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ORIGINAL PAPER

A spotted hyaena den in the Middle Palaeolithic of Grotta Paglicci (Gargano promontory, Apulia, Southern Italy)

Jacopo Crezzini[1,2] **· Paolo Boscato**[1] **· Stefano Ricci**[1] **· Annamaria Ronchitelli**[1] **·**
Vincenzo Spagnolo[1] **· Francesco Boschin**[1,2]

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Abstract The Palaeolithic sequence of Grotta Paglicci (Gargano promontory, Apulia, Southern Italy) is one of the most important in the Mediterranean area: It comprises the whole Upper Palaeolithic cultural sequence known for the region, as well as Early Middle Palaeolithic and Lower Palaeolithic levels. These earlier phases are best represented in a collapsed room located outside the present-day cave (the so called "external rock shelter"). In this area, a new excavation, started in 2004, brought to light Middle Palaeolithic animal remains associated with evidence of spotted hyaena (SU 64 and 53). The spatial distribution analysis of remains from SU 53 revealed the presence of a bone accumulation area and a wider dispersal of hyaena coprolites. Three main ungulate species (aurochs, fallow deer and red deer) as well as carnivores (spotted hyaena, wolf, fox, wild cat and lynx) and lagomorphs have been identified. The majority of aurochs remains are located in the main accumulation; among these specimens, a complete metatarsal connected with three tarsal bones has been found; a talus and a complete tibia, probably belonging to the same limb, have also been identified. The multidisciplinary study carried out in this paper highlights a specific bone accumulation and scattering pattern in a spotted hyaena (*Crocuta crocuta*) den. In addition, taphonomy of lagomorph remains indicates the presence of other depositional agents.

Keywords Hyaena den · Taphonomy · GIS · Spatial analysis · Grotta Paglicci · Middle Palaeolithic

Introduction

The taphonomic study of hyaenas is essential for a better understanding of hominin subsistence strategies. Hyaena's geographical distribution overlapped with that of hominins in Africa and Eurasia, and the interactions between these taxa are considered of crucial importance for human evolution. Moreover, since hyaenas are bone accumulators, the understanding of modifications induced by these taxa on bones is important for shedding light on the origin of zooarchaeological assemblages (Pokines and Kerbis Peterhans 2007).

Bone remains from Atapuerca (Spain) attested that from at least 800 ka, the spotted hyaena (*Crocuta crocuta*) entered Europe via the Middle East (García and Arsuaga 2001; Martinez-Navarro et al. 2009). The earliest evidence of this taxon in Italy is from Casal Selce (Italy), Ponte Galeria Formation, referred to as MIS 18 (Sardella and Petrucci 2012). Both dating and evidence from faunal assemblages seem to show that disappearance of this taxon in Europe occurred before the Last Glacial Maximum (Stuart and Lister 2015). The latest evidence in Italy was found at Grotta Paglicci (Foggia, Italy) where an early Epigravettian layer yielded two spotted hyaena remains (Boscato and Palma di Cesnola 2000).

The coexistence of humans and hyaenas in Europe is recorded by a number of sites from the early to the late Pleistocene (Brugal and Jaubert 1991; Moullé 1992; Fernández Rodríguez et al. 1995; Villa and Bartram 1996; Arrizabalaga and Altuna 2000; Enloe et al. 2000; Diedrich 2010; Villa et al. 2010; Patrocinio Espigares et al. 2013). This evidence has also been attested in some palaeolithic sites in Italy (Pitti and Tozzi

✉ Jacopo Crezzini
jacopocrezzini@gmail.com

[1] U.R. Preistoria e Antropologia, Dipartimento di Scienze Fisiche, della Terra e dell'Ambiente, Università degli Studi di Siena, via Laterina 8, 53100 Siena, Italy

[2] Centro Studi sul Quaternario Onlus, via Nuova dell'Ammazzatoio 7, 52037 Sansepolcro, Arezzo, Italy

1971; Piperno and Giacobini 1991; Stiner 1991, 2004; Boscato 1994; Bonfiglio et al. 2001; Boscato and Crezzini 2005; Moroni Lanfredini et al. 2010); intensive competition between hominins and hyaenas to access carrion is documented at some sites (Patrocinio Espigares et al. 2013).

The result of the alternation of humans and spotted hyaena within the same site, or the mutual food scavenging is the reason for the contemporary presence of both human and hyaenid modifications on bones in some assemblages. Since this may confuse the interpretation of the origin of bone accumulations, a number of studies on the taphonomy of hyaenas have been carried out in the recent decades (Mills and Mills 1977; Hill 1984; Skinner et al. 1986; Binford et al. 1988; Cruz-Uribe 1991; Boaz et al. 2000; Pickering 2002; Pokines and Kerbis Peterhans 2007; Fourvel 2012).

Spotted hyaena can be considered as a ubiquitous taxon living at present in a wide range of environments, including arid areas (rarely deserts), savannah, woodlands (rarely rainforests), and high-altitude habitats up to 4100 m above sea level (a.s.l.) (Höner et al. 2008). The occurrence of spotted hyaena in Europe during the Pleistocene is recorded in both temperate and glacial episodes up to 600 m a.s.l (Clot and Duranthon 1990; Döppes and Rabeder 1997; Stuart and Lister 2015).

Studies on extant spotted hyaenas demonstrate that these carnivores hunt the great part of their own prey, which can vary seasonally (Salnicki et al. 2001). It is assumed that Pleistocene spotted hyaena in Europe had a broad spectrum of prey and was an active hunter rather than a scavenger (Stiner 2004; Bocherens et al. 2005; Diedrich 2010). Extant spotted hyaenas consume the choicer parts of a carcass at the killing site and then dismember and transport other parts (Kruuk 1972). Transport of bones or meat to provision the offspring is rarely attested (Kruuk 1972; Hill 1980a). This only occurs until the juvenile individuals are grown-up enough to feed at the killing sites. This is confirmed by the rate of bone accumulation observed by Pokines and Kerbis Peterhans (2007) in a cave den in the Masai Mara National Reserve (Kenya): About 30 identified specimens and four individuals were accumulated per year.

In Europe, other large carnivores frequenting caves do not accumulate bones, even if part of the carcass is brought to the den for feeding offspring, such as for instance the case of the wolf (*Canis lupus*) (Peters 1993). Among smaller carnivores, the fox (*Vulpes vulpes*) and the badger (*Meles meles*) can transport carcasses into caves. Whilst the fox accumulates bones in its sett (Mallye et al. 2008), the badger cleans up its setts accumulating bones in the area next to the entrances (Roper et al. 1991; Lüps and Wandeler 1993). Both species mostly accumulate mesomammal and bird remains and, therefore, their accumulations can be separated from those of hyaena.

The aim of this work is to carry out an in-depth study of a Middle Palaeolithic bone assemblage from the so-called "external rock shelter" of Grotta Paglicci (Apulia, Southern Italy) that is supposed to be the result of hyaena activities.

The site

Grotta Paglicci opens on the southwestern side of Gargano promontory (Rignano Garganico, Foggia), in Southern Italy at an altitude of about 143 m a.s.l. (Catasto delle Grotte della Puglia - N. 300). The site comprises the present-day cave and a rock shelter that originated from the collapse of a first chamber of the same hypogean system (Fig. 1). The first excavations, carried out in the cave, were directed by the Natural History Museum of Verona from 1961 to 1963. From 1971 to 2001, excavations were led by Prof. A. Palma di Cesnola of the University of Siena, who also extended the stratigraphic research to the rock shelter. From 2002 until today, the research activities have been directed by Prof. A. Ronchitelli of the same University. Grotta Paglicci is one of the most important Palaeolithic sites of southern Europe, where human occupation is attested during the Lower, Middle and Upper Palaeolithic (Palma di Cesnola 1993, 2004, 2006; Wierer 2013; Revedin et al. 2015; Ronchitelli et al. 2015; Ricci et al. 2015).

The first excavations in the rock shelter area uncovered four layers (numbered from 1 to 4) yielding Middle Palaeolithic and Acheulean stone tools (Mezzena and Palma di Cesnola 1971). More recent excavations, carried out from 2003 to 2006, explored a wider area of 20 m^2 (Fig. 2) and led to a better understanding of the stratigraphy, characterised by alternate of human/carnivore occupation phases and cave vault collapsing phases (Boscato and Ronchitelli 2006). In particular, it was discovered that at the time of the identified periods of occupation, the excavated area was part of a cave, the extension of which progressively reduced phase after phase. More specifically, the northern area collapsed first, as documented by the immersion of the limestone rocks at the top of layer 2. Then, the southern area collapsed (SU 53). In the northwestern part of the cave, a Middle Palaeolithic human occupation is attested in the squares O/P 6/7 (SU 56/55/54/64), where a rock shelter was probably still existing. In SU 50 and in the superimposed layer 1, evidence of Middle Palaeolithic human activities was found (Palma di Cesnola 2001; Boscato 2001). Finally, the large rocks in the eastern area attest the last collapse of the cave. No radiometric dates are available for the rock shelter area. However, layer 1 related to the excavation directed by A. Palma di Cesnola yielded two remains of *Iberomys brecciensis* that became extinct in Italy during the Late Middle Pleistocene–Early Late Pleistocene (Lopez Garcia et al. 2015). Such evidence can be considered a terminus *post quem* for the archaeological context investigated in this work.

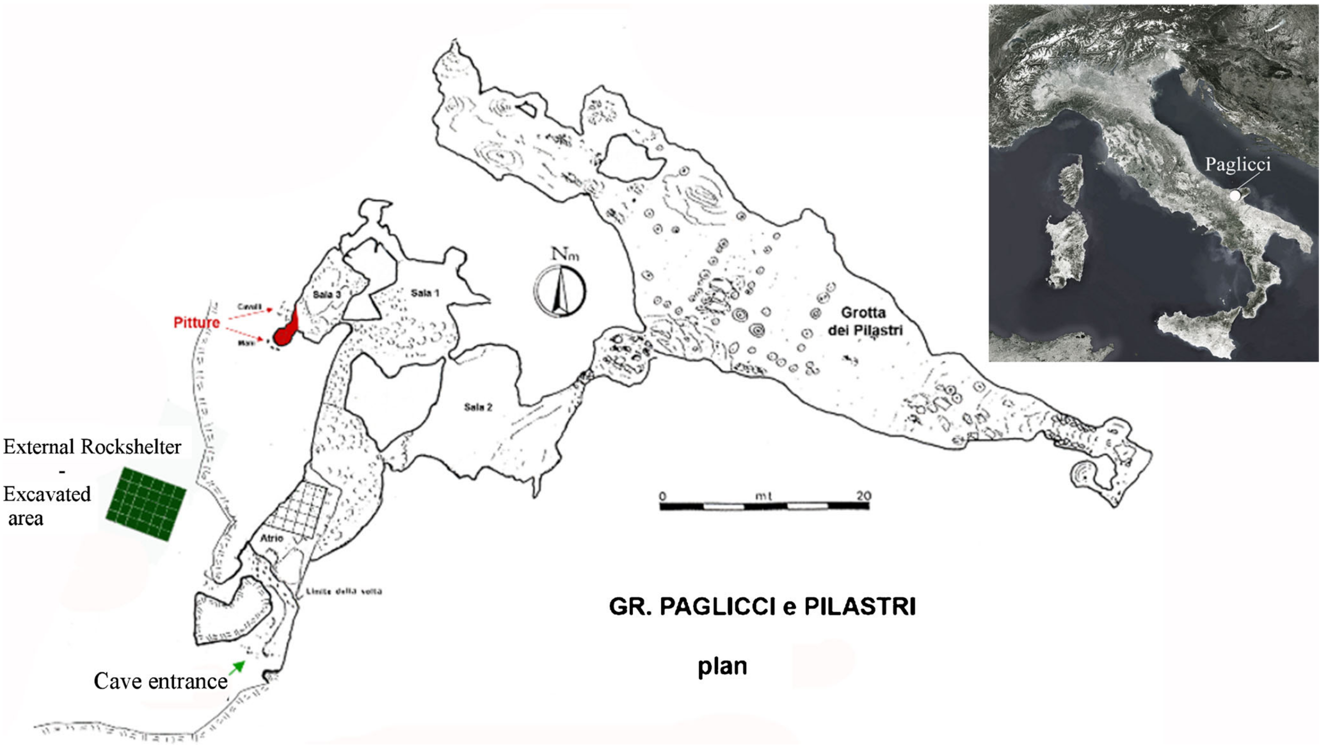

Fig. 1 Site location and excavated areas

SU 53/2 shows peculiar characteristics that have not been observed in other layers: In particular, a bone accumulation area and several hyaena coprolites have been discovered. Some bones (aurochs limb bones) are complete and, among these specimens, a complete metatarsal connected with three tarsal bones, a talus and a complete tibia, probably belonging to the same limb, have been identified. In addition, one unilateral straight scraper (square P8), one burnt denticulate point (northeastern quadrant of Q10), sporadic little flakes and rare flint debris (the intrusive origin of which cannot be excluded) are the only evidence of human presence in this stratigraphical unit.

Faunal remains found in layer 53/2 were accumulated between collapsed rocks. It has to be pointed out that at the time of this bone accumulation, a part of the cave vault still existed. Voids formed between the collapsed limestone blocks were suitable for carnivore or lagomorph dens. Layer 64, which yielded few traces of human use as well as marks left by carnivores, covered layer 53/2. After this phase, the cave vault collapsed in this area (SU 50) (Boscato and Ronchitelli 2006) (Fig. 3).

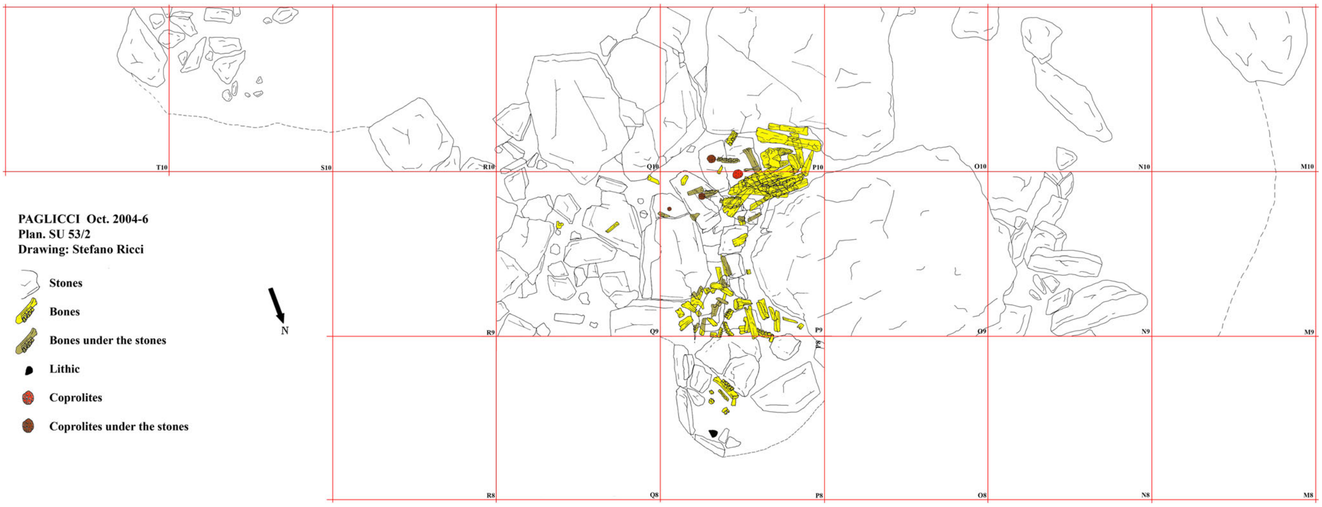

Fig. 2 SU 53/2: excavated area showing bone accumulations

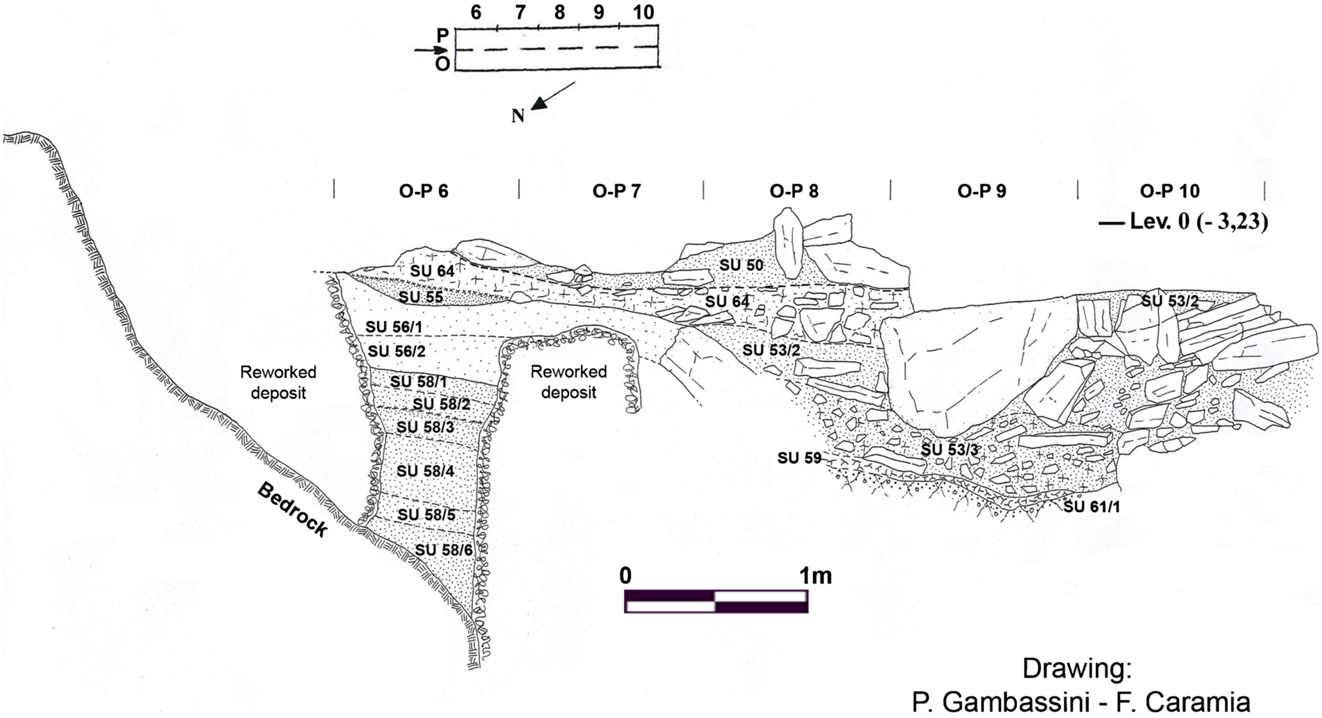

Fig. 3 Site stratigraphy

Material and methods

The archaeological excavation was carried out recording the precise position of rocks in the whole area and bones where the main bone accumulations were detected. The whole removed sediment was sieved through 1-mm mesh. Spatial distribution of remains was elaborated using ArcGIS® 10.2. Spatial data were managed through a specifically designed geodatabase for data collection and analysis. Spatial patterns of the finds were analysed through the Square Count Method (Connolly and Lake 2006) referring to the grid of excavation (squares 100 cm × 100 cm).

The total assemblage presented here consists of 5742 faunal remains, of which 622 were identified at a taxonomic level using the osteological reference collection housed at the University of Siena.

Skeletal frequencies were evaluated using the minimum number of elements (MNE, *sensu* Lyman 1994) and the minimum number of animal units (MAU, Binford 1984), even if it must be taken into account that these are derived measures and should be used carefully (see Lyman 2008 for a synthesis). The standardised percentage of MAU (%MAU) was obtained dividing each value by the highest MAU value in the assemblage. Structural density data of skeletal elements proposed by Pavao and Stahl (1999) and Lam et al. (1999) were used to quantify bone attrition in lagomorphs and cervids. Scan sites in the same element were considered separately. The density of every scan site has been compared with its abundance in the assemblage, expressed as a %MAU value.

Skeletal frequencies of cervids were also discussed considering utility indexes proposed by Binford (1978) for caribou, whilst skeletal frequencies of lagomorphs were discussed using some indexes proposed by Lloveras et al. (2008a, b). As explained by the authors, these indexes are as follows:

PCRT/CR - total numbers of postcranial elements compared with total numbers of mandibles, maxillae and teeth
PCRAP/CR - appendicular skeleton elements compared with mandibles, maxillae and teeth
PCRLB/CR - humerus, radius, ulna, femur and tibia compared with mandibles and maxillae
AUT/ZE - metapodials, carpals, tarsals and phalanges compared with tibia, radius, ulna, humerus, femur and patella
Z/E - tibia, radius and ulna compared with femur and humerus
AN/PO - humerus, radius, ulna and metacarpus compared with femur, tibia and metatarsus

Carnivore-induced bone modifications were recorded according to Binford (1981) and, in addition, ungulate limb specimens were divided into the following categories according to the intensity of bone consumption:

1. Complete elements bearing tooth marks
2. Complete elements showing partially destroyed epiphyses

3. Diaphysis cylinders
4. Diaphysis fragments showing tooth marks
5. Digested fragments

The unidentified bones were divided into the anatomical categories proposed by Boscato and Crezzini (2012). Once anatomically classified, all specimens were further divided into four metric classes (considering the maximum length), with a size between 1–3 cm, 3–6 cm, 6–10 cm, and >10 cm. Taphonomic analysis was carried out on bone fragments of all sizes. Fresh-bone fractures of diaphysis fragments were recorded using the Fracture Freshness Index (FFI) proposed by Outram (2002).

Results

The taxonomic identification was strongly influenced by fragmentation, since the bulk of the assemblage (94 % of remains) is grouped in the size class “1–3 cm” (Table 1). The faunal association indicates mild climatic conditions. Among the ungulates, taxa belonging to the cervids (fallow deer, red deer and roe deer) represent about 80 % of the number of identified specimens (NISP). Aurochs (*Bos primigenius*) is represented by the 17.52 % of NISP (Table 2). The absence of equids (horse and European ass) is remarkable, since their remains are abundant at Paglicci in colder and drier phases of Upper Palaeolithic (Sala 1983; Boscato 1994; Boscato and Crezzini 2005). A great variety of carnivore taxa, represented by few specimens, has been identified. The most frequent species are wolf (NISP=26) and red fox (NISP=35). Deciduous teeth of wolf and lynx (*Lynx lynx*) were also recorded. Lagomorph remains are also very abundant (NISP=310).

Table 2 Faunal composition

	NISP	%NISP	MNI			Carnivore modifications
			Young	Adult	Senile	
Sus scrofa	2	0.8				
Bos primigenius	41	17.6	2	1		2
Rupicapra sp.	3	1.3		3		
Cervus elaphus	76	32.5	2	1	1	1
Dama dama	99	42.3	2	3	1	12
Capreolus capreolus	5	2.1	1	2		1
Cervidae	8	3.4				
Tot ungulates	234	100				
Lepus corsicanus	18	4.6				3
Oryctolagus cuniculus	212	54.5				17
Leporidae	81	20.8				
Tot Lagomorpha	311		2	7		
Ursus arctos	1	0.3		1		
Lynx lynx	3	0.8	1	1		
Felis silvestris	6	1.5		1		
Crocuta crocuta	4	1		1		
Canis lupus	26	6.7	1	1		
Canis sp.	3	0.8				
Vulpes vulpes	35	9.00		3		
Tot Carnivora/ Lagomorpha	389	100				

NISP number of identified specimens, *MNI* minimum number of individuals

The skeletal profiles of the main ungulate taxa are shown in Table 3. Ungulate skulls and mandibles are over-represented due to the presence of well-preserved teeth. Axial elements are rare (there are rib and vertebral fragments among the unidentified specimens). Regarding the fallow deer (*Dama dama*) (the most frequent ungulate), elements of the appendicular skeleton are not abundant. Carpal and tarsal bones are rare whilst phalanx 3 is the most highly represented post-cranial element (Table 3). Considering lagomorph remains (Table 4), the skeletal representation differs: long bones, as well as talus and calcaneum, are well represented. The relative abundance of elements (RA%), as defined by Dodson and Wexler (1979), indicates a substantial loss of bones (RA% mean=28.78). Indexes proposed by Lloveras et al. (2008a) indicate the following: A general deficiency in the number of postcranial remains (PCRT/CR=40.66; PCRAP/CR=57.84), a

Table 1 Size of specimens

	Squares												
Size classes	M9	M9-10	N9	N10	O10	P8	P9	P10	Q9	Q10	R10	TOT	TOT%
1–3 cm	54	8	864	252	261	3	1396	514	1596	244	201	5393	93.9
3–6 cm	5	1	39	9	21	3	102	1	69	5	6	261	4.5
6–10 cm	0	0	3	0	0	2	31	4	9	0	1	50	0.9
>10 cm	0	0	0	0	0	1	27	9	1	0	0	38	0.7
TOT	59	9	906	261	282	9	1556	528	1675	249	208	5742	

Table 3 Skeletal frequencies of main ungulate taxa

	MNE			MAU		
Elements	*Bos primigenius*	*Cervus elaphus*	*Dama dama*	*Bos primigenius*	*Cervus elaphus*	*Dama dama*
Skull	4	5	2	4	5	2
Mandible	2	9	6	2	9	6
Vertebra	0	1	0	0	0.04	0
Scapula	0	0	1	0	0	0.5
Humerus prox.	0	0	0	0	0	0
Humerus dist.	0	0	4	0	0	2
Radius prox.	2	1	2	1	0.5	1
Radius dist.	0	0	0	0	0	0
Metacarpal prox.	2	1	1	1	0.5	0.5
Metacarpal dist.	1	1	0	0.5	0.5	0
Innominate	0	1	0	0	0.5	0
Femur prox.	0	0	0	0	0	0
Femur dist.	0	0	1	0	0	0.5
Tibia prox.	1	0	0	0.5	0	0
Tibia dist.	1	1	2	0.5	0.5	1
Calcaneum	1	0	0	0.5	0	0
Astragalus	4	0	1	2	0	0.5
Other tarsal bone	4	2	2	0.67	0.33	0.33
Metatarsal prox.	4	1	3	2	0.5	1.5
Metatarsal dist.	3	0	0	1.5	0	0
Metapodial dist.	2	0	2	0.5	0	0.5
Phalanx 1 prox.	0	0	2	0	0	0.25
Phalanx 1 dist.	0	1	2	0	0.13	0.25
Phalanx 2 prox.	2	0	1	0.25	0	0.13
Phalanx 2 dist.	2	2	2	0.25	0.25	0.25
Phalanx 3	1	5	14	0.13	0.63	1.75

MNE minimum number of elements, *MAU* minimum number of animal units, *prox.* proximal, *dist.* distal

good representation of long bones (PCRLB/CR=116.13), a loss of distal elements among limb bones (AUT/ZE=50.46), a better representation of stylopodium elements compared to the zygopodium (Z/E=59.65), and a similar representation of anterior and posterior limbs (AN/PO=91.94).

Faunal remains bearing carnivore-induced bone modifications are reported in Tables 1 and 5. These are referred both to ungulates and lagomorphs. Diaphyseal fragments show fresh-bone fractures as demonstrated by the low FFI values (Table 6). A number of specimens bearing dry-bone fractures are also represented by high FFI values.

In spite of the depositional context characterised by cave collapse, destruction of bones does not seem to be density-mediated: Even if not significant (R=0.2; p=0.48), a negative regression between bone density and patterning of skeletal part frequencies of red deer and fallow deer has been observed (Fig. 4a). This evidence also seems to be confirmed also by a weak and not significant relationship between skeletal part frequencies of lagomorph taxa and bone density (R=0.02; p=0.46; Fig. 4b).

A negative regression between cervid skeletal parts frequencies and the grease content within the bone tissue (R=0.15; p=0.07) was also observed. Although not significant, the p value has to be treated as borderline (Fig. 4c).

The spatial evidence both for the faunal remains and the coprolites highlights a marked concentration in squares P9 and Q9 (Fig. 5a). The main concentration of faunal remains seems to fill the space between the large stones found in this stratigraphic unit (Fig. 2).

Significant differences have been observed in the frequency of the main taxa (lagomorphs, fallow deer, red deer and aurochs) and the distribution patterns (Figs. 5b and 6). As demonstrated by the χ^2 test, this pattern is not attributable to a random model (null hypothesis). In the χ^2 contingency table (Table 7), the individual distribution of the main identified taxa (lagomorphs, fallow deer, red deer and aurochs) was compared in the areas bearing a significant number of

Table 4 Lagomorph remains: skeletal frequencies and relative abundance (RA%) of elements

Elements	MNE	MAU	RA%
Skull	14	7	77.78
Mandible	12	6	66.67
Vertebra	3	0.13	1.39
Rib	3	0.13	1.39
Scapula	3	1.5	16.67
Humerus	10	5	55.56
Ulna	5	2.5	27.78
Radius	3	1.5	16.67
Metacarpal	20	2	22.22
Pelvis	2	1	11.11
Femur	9	4.5	50
Patella	3	1.5	16.67
Tibia	9	4.5	50
Calcaneum	8	4	44.44
Astragalus	10	5	55.56
Other tarsal bone	1	0.13	1.39
Metatarsal	13	1.63	18.06
Metapodial dist.	32	1.78	19.75
Phalanx 1	33	1.83	20.37
Phalanx 2	25	1.56	17.36
Phalanx 3	22	1.22	13.58

MNE minimum number of elements, *MAU* minimum number of animal units

Table 6 FFI values recorded on diaphysis fragments following Outram (2002)

FFI	NISP
0	16
1	20
2	20
3	13
4	10
5	8
6	12
TOT	99

FFI Fracture Freshness Index, *NISP* number of identified specimens

identified faunal remains (χ^2=85.53; *d.f.* = 12; $p<0.001$). The measures of the clustering degree of each taxa have been evaluated using Getis-Ord General G statistic (ArcGIS® 10.2). Given the *z*-scores of the lagomorphs, the fallow deer and the red deer do not appear to be significant, while for the aurochs (*z*-score=1868), it is possible to assert that there is less than 10 % probability that the high-clustered pattern could be the result of random chance (Table 8).

In contrast with the extremely clustered distribution of *B. primigenius* remains, the dispersal mode of the cervids and, particularly, of the lagomorphs is wider. The high concentration of *B. primigenius* remains in P9 can be related to the presence of remains attributable to the same limb, as documented by the anatomical connection of some elements (tibia, tarsals and metatarsus). In the same square P9, the remarkable number of juvenile lagomorph remains could also have the same meaning, namely, the presence of several elements of a single individual.

Furthermore, also the spatial pattern of the long bone reduction stages (clearly correlated with the spatial configuration of dimensional classes) produces a varied frame. The first stages of the reduction sequence are well clustered in and around square P9, while the advanced stages of reduction and digestion are more dispersed (Fig. 7). This distribution is only partially related to the presence of the almost complete aurochs hind limb, since in P9 ungulate bones grouped in classes 1 to 3 belong to at least eleven limbs.

Table 5 Carnivore-induced bone modifications following Binford (1981)

	M9-10 L.M.	M9 L.M.	M9 Lag.	N9 L.M.	N10 L.M.	N10 Lag.	P9 L.M.	P9 Lag.	P10 L.M.	O10 L.M.	O10 Lag.	Q9 L.M.	Q10 L.M.	Q10 Lag.	R10 L.M.	TOT Lag.
Crenulated edges	0	0	0	0	1	0	5	0	0	0	0	1	0	0	0	7
Pitting	0	0	0	1	0	2	4	3	1	0	3	4	0	0	0	18
Punctures	0	0	0	2	0	0	7	0	2	1	0	4	0	0	0	16
Scoring	0	0	0	1	0	2	1	0	0	1	1	0	1	0	2	9
Furrows	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	3
Scooping out	0	0	0	1	0	0	3	0	1	0	0	0	0	0	0	5
Digested bones	0	0	1	4	0	4	3	2	1	4	1	10	2	1	0	33
Cones	1	0	0	3	0	0	1	0	0	0	0	5	0	0	0	10
Notches	0	0	0	0	0	0	3	0	0	0	0	3	0	0	0	6
TOT	1	0	1	12	1	8	27	5	5	6	5	29	3	1	3	107

Data are divided per squares

L.M. large mammals, *Lag.* lagomorphs

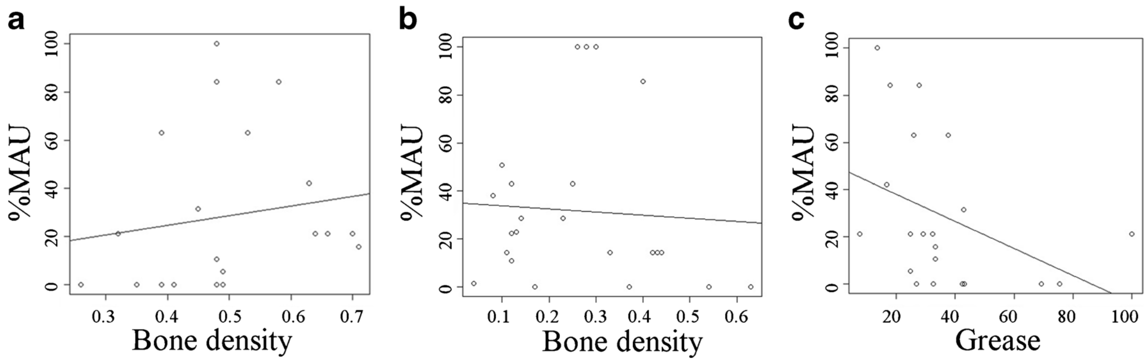

Fig. 4 **a** Relation between %MAU of red and fallow deer and bone density. **b** Relation between %MAU of lagomorphs and bone density. **c** Relation between %MAU of red and fallow deer and grease content within bone tissue

Discussion

Since the first pioneering researches on carnivores as taphonomic agents, scholars focused mainly on the identification of chewing and digestion marks on faunal assemblages (e.g. Henschel et al. 1979; Binford et al. 1988; Pokines and Kerbis Peterhans 2007; Egeland et al. 2008; Conti et al. 2012; Fourvel et al. 2012, 2014). The spatial component of the

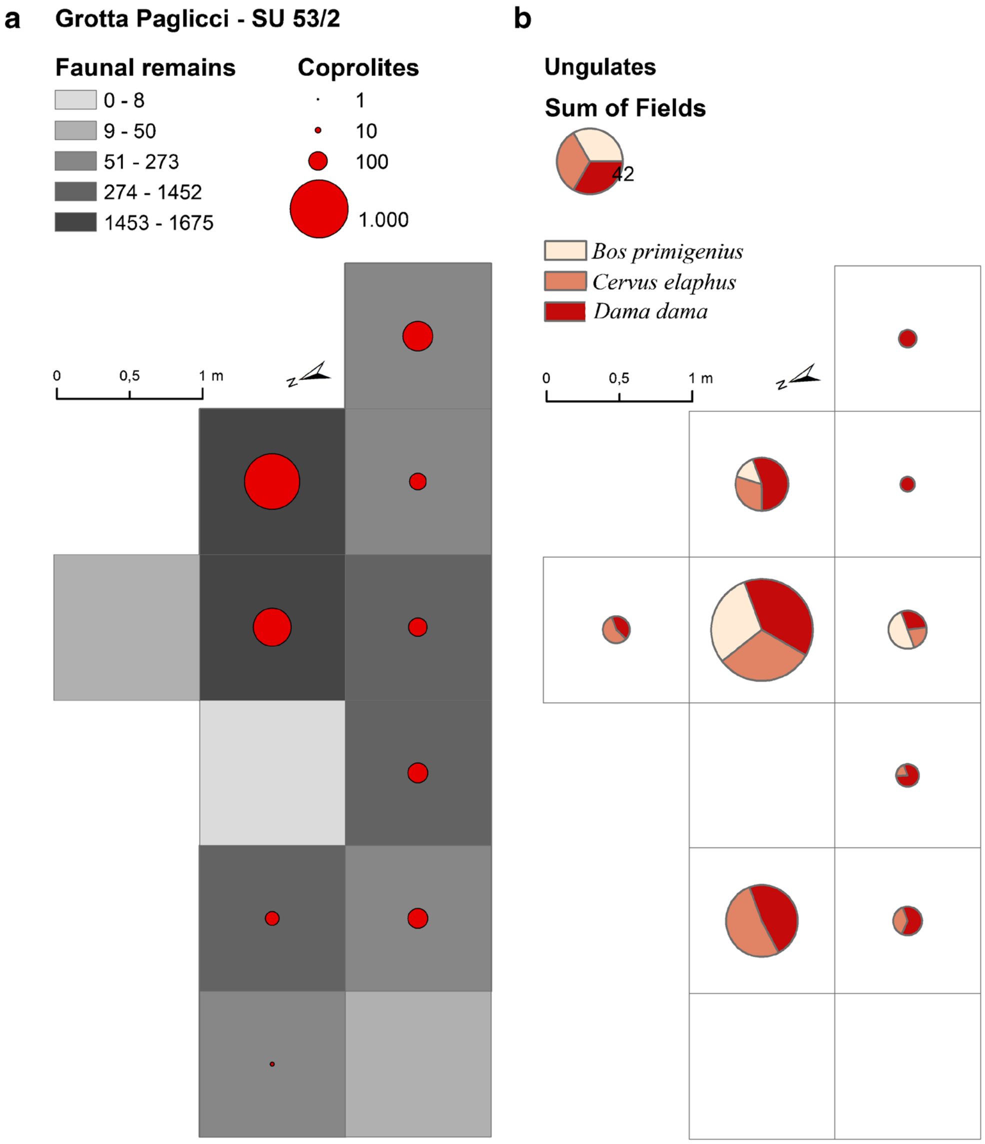

Fig. 5 **a** Density map of the faunal remains (NISP) and coprolites (g) distribution. **b** Distribution of the main ungulate taxa

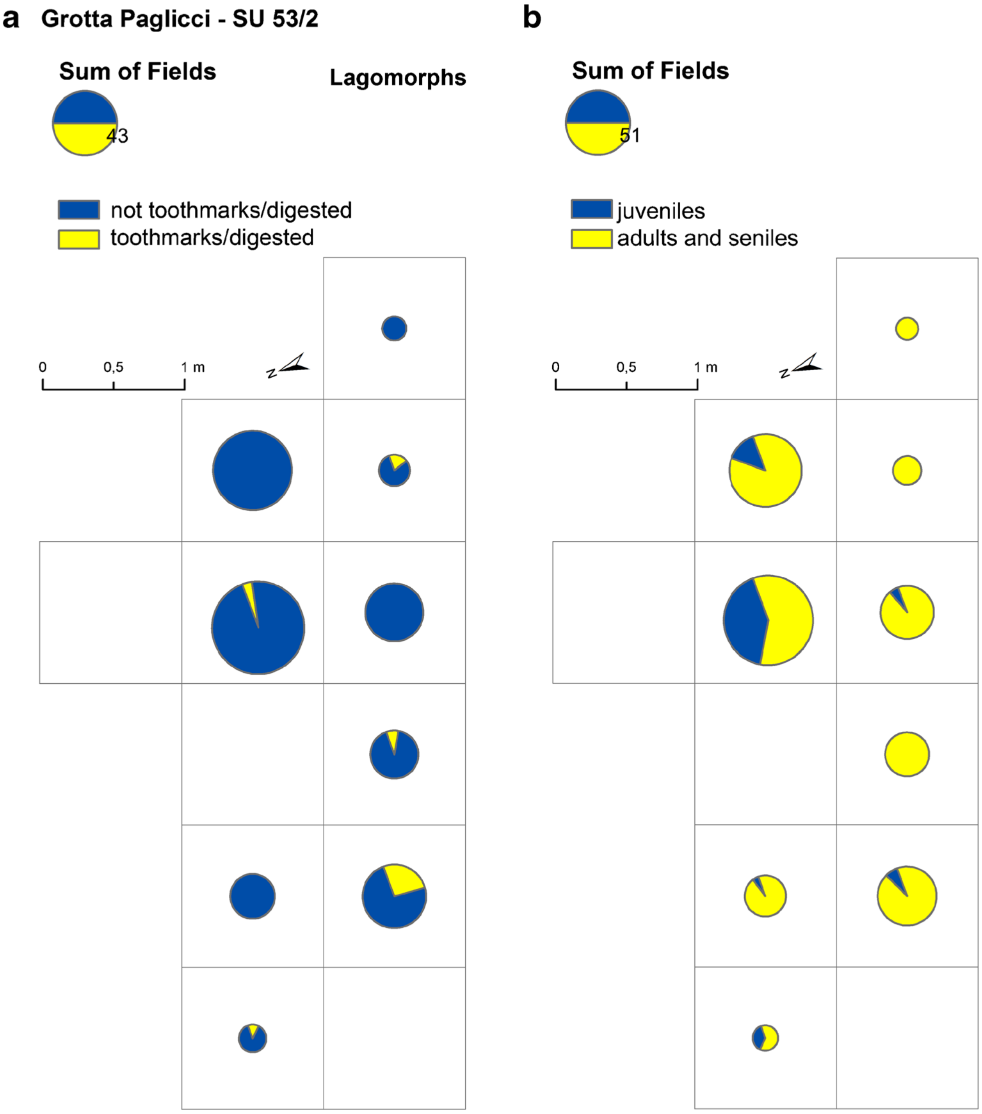

Fig. 6 Lagomorphs. **a** Tooth-marked/digested bones in relation with carnivore-unmodified specimens. **b** Distribution of remains in relation with the age classes

spotted hyaena dens was mainly debated in some taphonomic studies and, often marginally, in some ethological researches (e.g. Potts et al. 1988; Arribas and Palmqvist 1998; Boydston et al. 2005, 2006; Fourvel 2012).

The study of SU 53/2 of Grotta Paglicci has clearly evidenced a bone accumulation produced by carnivore activity. The presence of spotted hyaena coprolites, together with the evidence of transport at the site of partial carcasses of large-

Table 7 Contingency table of the χ^2 for the distribution of lagomorphs, fallow deer (*Dama dama*), red deer (*Cervus elaphus*) and aurochs (*Bos primigenius*), with the observed values (O), the expected values (E) and the χ^2

	Lagomorphs			*Dama dama*			*Cervus elaphus*			*Bos primigenius*			TOT	
	O	E	χ^2	O	E	χ^2	O	E	χ^2	O	E	χ	O/E	χ^2
N9	20	39	9.033	24	14	7.774	26	11	19.696	0	6	6.449	70	42.953
P9	93	107	1.757	39	38	0.043	31	31	0.001	30	18	8.395	193	10.196
Q9	60	48	2.947	15	17	0.237	8	14	2.492	4	8	2.012	87	7.688
N10	38	25	6.214	5	9	1.773	3	7	2.566	0	4	4.238	46	14.791
P10	35	27	2.311	4	10	3.250	3	8	2.969	7	5	1.368	49	9.899
TOT	246		22.263	87		13.077	71		27.723	41		22.463	445	85.526

Table 8 Results of the Getis-Ord General G analysis on the distribution of lagomorphs, fallow deer (*Dama dama*), red deer (*Cervus elaphus*) and aurochs (*Bos primigenius*)

	Lagomorphs	*Dama dama*	*Cervus elaphus*	*Bos primigenius*
Observed General G	0.532	0.416	0.328	1.000
Expected General G	0.394	0.394	0.394	0.394
Variance	0.011	0.021	0.041	0.105
z-score	1.304	0.151	−0.325	1.868
p value	0.192	0.880	0.745	0.062

sized prey (aurochs), implies that the bone accumulation was mainly due to hyaena activities. Other large carnivores identified at the site (wolf and lynx) are not bone accumulators (Hemmer 1993; Peters 1993). The bones appear to fill the spaces between stones; their disposal pattern and orientation probably were influenced by several biostratinomic processes. The analysis of the spatial arrangement of large mammal remains highlights a recurrent bone processing pattern: In particular, the first carcass processing phases (transport of the anatomical district, incipient disarticulation and initial gnawing of epiphysis) seem to take place within a specific area (around square P9). Here an almost complete lower hind limb of aurochs was also recovered in an anatomically coherent disposition. This evidence could indicate an abandonment of the den by the hyaenas before the exploitation of this anatomical part. Fragments related to advanced stages of bone destruction processes (phases 4 and 5) are dispersed over a wider area. As would be expected, there is a spatial correlation

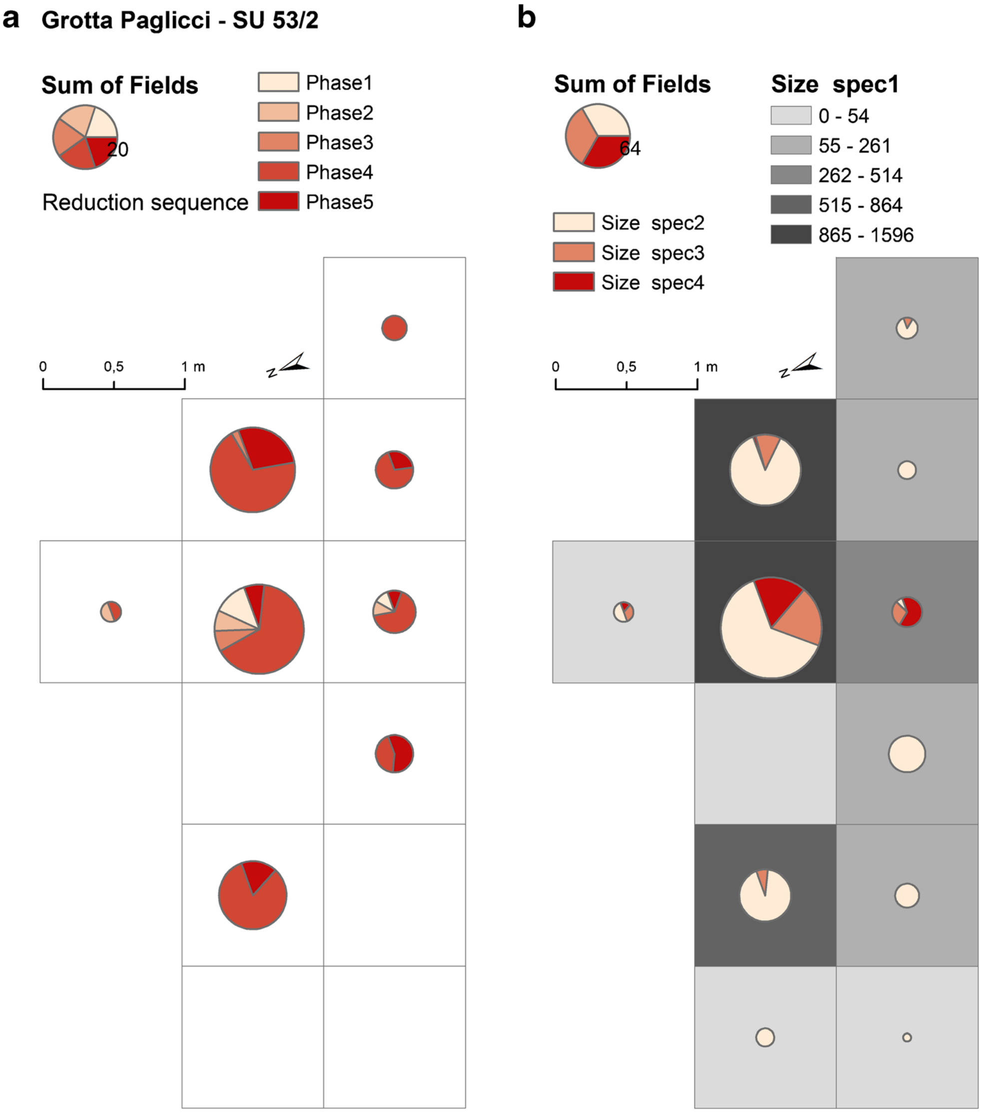

Fig. 7 **a** Long bone reduction sequence. **b** Dimensional classes of bone specimens

between the bone processing stages and the dimensional classes, namely, the bigger specimens are clustered in the same area of the first reduction stages, while the smaller ones follow a more dispersed pattern.

Faunal association, characterised by an overwhelming presence of cervid taxa could indicate an active hunt to mid-sized ungulates carried out by spotted hyaena, confirming modern data (Fourvel 2012; Kruuk 1972; Mills 1985). On the other hand, scavenging activities cannot be excluded given the presence of aurochs remains. Regarding the lower hind limb from square P9, the presence of tooth scores on the metatarsal shaft can attest to an action of disarticulation and transport of the limb to the den; since the shaft of the tibia does not bear tooth marks, the absence of muscular masses at the moment of disarticulation can be supposed (thus indicating scavenging). A characteristic of hyaena accumulations is that the cranial/postcranial ratio decreases with ungulate size (a pattern almost certainly related to transportation, Hill 1980b; Cruz-Uribe 1991). In SU 53/2, cervids are better represented by cranial bones and aurochs is better represented by postcranial ones; cranial/postcranial ratios, calculated with MNE, are 0.34 and 0.28, respectively (Table 3). As suggested by some authors, the consumption of limb bones by spotted hyaena follows a precise sequence (Zapfe 1942; Wernert 1955; Hill 1980b). To this regard, distal humerus, proximal radius, proximal metapodials and distal tibia are more frequent than the opposite epiphyses of the same elements. One exception is represented by aurochs metacarpal and metatarsal bones, due to the high frequency of complete elements. It has to be pointed out that destruction of ungulate spongy bones in US 53/2 seems to be correlated to grease consumption carried out by hyaenas (even if p value is borderline, $p=0.07$). The lower hind limb of aurochs from square P9 could point to an initial exploitation of this anatomical part by hyaenas: The only missing tarsal bone is the calcaneum, which is frequently the first one to be consumed (Zapfe 1942; Hill 1980b). Lagomorph remains show a different spatial distribution pattern from that of ungulates; the concentration of juvenile lagomorph specimens in the square P9 is characterised by the presence of right and left metapodials clearly belonging to the same paws, of right and left unfused epiphyses of the same size, and of other skeletal elements (e.g. phalanges, tarsal bones and one mandible with deciduous teeth) referable to the same growth stage. This indicates the presence of a not scattered carcass of an individual whose age-at-death was less than 3 to 5 weeks (Habermehl 1985). The skeletal element representation of lagomorph taxa is very different from that recorded in bone accumulations resulting from terrestrial carnivore activities (not ingested bones) (Lloveras et al. 2012; Rodríguez-Hidalgo et al. 2013). On the contrary, it is similar to that referable to accumulations due to bird raptors and terrestrial mammals (scat) (Lloveras et al. 2008a,b, 2009, 2012, 2014a,b). These accumulations differ from that found at Paglicci due to a much higher presence of digested remains, which are quite rare in the SU 52/2 (Table 5), and to a different representation of long bone's proximal epiphyses in comparison to the distal ones (at Paglicci, the proximal/distal epiphyses ratio, P/D, is 1.1). Thus, the peculiar characteristics of the lagomorph assemblage at Paglicci can be due to a mixing of both *Lepus*/*Oryctolagus* natural accumulation (den?) and predator activities.

Conclusions

Our multidisciplinary study (including zooarchaeological, taphonomic and spatial distribution analyses) allowed us to shed light on patterns of bone accumulation and scattering indicating a specific behaviour of *Crocuta crocuta*. SU 53/2 has to be considered as a palimpsest representing an interruption of Middle Palaeolithic human occupation at Grotta Paglicci. The faunal assemblage and taphonomic interpretation suggest a sequence of site occupation by different taxa, at different times. In addition to the spotted hyaena den, which was probably abandoned before the complete exploitation of some transported carcasses, other occupations can be hypothesised. Different mammal carnivores or bird raptors were responsible for a part of the lagomorph bone accumulation, but also the presence of *Lepus*/*Oryctolagus* dens cannot be excluded. Furthermore, our study confirmed observation carried out by other authors regarding patterns of bone transport and exploitation by spotted hyaena (e.g. Zapfe 1942; Wernert 1955; Hill 1980b; Cruz-Uribe 1991), thus corroborating the hypothesis that archaeological bone accumulations due to spotted hyaena can be distinguished from those due to human activities. Results obtained by spatial analysis indicates that this study can further contribute to our knowledge on past carnivore behaviour. Further studies on other archaeological assemblages or observations of living populations are needed to confirm if the spatial pattern of accumulation and scattering of carcasses observed in the SU 53/2 of Grotta Paglicci was induced by local environmental characteristics or if it can be considered as a distinctive behaviour of spotted hyaena. If confirmed, spatial analysis could provide new useful information for characterising bone accumulations of different carnivore species. In addition, the active hunting of cervid populations (red deer and fallow deer) carried out by spotted hyaena in the surroundings of Grotta Paglicci should be considered in discussing Middle Palaeolithic human subsistence strategies in Apulia.

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Author contributions J.C., F.B. and P.B. designed research; J.C., F.B. and P.B. performed taphonomy and zooarchaeological research; A.R., S.R. and V.S. analysed excavation data; V.S. performed spatial distribution analysis; J.C., F.B., P.B., A.R. and V.S. wrote the paper.

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