearing tooth

marks and three with digestion damage. These low numbers reflect the extremely limited involvement of secondary scavenging by a small terrestrial predator in the cavity. This observation differs from that recorded on micromammal bones (i.e. rodents and insectivores), which might be the result of pellets produced by nocturnal raptors, such as the snowy owl (*Bubo scandiacus*; Crégut-Bonnoure *et al.*, 2018).

Post-depositional processes are most likely responsible for the majority of *post mortem* bone surface modifications and could be the most relevant indices for identifying accidental mortality in the fossil record. Firstly, most of the breaks in the Coulet des Roches assemblage occurred on dry bones, suggesting processes such as pressure and sedimentary movements, roof collapse or weathering. In addition, many individuals have been found in loose anatomical connection, i.e. sets of bones congruent with the skeletal organisation, or by piles of bones resulting from the disturbance of carcasses within the cavity (Fig. 3). Most of the leporid remains found were isolated and were mainly collected in the south-southwestern part of the deposit. This lack of strict connection among leporids coincides with the random dispersion of skeletal elements during the decomposition of carcasses on a debris cone and/or following the flow of water on it (Costamagno, 1999; Cochard, 2004a). On the contrary, large herbivore skeletons are mainly found in strict anatomical connection (Crégut-Bonnoure *et al.*, 2018). However, leporid bones are relatively lightweight compared with those of large fauna, and are more easily transportable by runoff. Given the climatic context that led to the deposition of the sediment (i.e. cold periods of the Late Pleniglacial and the Early Late Glacial), it has been considered that the presence of a névé at the bottom of the pitfall on a cone was mainly constituted by US3 sediments, and that this channelled the carcasses to a specific part of the deposit (Crégut-Bonnoure *et al.*, 2017). This could explain, among other things, the relatively high frequency of skeletal remains with abrasion grooves (2%). However, some of these grooves undoubtedly are very reminiscent of anthropogenic cut marks (Fig. 7E–F). At Coulet des Roches, there is no trace of human presence or any anthropogenic activity. Therefore, to avoid any erroneous interpretation, it is essential to characterise the whole assemblage to make interpretations, since these isolated marks could easily be confused with anthropic marks. Finally, the flow of water within the cavity is also a phenomenon that significantly impacted the surface of the bones. Indeed, many bones present pits of dissolution (NISP = 1752), weathering (NISP = 134), or evidence of concretion (NISP = 41).

A taphonomical referential framework from an archaeological perspective

Several diagnostic taphonomical criteria were initially put forward to identify accidental mortality at archaeological sites (Cochard, 2004a). While the leporid assemblage from Coulet des Roches shares several similarities with this theoretical model, our results nuance some criteria previously proposed by some authors. In terms of spatial organisation, the density of the remains, both in terms of the number of remains and individuals, is indeed very high and mostly concentrated at the base of a scree cone. The theoretical model also suggests the preservation of a high number of strict anatomical connections as a discriminating criterion. However, the individuals were mainly found by sets of bones or represented by isolated remains, and no clearly articulated bones were documented at Coulet des Roches. The absence of strict anatomical connections noted during the excavation may be explained by the sedimentary movements (gravity) that caused a random

dispersion of the skeletal elements. However, their presence or absence cannot be considered as a sufficiently reliable indicator to identify accidental mortality in an archaeological assemblage, because it is also possible to find bones in approximately anatomical positions in the regurgitated pellets of certain birds of prey or in carnivore dens (Sanchís, 2000; Cochard, 2004a), as well as at anthropogenic sites (Cochard, 2005).

As expected, the anatomical representation is consistent with whole skeletons introduced into the deposit. However, indices calculated from the skeletal profile can also be found in bone assemblages accumulated by several terrestrial carnivores and are therefore not agent-specific. It is important to remain cautious as to the meaning and interpretation of anatomical representations, both in modern reference collections and in the fossil record, because of the great variability of the profiles generated by these different predators (Fig. 5). Moreover, it is also important to note that quite a few of the comparative experimental studies have been carried out with captive animals (e.g. Lloveras *et al.*, 2008b, 2012a, 2018; Álvarez *et al.*, 2012; Cohen and Kibii, 2015; Rodríguez-Hidalgo *et al.*, 2015; Armstrong, 2016a). Thus, Gidna *et al.* (2013) warn that the inappropriate use of actualism in some experimental studies, derived from inadequate contexts, can lead to erroneous analogies and, subsequently, to unsuitable interpretations when analysing prehistoric faunal assemblages.

Unlike birds of prey, which usually disarticulate their prey, preferably consuming the fleshiest portions and creating specific anatomical profiles, predators of a relatively large size such as lynxes, badgers, foxes or dholes transport their complete prey to the consumption site. Nevertheless, traces of scavenging have been found in the pitfall, but are probably the result of a secondary modification by a small terrestrial carnivore. In addition, although fractures on dry bone are the most common, some evidence of fractures on green bones was recorded at Coulet des Roches but at very low frequencies. In terms of age classes, the assemblage of Coulet des Roches is characterised by an age structure that corresponds more to the theoretical structure of a living natural population.

Ultimately, our analysis revealed five main criteria for reliably identifying the type of accidental accumulation at a fossil site:

- The lack of evidence of human exploitation of carcasses and a very low presence of predator marks.
- A relatively balanced proportion between immature and adult individuals in mountain hares, and mostly immature individuals in rabbits. This peculiarity follows the ethology of both species and differs relatively well from: 1) attritional-natural accumulations, defined by a high proportion of infants; 2) anthropogenic catches, mainly focused on adults; and 3) non-human predations characterised by a predominance of juveniles and/or subadults.
- A considerable presence of complete skeletons found in loose anatomical connection. Although few strict anatomical connections have been found at Coulet des Roches, their potential presence in a deposit remains a strong aspect in identifying natural mortality because they are generally not found in contexts related to predation.
- A relatively high proportion of complete bones coupled with moderate fracturing mainly on dry bones related to natural post-depositional processes, such as pressure and sedimentary movements or roof collapse.
- A low degree of bone surface modification, mainly related to natural phenomena such as water circulation within the karst (i.e. dissolution) or post-mortem bone movements (i.e. abrasion grooves).

Some of these features are shared with other potential agents, which may make it difficult to identify the specific agent(s) responsible for leporid bone accumulations at an archaeological or palaeontological site. Furthermore, in fossil contexts, leporid accumulations can result from successive events involving several different agents. In some cases, it is also difficult – if not impossible – to discern all the agents that contributed to the accumulation, as well as their relative shares. Relying on a single criterion is therefore unsatisfactory for determining the origin of a taphocenose or distinguishing between the multiple mechanisms and agents responsible for the creation of a bone assemblage. Consequently, it is fundamentally important to combine various taphonomic arguments (mortality profiles, skeletal-part representation, breakage patterns, degree of ossification or macro-traces) with different forms of available geoarchaeological or contextual data, including spatial distributions. Thus, considering all these indices together, it would be easier to distinguish the taphonomic signature of an accidental-natural accumulation.

Conclusion

During the Quaternary, various predators and human groups shared similar ecological niches, as well as the same habitat types in karst cavities. The remains of their respective bone accumulations can then be conjugated. As a result, in the last two decades, the study of the modifications produced by human and non-human predators on leporids, small mammals that are found very frequently and often in large numbers at archaeological sites, has occupied an increasingly significant place in (neo-)taphonomic analyses. Before being able to decide on the origin of the accumulation of their bone remains, these analyses must measure the loss of information and the sets of biases likely to be introduced by multiple agents, especially since their presence may also come from natural deposits without predation. The taphonomic study of natural sites allows the creation of frames of reference, directly comparable with data from archaeological sites. This study, concerning the accidental-natural accumulation of leporids from Coulet des Roches, presents a set of taphonomic characteristics that can help to better discern this type of accumulation.

The accumulation at Coulet des Roches is mainly characterised by a large concentration of hare and rabbit bones and individuals located in a specific part of the deposit. This bone concentration is probably related to the configuration of the pitfall and the duration of sedentary implementation, which should increase significantly over longer time periods at Coulet des Roches, and vice versa. The differences observed in this study between the two leporid species are most certainly related to their eco-ethological characteristics, which also show the importance of studying each taxon separately in fossil taphonomic studies. In general, the different anatomical elements are relatively complete, and the breaks identified are mainly due to post-depositional fragmentation. The post-depositional processes are responsible for the dislocation of the carcasses after their falls and their decompositions in the pitfall, and the fact that strict anatomical connections have never been observed. However, these patterns should be treated with some caution, as the recovery of skeletons in anatomical connection at archaeological or palaeontological sites still remains a reliable argument in situations of natural death without predation. Unlike small mammals (rodents and insectivores), minimal traces of predation (i.e. digestion or tooth marks) were observed *in situ*.

Until now, this type of accumulation has only been recognised within archaeological sites, where a presence, albeit a marginal one, of humans had been noted in the deposits. The use of the criteria presented in this study can help to evaluate the potential contribution of natural mortalities in accumulations of leporid remains at archaeological sites, which is a fundamental preliminary step for establishing the integrity of palaeo-ethnographic and palaeo-environmental interpretations.

Supporting information

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Supporting information.

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Data availability statement

Data available on request from the authors.

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