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# The faunal assemblage from La Sassa cave (Latium, Italy): Environmental perspective of a Late Pleistocene cave hyena – Brown bear den

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## ARTICLE INFO

## ABSTRACT

La Sassa cave (Sonnino, central Italy) is a recently investigated MIS 3 site of southern Latium, a region characterised by a large number of caves and open-air Late Pleistocene sites. This paper describes the large faunal assemblage discovered at La Sassa cave, providing taphonomic and stratigraphic analyses which allow us to interpret the outer rooms of the cave as a cave hyena communal den and the inner area as a possibly coeval brown bear hibernating shelter. Archaeological evidence also indicates a human frequentation of the surrounding area occurred. In addition, a first environmental reconstruction of the area is provided based on faunal data. Results suggest a composite hilly landscape, with forests and grasslands interspersed by scrubland areas, rocky bands and wetlands, between the Pontine Plain and the modest peaks of the Ausoni Mountains. This contribution improves our palaeoecological perspective of the area around the time of the Last Glacial Maximum with intense human occupation.

## 1. Introduction

The Pontine Plain is a small plain in central Italy naturally bounded between the Tyrrhenian Sea and the Lepini and Ausoni Mountains. It is characterised by the coexistence of different habitats within a few kilometres of an extremely varied and complex landscape shaped by karst and volcanic activities, intense hydrogeology and coastal erosion.

This region has been the subject of an increasing number of multidisciplinary investigations in recent years. Archaeological and paleontological studies pointed out this small territory was densely populated with hundreds of human and faunal cave and open-air sites during the Late Pleistocene (Gatta et al., 2016a; 2019; Grimaldi and Spinapolice, 2010; Petronio et al., 2021; Vitagliano and Bruno, 2012). The main hypothesis is that this was probably due to the hospitable environmental features of the area during the Last Glacial, conversely to what would be expected from a period that is commonly interpreted as one of drastic climate oscillations and widespread unfavourable habitats. Marine Isotope Stage 3 (MIS 3) features several extreme natural events with global consequences such as Heinrich Event 4, Dansgaard-Oeschger

events and the neighbouring Archiflegreo Volcano eruption. Nevertheless, these factors affected the climate with varying intensity on a regional scale, therefore small-scale analyses are strongly required to obtain reliable reconstructions of past environments. Unfortunately, the Late Pleistocene environment of the Pontine Plain has long been based on pollen records from distant lacustrine deposits (Follieri et al., 1989, 1998; Magri and Sadori, 1999).

New studies suggest the region was extremely diversified during the Late Pleistocene and its complex landscape provided several ecosystems acting as "*refugia*" for faunal and floral species (Gatta et al., 2016b, 2019, 2021). This hypothesis is further supported by the Neanderthals recently discovered at Grotta Guattari (Petronio et al., 2021), which significantly improved the neanderthalian population of Europe, and the presence of one of the latest narrow-nosed rhinoceros of Europe (Pandolfi et al., 2017). Nevertheless, further investigations of chronologically relevant sites are strongly needed to improve our knowledge of this area by improving the temporal resolution.

The aim of this paper is to interpret the Late Pleistocene deposit of La Sassa cave, a recently discovered site situated at the southern border of

the Pontine Plain (Alessandri et al., 2020; Alessandri et al., 2019; Alessandri et al., 2021). A large collection of almost five thousand faunal remains has undergone detailed paleontological and chronostratigraphic analyses. Results suggest *Crocuta crocuta* and *Ursus arctos* possibly coexisted using different rooms of the cave as dens. This behavioural pattern has been already attested in Europe (Diedrich and Žák 2006; Diedrich, 2006, 2013, 2017) while it has never been documented in Italy to the knowledge of these authors. Finally, the palaeoenvironmental/paleoclimatic contribution of this faunal assemblage to

the understanding of the Pontine Plain during MIS 3 will be discussed.

## 2. Archaeological setting

The archaeological site of La Sassa (Sonnino, central Italy; 41°25′29.4″N 13°14′11.6″E) is located at 140 m a.s.l., on the left bank of the river Rio Sassa in the Ausoni Mountains, the southern natural border of the Pontine Plain (Fig. 1). La Sassa is a small karst cave (Fig. 2) characterised by a large entrance room (i.e., Room 1) of 151 m$^2$ with the present-day vertical access in the 3 m-high ceiling. The prehistoric sub-horizontal access to the cave has been recently identified along the northern wall of Room 1. The entire western portion of this chamber is currently occupied by a huge pile of rock debris, which may cover further archaeological deposits. The eastern part has a sub-horizontal floor slightly inclined towards S-E, where the caves is divided into two branches: an eastern one, which leads after a bottleneck to a small-size room (i.e., Room 2) on the same floor level, and a southern branch, which through a steep access led to a series of uneasy and dark areas. The first of these is Room 3, after which it is necessary to crawl to have access to next Rooms 4 and 5 in which the ceiling is about 30–50 cm high. The adjacent Room 6 and following Rooms 7, 8 and 9 represent the inner part of La Sassa, characterized by well-preserved geological formations, such as stalactites and stalagmites in an extremely tight and uncomfortable environment (Alessandri et al., 2021).

The archaeological potential of the cave was unknown until 2014, when a local speleological group discovered abundant protohistoric pottery in Room 1 and identified a few bones on the surface floor of the inner Room 6. Following a surface survey campaign in 2015, four archaeological excavations were carried out between 2016 and 2019 under the direction of the University of Groningen (Netherlands) in collaboration with the University of Rome "Tor Vergata" (Italy). All the rooms of La Sassa have been investigated with the exceptions of Rooms 7, 8 and 9, in which the floor is formed by an extremely thick limestone crust preventing careful excavations. The cave yielded a considerable Copper to Early Bronze Age burial ground in Rooms 1 and 2 and Middle Bronze Age frequentation evidence (e.g., hearths and pottery) in Rooms 1, 2, 3 and 4 (Alessandri et al., 2021). Very rare Upper Palaeolithic lithic industry has been discovered in Room 1. Very rare pottery shards and bone remains suggest that a brief frequentation occurred in Rooms 1 and 2 during Roman, Middle Age and Renaissance, together with a modern occupation during World War II confirmed by elderly citizens of the town.

The faunal remains from the Late Pleistocene layers in Rooms 1, 2, 3 and 6 at La Sassa will be discussed in this paper. The paleontological deposit is widespread in the eastern perimeter of Room 1 and the entire
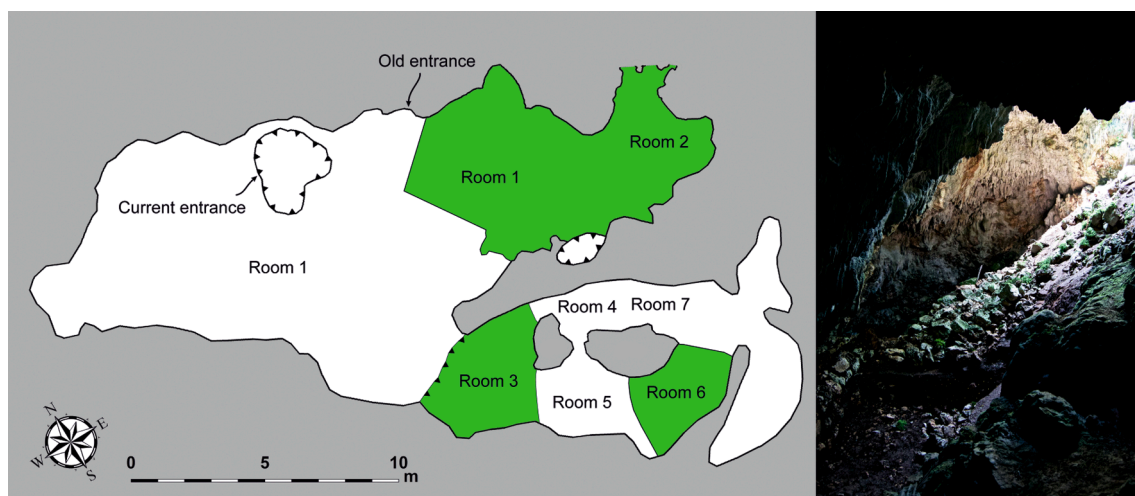


**Fig. 2.** Map of La Sassa cave. Areas with late Pleistocene deposit in green.

**Table 1**

Results of AMS radiocarbon dating from La Sassa cave. Dates were calibrated with the IntCal20 curve in OxCal v4.4 (Bronk Ramsey 2009; 2017). Oxford dates were obtained using methods described in Brock et al. (2010). OxA-X-2772–34 was obtained without ultrafiltration (lab protocol code 'AG') and has a health warning due to low carbon content on combustion (25%); others were obtained with ultrafiltration (protocol 'AF').

| **LA SASSA PLEISTOCENE** | | | | | |
|---|---|---|---|---|---|
| **Find** | **ID** | **Room** | **Laboratory No.** | **14C age BP** | **Cal BC (OxCal4.4, IntCal20)** |
| 516A | *Crocuta crocuta* | 3 | OxA-37219 | 30150 ± 350 | 33385–32111 (95,4%) |
| 516B | *Crocuta crocuta* | 3 | OxA-37218 | 29190 ± 310 | 32493–30950 (95,4%) |
| 23 | *Panthera spelaea* | 1 | OxA-X-2772–34 | 29300 ± 400 | 32661–30879 (93,7%) |
| 3 | *Ursus arctos* | 6 | OxA-37283 | 30220 ± 360 | 33438–32156 (95,4%) |
| 35 | *Ursus arctos* | 6 | GrA64830 | 30210 ± 180 | 33190–32360 (95,4%) |

Room 2, between −0,4/-0,8 m below the original surface floor, following a light and constant S-E gradient. Homogeneity of layers, spatial and taphonomic analysis of bone distribution suggest a contemporaneity of deposit formation in these two rooms, which has been interpreted as a primary deposition, albeit finds inclination indicate a slight alluvial activity took place in this area. Radiocarbon dating confirms remains from Rooms 3 and 6 are also coeval (Table 1), however these contexts have a completely different formation: Pleistocene remains in Room 3 are resulting from the massive collapse of the southern part of Room 1 and its deposit, which is particularly evident from the vertical disposition of bones in a cone of detritus and large stones (Alessandri et al., 2021). Room 6 is the only area of the cave in which Pleistocene remains belonging to two specimens of *Ursus arctos*, one of which in partial anatomical connection, were found in primary deposition encrusted on the surface floor.

## 3. Materials and methods

### 3.1. Excavation and chronology

The faunal assemblage analysed here consists of 4739 bone remains collected from the Late Pleistocene layers of La Sassa cave between 2015 and 2019. All finds were recorded on a grid system, to permit a detailed study of their spatial distribution and stratigraphic integrity of sediments. Sieving of all sediments, with a 2-mm mesh, was performed to avoid the loss of data and no selection based on size or significance of specimens was applied. The excavation also returned a large number of coprolites, on which the morphological study was conducted, while pollen and ancient DNA analyses are in progress.

In order to define the chronological framework, five radiocarbon dates have been performed on bone remains from the supposed Late Pleistocene layers of La Sassa (see Table 1). A first dating was performed on a brown bear right radius from the strongly concreted surface (SU 16) in Room 6 at the University of Groningen (i.e., GrA-64830), and four further bones were submitted to the Oxford Radiocarbon Accelerator Unit. Overall, two dates each from Room 3 and 6 were yielded respectively from cave hyena and brown bear remains, and a single dating was obtained on a cave lion from Room 1. Results returned a short and well delineated chronological range between 33 and 31 ka cal BP (Table 1), without notable chronological differences between rooms.

### 3.2. Paleontological study

The paleontological study has been carried out at the Laboratory of Prehistory of the University of Rome Tor Vergata. Aims of this work were to (i) understand the agents behind the fossil accumulation and (ii)

to propose a preliminary palaeoenvironmental reconstruction based on fauna ecology, allowing a comprehensive interpretation of the site and its surroundings during the late MIS 3.

The taxonomic attributions were determined by comparing the fossil remains to the osteological collections stored at the Laboratory of Prehistory of the University of Rome Tor Vergata, also consulting Pales and Lambert (1971) and Schmid (1972). The estimates of the minimum number of individuals (MNI) were calculated according to Bökönyi (1970) and Stiner (1990), based on the stage of teeth eruption, replacement and wear. The results were integrated with the analysis of the metrical characters and age profiles of the other skeletal elements. The number of identified specimens (NISP; Grayson, 1984), their taxonomic and taphonomic analyses as well as the minimum number of elements (MNE; Binford, 1981; Klein and Cruz-Uribe, 1984; Stiner, 1994) and age class at death are provided according to available criteria. The estimated age of death was performed taking into consideration the observations of Gipson et al. (2000) on North American wolves, Guskov (2014) for Balkan and North American brown bears, Brugal et al. (1997) for Pleistocene hyenas, Bull and Payne (1982) for *Sus scrofa* from Turkey, Mariezkurrena (1983) for *Cervus elaphus* from Cantabria (Spain) (for red deer and fallow deer), Tomé and Vigne (2003) for *Capreolus capreolus* from northern France, and Barone (1974, 1981) and Grant (1982) for present-day domestic cattle and horse (as a proxy for equids and *B. primigenius*). The fragmentation index and the survival coefficient of the anatomical elements (Binford, 1981; Lyman, 1994) were calculated to evaluate the skeletal survival rate of different species. The study of body parts distribution was carried out on the most present ungulates: *Cervus elaphus* and *Dama dama*. The skeleton has been divided into seven anatomical regions (RA), according to the method established by Fosse (1994) and Fourvel & Fosse (2017): cranial elements (RAI), vertebrae (RAII), ribs (RAIII), pelvis (RAIV), long bones (RAV), metapods (RAVI) and short bones (RAVII).

The taphonomic study was carried out on the entire assemblage (identified and indeterminate remains) through the use of a Leica S9I Stereomicroscope and a 10x magnifier. Bone surface modifications were analysed to identify their origin, trampling abrasions and other post-depositional traces (Fernandez-Jalvo and Andrews, 2016). Carnivore traces were identified as deep punctures in the cortical bone surface, concentrated on the articular ends of the bones, as well as pits and scores with U-shaped striations on bone surfaces (Binford 1981). The results were compared with those from other well-known cave hyena sites and to studies of bone assemblages produced by large carnivores (e.g., Arriaza et al., 2016; Diedrich, 2012b, 2012c; Gatta et al., 2019; Stiner, 1991; Yravedra et al. 2011, 2012). In addition, digestion traces, gnawing of rodents and ichnotraces were also examined (Bocheński et al., 1998; Fernandez-Jalvo and Andrews, 2016; Fernandez-Jalvo et al., 1998; Lloveras et al., 2009; Pirrone et al., 2014; Thompson et al., 2018; Gatta et al., 2021). Taphonomic observations were integrated by a ternary diagram made to investigate the mortality profile of the red deer population, the most abundant ungulate taxon, to help identify the main accumulation agent of the faunal assemblage, following the methodology of Stiner (1990), later used also by Pandolfi et al. (2013) and Gatta et al. (2019).

## 4. Results

### 4.1. Taxonomy and taphonomy of faunal remains

#### 4.1.1. Rooms 1, 2 and 3

A total of 4675 macromammals bone remains from Room 1 (=2581), then Room 2 (=1718) and Room 3 (=376) have been analysed. The 21 % of the collection was taxonomically identified, highlighting the presence of at least 23 taxa, among which *Lepus* sp., *Canis lupus*, *Vulpes vulpes*, *Ursus arctos*, *Meles meles*, *Felis silvestris*, *Panthera spelaea*, *Crocuta crocuta*, *Equus ferus*, *Equus hydruntinus*, *Sus scrofa*, *Capreolus capreolus*, *Cervus elaphus*, *Dama dama*, *Bos primigenius* and *Rupicapra* sp. (Table 2; Figs. 3

**Table 2**
Distribution of anatomical elements from Room 1 and 3 at La Sassa cave.

| BodyPart | Testudinata | Aves | *Talpa sp.* | Rodentia | *Castor fiber* | *Arvicola italicus* | *Lepus sp.* | Carnivora | *C. lupus* | *V. vulpes* | *U. arctos* | *Mustela sp.* | *Meles meles* | *F. silvestris* | *P. spelaea* | *C. crocuta* | Rhinoceratidae | *E. ferus* | *E. hydruntinus* | *S. scrofa* | Cervidae | *C. capreolus* | *C. elaphus* | *Dama dama* | *B. primigenius* | *Rupicapra sp.* | Small ruminants | **Total** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Horn/Antler | | | | | | | | | | | | | | | | | | | | | 17 | 1 | 9 | | | | | **27** |
| Skull | | | | | | | | | | 1 | | | | | | 1 | | | | | | 1 | | 1 | | 1 | 1 | **6** |
| Maxillary | | | | | | | 1 | | | | | | | | | 6 | | | | | | 1 | 6 | 2 | 1 | 3 | | **20** |
| Upper teeth | | | | 3 | 1 | | | | 6 | 5 | 14 | 1 | | | 7 | 25 | | 9 | 4 | 8 | | 12 | 97 | 21 | 23 | 3 | | **239** |
| Mandible | | | | | | | | | | 3 | 3 | | | | 2 | 2 | | 1 | | 2 | 3 | 9 | 14 | 3 | 2 | 1 | 1 | **46** |
| Lower teeth | | | | 2 | | | | | 3 | 6 | 11 | | | | 4 | 18 | | 3 | | 5 | 4 | 14 | 63 | 30 | 17 | 10 | | **190** |
| Indeterminate teeth | | | | | | 1 | | 1 | 1 | 3 | | | | | | 6 | | 1 | | | 6 | 1 | 8 | 1 | 2 | 1 | | **32** |
| Epistropheus | | | | | | | | | | | | | 1 | | | | | | | | | 1 | | | | | | **2** |
| Vertebrae | | | | | | | | | | 2 | | | | | | | | | | | | | | | | | | **2** |
| Rib | | | | | | | | | | 4 | 1 | | | | | | | | | | | | | | | | | **5** |
| Turtle shell | 3 | | | | | | | | | | | | | | | | | | | | | | | | | | | **3** |
| Scapula | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | **1** |
| Humerus | | | 1 | 1 | | | 1 | 1 | 1 | 1 | 2 | | | 1 | | | | | | 1 | | 2 | 3 | 2 | 1 | 3 | 1 | **22** |
| Radius | | | | | | | | | 1 | 1 | 2 | | | | 1 | 1 | | | | | | | 4 | 2 | 2 | 2 | 1 | **17** |
| Ulna | | | | 1 | | | | | | | 1 | 1 | 1 | | 1 | | | | | 2 | | | | | 2 | 1 | | **10** |
| Carpal bones | | | | | | | | | | 1 | 5 | | | | | 2 | | | | 1 | 1 | | 10 | 3 | 3 | 1 | | **27** |
| Metacarpus | | | | 3 | | | | | 1 | 5 | 11 | | | | | 4 | | | | 2 | 2 | 2 | 16 | 20 | 5 | 4 | 1 | **76** |
| Pelvis | | | | 1 | | | | | | | 1 | | | | | | | | | | | | | | | | 4 | **6** |
| Femur | | | | 1 | | | | | 1 | 1 | 2 | | | | | | | | | 2 | | | 1 | | 1 | 1 | 1 | **11** |
| Knee bone | | | | | | | | | | 1 | 1 | | | | | | | | | | | 1 | 3 | | | 1 | | **8** |
| Tibia | | | | 2 | | | | | | 2 | 1 | | | | | 2 | | | 1 | 2 | | 1 | 5 | 1 | | | | **17** |
| Fibula | | | | | | | | | | | 1 | | | 1 | | 1 | | | | | | | | | | | | **3** |
| Tibia-Fibula | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | **1** |
| Astragalus | | | | | | | | | | 1 | 2 | | | | | 1 | | | | | | 2 | | | | 1 | | **7** |
| Calcaneus | | | | 1 | | | | | | 1 | 1 | | | | | | | | | | | | | 1 | | | 1 | **5** |
| Malleolar bone | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | **1** |
| Tarsal bones | | | | | | | | | 1 | 1 | 5 | | | | | | | | | | | | | | | | | **7** |
| Sesamoid | | | | | | | | | 2 | 1 | 3 | | | | | | | | | | | 2 | 3 | | 1 | | 1 | **13** |
| Metatarsus | | | | | | | 4 | 1 | 1 | 4 | 3 | | | | | | | | 1 | 2 | 2 | 2 | 2 | 28 | 33 | 2 | 1 | **86** |
| Metapodial bones | | | | | | | 2 | | | 3 | 4 | | | | 2 | 3 | | | | | 3 | 3 | | 2 | 2 | | 2 | **26** |
| Phalanx I | | 3 | | | | | 6 | | 4 | 3 | 15 | | | | | 2 | | | | | 10 | 1 | 3 | 10 | 1 | 2 | 1 | **61** |
| Phalanx II | | | | 1 | | | | | | 3 | 4 | | | | | 1 | | | | | 1 | 2 | 3 | 6 | 2 | 1 | 1 | **25** |
| Phalanx III | | | | | | | | | | | 2 | | | | | 2 | | | 1 | 3 | | | 1 | | | 1 | | **10** |
| **Total** | 3 | 3 | 1 | 8 | 1 | 2 | 21 | 6 | 27 | 46 | 96 | 2 | 2 | 2 | 17 | 77 | 1 | 14 | 6 | 44 | 45 | 59 | 288 | 122 | 67 | 35 | 17 | **1012** |

**Fig. 3.** La Sassa cave, Late Pleistocene. A) Cranium of *Dama dama* in frontal (up) and ventral (down) view; B) Femur of *Ursus arctos* in posterior (left) and anterior (right) view; C) Mandible *Panthera spelaea* in labial view.

and 4A). A limited number of reptiles (=3 turtle shells), birds (=3) and small mammals (=11, i.e., *Talpa* sp., *Arvicola italicus* and undetermined Rodentia) have also been recovered (Table 2).

The MNI counts estimate the most common taxon is red deer, followed by fallow deer and cave hyena (Table 3) but, due to the high fragmentation rate, the number is probably belittled. Age at death estimation (Table 3) display a strong preponderance of adult individuals (57,5% of total MNI), followed by young (27,6%) and old ones (13,8%). The main taxa of the site also reflect this trend, with a minor exception among red deer where a dominance of adult individuals (=11) is followed by old (=5) and lastly young (=4).

Fossilisation of bone remains is generally good, probably due to the closed environment of the cave with steady temperature and humidity during the entire year, but the faunal assemblage is mainly composed of fragmented specimens (88 %), often of very small size (≤5 cm), whilst intact long bones are extremely rare. Patinas are also consistent within the assemblage regardless of the room in which the finds were collected and varies between yellowish, when remains laid on soft soil, and whitish, when sticked on limestone crusts. On the surface of the fossil bones, no cut marks or other obvious traces of human activity have been observed. Instead, clear carnivore activity is widespread on over 53 % of total remains: fragmented diaphysis with cracks and perforations typical of a strong bite are ubiquitous, with pits and punctures on 37 remains (1,4%) and widespread scores (Fig. 5); epiphyses are underrepresented and consistently display furrows (Fig. 4C); chewed shed antlers are abundant, together with metapodial bones and ribs (Table 4). Digested

bones between 1 and 4 cm are also common (34 % of total remains; Table 5 and Fig. 4B) and a few long fragments gnawed to produce nibbling sticks have also been recovered (Fig. 4D). Rodent marks are also visible on a large part of the assemblage. Digestion traces by birds of prey have been found on two remains, while three bones display gnawing by a small carnivore. Lastly, four bone fragments present ichnotraces by necrophagous insects.

The anatomical compositions of the main species of ungulates (Table 6) shows a clear preponderance of skulls and teeth (57 %), followed by diaphysis of long bones (19 %) and rare epiphysis (8 %). Indeterminate remains mostly consist of diaphysis of long bones (96.2 %) from medium-large size ungulates and display traces of hyena activity. For red deer and roe deer, the most frequent species, the study of skeletal distribution is quite similar, showing a majority of cranial elements (RAI), followed by long bones (RAV) and metapods (RAVI), but almost all the anatomical parts have been found (Fig. 6).

Digestion by birds of prey has been found on two remains belonging to *Lepus* sp. (Fig. 7A). Acid secretions produced a moderate degree of modification localised on the epiphysis. A large part of the surfaces is consumed, showing a dark patina and the edges of the bones are smoothed and rounded. Three bones of the same taxon show pits left by the canine of a small carnivore (Fig. 7B). Four bone fragments display ichnotraces left by necrophagous insects (Thompson et al., 2018; Gatta et al., 2021). Lastly, rodent marks are also visible on a very low percentage (0,6%) of taphonomic remains.

In addition, over one hundred coprolites have been found in these

**Fig. 4.** La Sassa cave, Late Pleistocene. A) *Crocuta crocuta*: maxillary fragment in labial and lingual view and cranium in frontal view; B) Bone fragments partially digested; C) Systematic bone exploitation by cave hyena; D) Nibbling stick.

**Table 3**
Number of identified specimens (NISP) and Minimum number of individuals (MNI) by age at death at La Sassa cave.

| | NISP | % | MNI | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Young | Adult | Old | Indet | Total | % |
| Testudinata | 3 | 0.3 | | | | | | |
| Aves | 3 | 0.3 | | | | | | |
| *Talpa* sp. | 1 | 0.1 | | 1 | | | 1 | 1.1 |
| Rodentia | 8 | 0.7 | | | | | | |
| *Castor fiber* | 1 | 0.1 | 1 | | | | 1 | 1.1 |
| *Arvicola italicus* | 2 | 0.2 | | 1 | | | 1 | 1.1 |
| *Lepus* sp. | 21 | 2.0 | 2 | 1 | | | 3 | 3.4 |
| Carnivora | 6 | 0.6 | | | | | | |
| *Canis lupus* | 27 | 2.5 | 1 | 2 | | | 3 | 3.4 |
| *Vulpes vulpes* | 46 | 4.3 | 1 | 3 | | | 4 | 4.6 |
| *Ursus arctos* | 160 | 14.9 | 1 | 3 | | | 4 | 4.6 |
| *Mustela* sp. | 2 | 0.2 | | 1 | | | 1 | 1.1 |
| *Meles meles* | 2 | 0.2 | | 1 | | | 1 | 1.1 |
| *Felis silvestris* | 2 | 0.2 | | 1 | | | 1 | 1.1 |
| *Panthera spelaea* | 17 | 1.6 | | 2 | 1 | | 3 | 3.4 |
| *Crocuta crocuta* | 77 | 7.2 | 2 | 4 | 2 | | 8 | 9.2 |
| Rhinoceratidae | 1 | 0.1 | | | | 1 | 1 | 1.1 |
| *Equus ferus* | 14 | 1.3 | 1 | 1 | 1 | | 3 | 3.4 |
| *Equus hydruntinus* | 6 | 0.6 | 1 | | 1 | | 2 | 2.3 |
| *Sus scrofa* | 44 | 4.1 | 1 | 2 | | | 3 | 3.4 |
| Cervidae | 45 | 4.2 | | | | | | |
| *Capreolus capreolus* | 59 | 5.5 | 2 | 3 | 1 | | 6 | 6.9 |
| *Cervus elaphus* | 288 | 26.8 | 4 | 11 | 5 | | 20 | 23.0 |
| *Dama dama* | 122 | 11.3 | 4 | 5 | 1 | | 10 | 11.5 |
| *Bos primigenius* | 67 | 6.2 | 2 | 4 | | | 6 | 6.9 |
| *Rupicapra* sp. | 35 | 3.3 | | 4 | | | 4 | 4.6 |
| Small ruminants | 17 | 1.6 | 1 | | | | 1 | 1.1 |
| **Total identified specimens** | **1076** | **100** | **24** | **50** | **12** | **1** | **87** | **100** |
| Identified specimens | 1076 | 22.7 | | | | | | |
| Indeterminate bones | 3663 | 77.3 | | | | | | |
| **Total remains of La Sassa** | **4739** | **100.0** | | | | | | |

rooms. These have been morphologically attributed to *C. crocuta* (Fig. 8A) except for a single specimen belonging to a small size canid, possible a fox (Fig. 8B), and a couple of larger coprolites possibly delivered by cave lions (Fig. 8C-D).
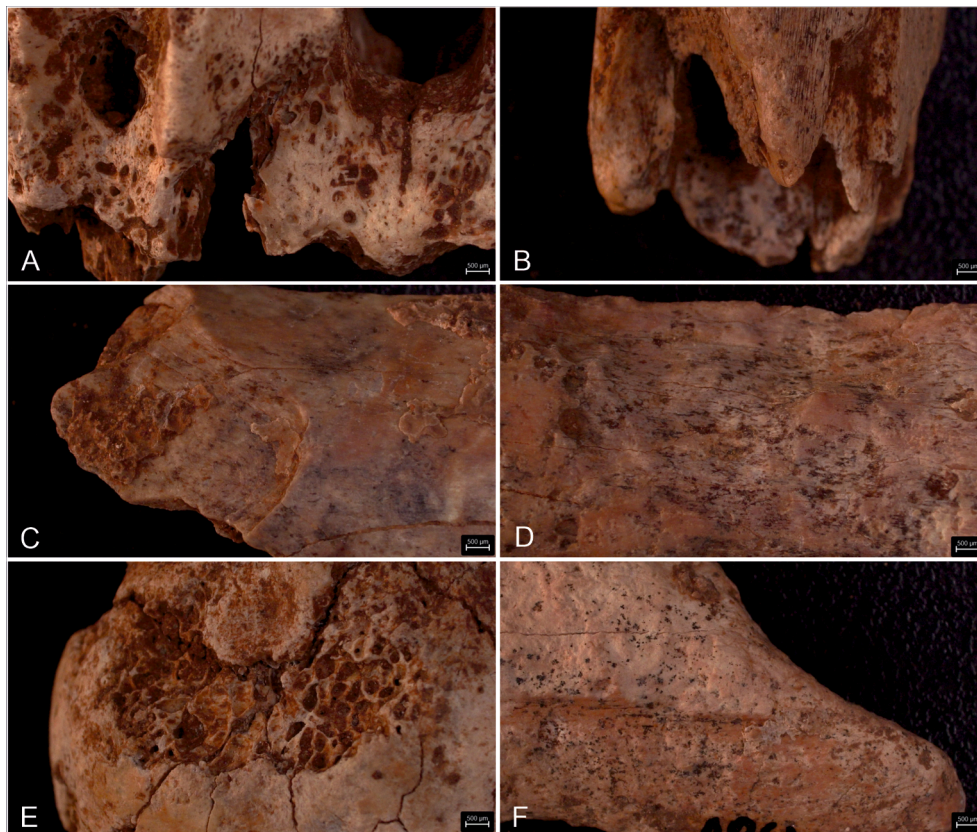
**Fig. 5.** Magnified view of bones with traces left by hyena activity at 0,5x/0,01: A-C) furrows; D-E) scores; F) digested. All scale bars represent 500 µm.

### 4.1.2. Room 6

About 60 bone remains were discovered in Room 6 during 2015 and 2016 (Table 7). These were partially visible in the surface floor, a highly concreted limestone crust 5–7 cm thick (SU 16), while part of them was lying on the soft brownish clay layer underneath (SU 17). The remains were strongly fossilized and well preserved. Large part of remains were collected still embedded in the concretion crust which was later removed in laboratory. The distribution and side of all anatomical parts was recorded. The veil of concretion covering the bones often incorporated microfauna remains.

An almost complete skull, overturned and dislocated in ancient, was collected in association with two hemimandibles and many permanent teeth, long bones with fused epiphyses, two scapulae (left and right), carpal and tarsal bones and phalanges with several ribs and vertebrae in partial anatomical connection. The morphological and morphometric study of teeth and long bones have allowed to ascribe the findings to *Ursus arctos* specimen (Torres Pérez-Hidalgo, 1984), excluding the presence of *Ursus spelaeus* (see Capasso Barbato et al., 1990, 1993; Petronio et al., 2003). All these bones are ascribable to an adult specimen (i.e., Specimen A in Table 7), as suggested by permanent teeth and completely fused epiphyses of long bones (Guskov, 2014). The remains, with the position of the right portion of the skeleton to north and left portion to south, suggests the individual died lying in a prone position with a west-east orientation.

Two more isolated fossil bones, a femur and a radius with both fused epiphyses, were found a little north of the other remains and are attributable to a second adult specimen (i.e., Specimen B in Table 7). The study of all bones, characterised by a yellowish patina, revealed the absence of both carnivorous activity and cut marks or other human manipulations, albeit the presence of concretions covering the surface of the 44 % of analysed remains prevented a more detailed study. However, the absence of anthropic layers in Room 6 agrees with this observation. Finally, gnawing marks and post-depositional movements

are mostly absent or due to minimal rodent activity (Fiorillo et al., in press).

## 5. Discussion

### 5.1. Interpretation of the site

The stratigraphic excavation and the laboratory studies of the faunal assemblage allow us to make several inferences on La Sassa cave. The main efforts were aimed to the interpretation of the site and the main agents responsible for the fossil accumulation. Our hypothesis is that of two distinct, but possibly coeval, frequentations within the cave, with hyenas in the outer rooms (i.e., Rooms 1, 2 and 3) while Room 6 served as a hibernation shelter to at least one brown bear.

The hyena frequentation was already preliminary proposed during the excavation and is based on several factors. Remains of cave hyenas are relatively abundant (the second carnivore after the brown bear, according to the NISP, but the first according to the MNI; Table 3) and the widespread presence of gnaw marks was already mentioned. Further studies highlighted a strong similarity with those of other current and Pleistocene hyena dens both in regards to the damage produced as well as the systematic exploitation of some anatomical parts (Diedrich, 2012b, 2012c; Fosse et al., 2010; Gatta et al., 2019; Stiner, 1991). For example, the presence of severely crunched shed fallen cervid antlers is typical of hyenas in the European Late Pleistocene (Lam, 1992). The over one-hundred coprolites from Rooms 1 and 2 also proved valuable to identify the bone collector. Fossil faeces were mostly assigned to *Crocuta crocuta* according to their morphometric analysis (Diedrich, 2012a) and comparison with the coprolite collection stored at the laboratory of Prehistory at University of Rome Tor Vergata. The presence within faeces of small-medium bone fragments is also typical of only a few Late Pleistocene European large carnivores, such as cave hyena, wolves and cave lions, but it is a common cave hyena behaviour to swallow and

**Table 4**

Body parts with gnaw marks from Room 1 and 3 at La Sassa cave.

| Gnaw marks | Lepus sp. | Carnivora | C. lupus | V. vulpes | U. arctos | Meles meles | F. silvestris | P. spelaea | C. crocuta | S. scrofa | Cervidae | C. capreolus | C. elaphus | Dama dama | B. primigenius | Rupicapra sp. | Small ruminants | Indet | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Horn/Antler | | | | | | | | | | | 12 | 1 | 12 | | | | | | 25 |
| Skull | | | | | | | | | 1 | | | 1 | | 1 | | | | | 3 |
| Mandible | | | | | | | | 1 | | | 2 | 3 | 3 | 2 | | 1 | | | 12 |
| Vertebra | | | | | | 1 | | | | | | 3 | | | | | | 2 | 6 |
| Rib | | | | | | | | | | | | | | | | | | 26 | 26 |
| Humerus | | | | | 1 | | 1 | | | | 1 | | 1 | 2 | 1 | 3 | 1 | | 11 |
| Radius | | 1 | | | | | | | | | 1 | 2 | 1 | 2 | 2 | | 1 | | 10 |
| Ulna | | | | | | 1 | | | | 1 | 1 | | | | | 1 | | | 4 |
| Carpal bones | | | | | | | | | 1 | | | | 4 | 1 | 1 | | | | 7 |
| Metacarpus | | | | 1 | 2 | | | | 1 | | 2 | 2 | 8 | 19 | 4 | 2 | | | 41 |
| Pelvis | 1 | | | | | | | | | | | | | | | | 2 | | 3 |
| Femur | 1 | | | | 1 | | | | | 1 | | | 1 | | 1 | 1 | 1 | 2 | 9 |
| Knee bone | | 1 | | | | | | | | | | 1 | | | | 1 | | | 3 |
| Tibia | | | | | | | | | 1 | | | 1 | 4 | 1 | | | | | 7 |
| Fibula | | | | | 1 | | | | | | | | | | | | | | 1 |
| Astragalus | | | | | | | | | | | | | | | | | | | 0 |
| Calcaneus | | | | 1 | | | | | | | | | 1 | | | | | | 2 |
| Sesamoid | | | | | 1 | | | | | | | | | | | | | | 1 |
| Metatarsus | | 1 | 1 | | 1 | | | | | 2 | 2 | 2 | 24 | 30 | 1 | 2 | | | 66 |
| Metapodial bones | | 2 | | | | | 1 | | 3 | 2 | 4 | 1 | 1 | | | | | | 14 |
| Phalanx I | | | | | 8 | | | | 2 | 3 | 1 | 1 | 2 | | 1 | | 1 | | 19 |
| Phalanx II | | | | | 2 | | | | | | | 2 | | 1 | | | | | 5 |
| Phalanx III | | | | | | | | | 1 | | | | | | | 1 | | | 2 |
| Indet. | | | | | | | | | | | | | | | | | | 2204 | 2204 |
| **Total remains w/ gnawing** | **2** | **5** | **1** | **2** | **17** | **2** | **1** | **2** | **9** | **10** | **28** | **18** | **62** | **59** | **11** | **12** | **6** | **2234** | **2481** |

**Table 5**
Body parts with digestion traces from Room 1 and 3 at La Sassa cave.

| Digested | Carnivora | C. lupus | V. vulpes | U. arctos | C. crocuta | Meles meles | S. scrofa | Cervidae | C. capreolus | C. elaphus | Dama dama | Rupicapra sp. | Small ruminants | Indet |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Horn/Antler | | | | | | | | 8 | | | | | | |
| Mandible | | | | | | | | 1 | 1 | 1 | 1 | | | |
| Vertebra | | | | | | 1 | | | | | | | | 1 |
| Rib | | | | | | | | | | | | | | 12 |
| Humerus | | | | | | | | | | | 1 | | | |
| Carpal bones | | | | | | | | | | 4 | 1 | | | |
| Metacarpus | | | | | | | 1 | 1 | | 1 | 5 | | | |
| Pelvis | | | | | | | | | | | | 1 | | |
| Femur | | | | | | | | | | | | | 1 | 1 |
| Knee bone | 1 | 1 | | | | | | | | | | | | |
| Astragalus | | | | | | | | | 1 | | | | | |
| Calcaneus | | | 1 | | | | | | | | | | | |
| Sesamoid | | | | | | | | | | | | | | 1 |
| Metatarsus | 1 | | | | | | 1 | 1 | 1 | 4 | 4 | 1 | 1 | |
| Metapodial bones | 1 | | | | 1 | | | 1 | 1 | 1 | | | | |
| Phalanx I | | | | | 1 | | 1 | 1 | 1 | | | | | |
| Phalanx II | | | | 1 | | | | | 1 | | | | 1 | |
| Phalanx III | | | | | | | | | 1 | | | 1 | | |
| Indet. | | | | | | | | | | | | | | 1505 |
| **Total remains w/ digesting traces** | **3** | **1** | **1** | **1** | **2** | **1** | **3** | **13** | **6** | **11** | **12** | **3** | **3** | **1520** |

regurgitate large bones partially digested such as those recovered in La Sassa (Fig. 4B; Fourvel et al., 2014; Jimenez et al., 2022; Linares-Matás et al., 2021; Suitcliffe, 1970).

The most common species at La Sassa cave is the red deer. Based on the tooth-wear classification reported by Stiner (1990), the species is represented by at least twenty individuals: four young (mainly represented by left deciduous teeth, d4), eleven adults and five old individuals (basing on very worn upper molars). The ternary diagram of the red deer population from La Sassa cave falls into the living-structure field (Fig. 9) and would suggests an attritional accumulation of skeletal remains of animals that died from natural causes as already recorded in several catastrophic death assemblages from Late Pleistocene to recent times sites (Pandolfi et al., 2013; Salari et al., 2019; Stiner, 1990 and references therein). Nevertheless, according to Stiner (1990), several bone accumulations by opportunistic predators who kill the prey according to availability in the territory, such as the extant lion, humans and, sometimes, wolves and cave hyenas, are also positioned in this field (Stiner, 1990). Finally, mass mortality can certainly be ruled out in La Sassa cave since intact bones are very rare and anatomical connections are completely missing (Pandolfi et al., 2013). A main role by wolves can also be excluded, since the number of gnaw-marks on the shafts is lower than those on the epiphyses (Yravedra et al., 2011) and the severity of damage on compact bones observed in the sample analysed is unusual for wolves (Haynes, 1983). Extant lions do not generally act as bone accumulators but consume their prey at the kill site or its proximity (Schaller, 1972; Palomares et al., 2022) and there is no evidence of this carnivore entering cave-like environments to hunt or scavenge (Palomares et al., 2022). Furthermore, the breakage patterns and the gnaw-marks typical of extant and Pleistocene lions of Africa described by Arriaza et al. (2016) are not observed at La Sassa cave. However, a couple of coprolites possibly referable to this large carnivore were found, suggesting a sporadic inspection of the cave, perhaps during moments of scarce presence or absence of hyenas.

These arguments allow us to sustain that the red deer mortality pattern supports the hypothesis that cave hyenas were the main accumulation agent at La Sassa cave. Different mortality profiles of the main taxa recognised in other Late Pleistocene cave hyena sites of central Italy, such as Buca della Iena and Cava Muracci (Figs. 1 and 9), could be explained with a different use of the den. Buca della Iena is a typical carnivore accumulation that show mortality pattern with dominance of young individuals (Stiner 1990), while the faunal assemblage from Cava Muracci shows a dominance of adult-old preys and hyena cubs and it was interpreted as a "cub raising" den (Gatta et al., 2019).

The anatomical composition of the main taxa (Table 6 and Fig. 6) allowed us to shed light on some hyena habits at La Sassa. The presence of all skeletal districts suggests that the entire carcasses of prey were transported inside the den and hyenas did not apply any body part selection. The overabundance of skull bones, a common feature within carnivores' accumulations, is due to the low nutritional value and hardness of these remains, which are rarely chewed to fragmentation favouring easier conservation within the fossil record. The significant number of diaphysis fragments (80 % among total remains of ungulates), as opposed to the very low attendance of proximal and distal epiphysis (Table 6), reveals a common subsistence strategy based on the complete gnawing of the spongy parts of the bone and the breakage of the diaphysis to access the bone marrow. Finally, the high number of cervid antlers does not reflect a preferential hunting choice but a diffuse scavenging activity of naturally shed antlers typical of cave hyenas.

The large number of small (≤5 cm) indeterminate bone fragments, albeit useless to taxonomy, revealed a widespread presence of gnaw and/or regurgitation marks and helped to understand the typology of den to which La Sassa cave belongs. High fragmentation rates are common in cave hyena dens defined as "communal" (Diedrich, 2011). This interpretation is further supported by the absence of cubs, which are usually weaned within specific dens (i.e., cub raising dens; Diedrich, 2014), whilst adult and senile are attested. Finally, "prey depot" den can

**Table 6**
Anatomical composition of the main ungulates species from Grotta La Sassa.

| Taxa | Intact bones | | Vertebrae | | Ribs | | Antlers | | Skull + Teeth | | Diaphysis | | Proximal epiphysis | | Distal epiphysis | | Tot. | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | N. | % | N. | % | N. | % | N. | % | N. | % | N. | % | N. | % | N. | % | N. | % |
| *E. ferus* | | | | | | | | | 14 | 3.5 | | | | | | | 14 | 2 |
| *E. hydruntinus* | | | | | | | | | 4 | 1 | | | | | 2 | 5 | 6 | 0.9 |
| *S. scrofa* | 14 | 18.7 | | | | | | | 15 | 3.8 | 7 | 5.3 | 1 | 3.7 | 7 | 17.5 | 44 | 6.3 |
| Cervidae | 2 | 2.7 | | | | | 17 | 63 | 13 | 3.3 | 12 | 9.2 | 1 | 3.7 | | | 45 | 6.5 |
| *C. capreolus* | 9 | 12 | 1 | 1 | | | 1 | 3.7 | 38 | 9.6 | 4 | 3.1 | 3 | 11.1 | 3 | 7.5 | 59 | 8.5 |
| *C. elaphus* | 31 | 41.3 | | | | | 9 | 33.3 | 188 | 47.5 | 42 | 32.1 | 7 | 25.9 | 11 | 27.5 | 288 | 41.3 |
| *Dama dama* | 6 | 8 | | | | | | | 58 | 14.6 | 49 | 37.4 | 5 | 18.5 | 4 | 10 | 122 | 17.5 |
| *B. primigenius* | 7 | 9.3 | | | | | | | 45 | 11.4 | 4 | 3.1 | 5 | 18.5 | 6 | 15 | 67 | 9.6 |
| *Rupicapra* sp. | 4 | 5.3 | | | | | | | 19 | 4.8 | 4 | 3.1 | 4 | 14.8 | 4 | 10 | 35 | 5 |
| Small ruminants | 2 | 2.7 | | | | | | | 2 | 0.5 | 9 | 6.9 | 1 | 3.7 | 3 | 7.5 | 17 | 2.4 |
| Tot. | 75 | 10.8 | 1 | 0.1 | 0 | 0 | 27 | 3.9 | 396 | 56.8 | 131 | 18.8 | 27 | 3.9 | 40 | 5.7 | 697 | 100 |
| Indet. | 8 | 9.6 | 96 | 99 | 185 | 100 | | | 15 | 3.6 | 3357 | 96.2 | 2 | 6.9 | | | 3663 | |
| Tot. | 83 | 1,9 | 97 | 2,2 | 185 | 4,2 | 27 | 0,6 | 411 | 9,4 | 3488 | 80,0 | 29 | 0,7 | 40 | 0,9 | 4360 | 100 |
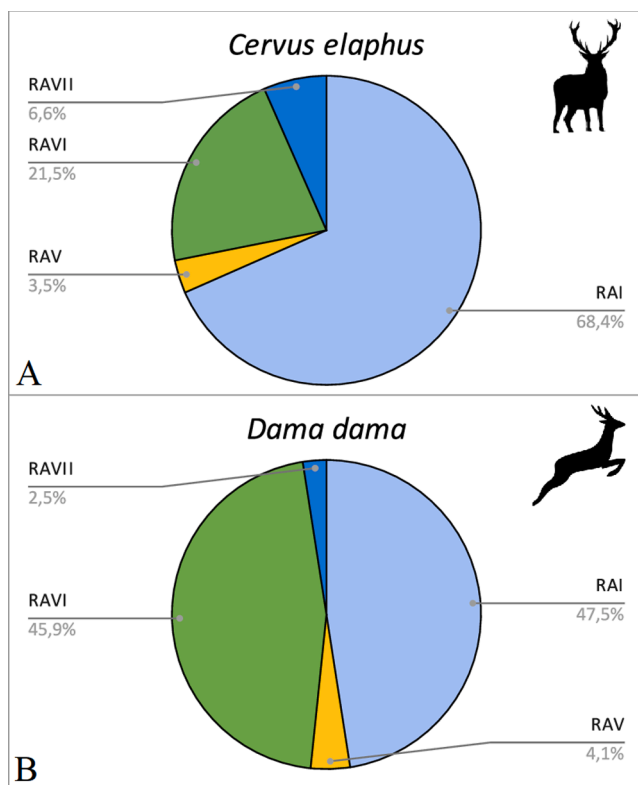


**Fig. 6.** Models of fragmentation of Cervus elaphus (A) and Dama dama (B) from Grotta La Sassa. Skeletons are divided, following Fosse (1994), into: cranial elements (RAI), vertebrae (RAII), ribs (RAIII), pelvis (RAIV), long bones (RAV), metapods (RAVI) and short bones (RAVII).



**Fig. 7.** Magnified view of remains belonging to Lepus sp. at 0,5x/0,01: A) digestion marks by birds of prey on two remains; B) pits left by a small carnivore. All scale bars represent 500 μm.

also be certainly excluded. Abundance of articulated anatomical districts, mostly without gnaw marks, and rare coprolites are key aspects of the latter typology of den (Diedrich, 2014) and none of these is reflected by La Sassa assemblage.

Bear sites can be interpreted as "cave/shelters dens" or "hibernation dens" depending on their function (Romandini et al., 2018). The interpretation of Room 6 as a brown bear hibernation den seems to be straightforward. Hibernation is the biological condition during which some animal species lose their sensitivity or movement force (Craighead and Craighead, 1972). It usually occurs in winter to save energy when food resources are decreasing. Starvation is the most common cause of death related to this process, especially for cubs and sub-adults (Stiner, 1998), while adults usually wake up if their energy reserves are scarce to

make food expeditions using the den as a base camp (Rogers, 1987). Death occurs if these quests are not achieved with minimal energy effort. The paleontological record within the wintering site is usually characterised by well-preserved bone remains in anatomical connections (Romandini et al., 2018). The discovery of the skeleton in the inner and darkest room of La Sassa cave, in a prone position and partial anatomical connection, without evidence of killing or exploitation of the carcass, strongly supports this unfortunate ending. The natural death and undisturbed deposition allowed optimal fossilization of the specimen which represents one of the best-preserved Late Pleistocene brown bears in central Italy (Fiorillo et al., in press). Moreover, brown bear remains are less frequent in Late Pleistocene caves in comparison with cave bears (Fortes et al., 2016), making this discovery noteworthy.

The presence of cave hyenas and bears within the same cave is well documented during all European Pleistocene. Remains of the latter are mostly found as preys within Italian hyena dens [i.e., Grotta di Fumane (Romandini et al., 2016), Grotta Cucigliana (Farina, 2011), Grotta

**Fig. 8.** La Sassa cave, Late Pleistocene. A) *Crocuta crocuta* coprolite; B) Small canid (probably *Vulpes vulpes*) coprolite; C-D) Possible *Panthera spelaea* coprolites.

**Table 7**
Number of identified specimens (NISP) of brown bear from Room 6 at La Sassa cave.

| Anatomical Part | SPECIMEN A | | SPECIMEN B | |
| --- | --- | --- | --- | --- |
| | Right | Left | Right | Left |
| Skull | | 1 | | / |
| Upper Canines | 1 | 1 | / | / |
| M1 | / | 1 | / | / |
| Hemimandible | 1 | 1 | / | / |
| Lower Canines | 1 | 1 | / | / |
| i1 | / | 1 | / | / |
| i3 | 1 | / | / | / |
| p4 | / | 1 | / | / |
| m1 | 1 | 1 | / | / |
| m2 | 1 | / | / | / |
| Vertebrae | | 4 | | / |
| Ribs | | 6 | | / |
| Scapula | 1 | 1 | / | / |
| Humerus | 1 | 1 | / | / |
| Radius | 1 | 1 | 1 | |
| Ulna | 1 | 1 | / | |
| Femur | 1 | 1 | 1 | / |
| Patella | | 1 | | / |
| Tibia | 1 | 1 | / | / |
| Fibula | 1 | 1 | / | / |
| Astragalus | 1 | 1 | / | / |
| Calcaneum | 1 | 1 | / | / |
| Tarsus | | 2 | | / |
| Mt I | | 1 | | / |
| Mt II | | 1 | | / |
| Sesamoidi | | 2 | | / |
| I Phalanx | | 4 | / | / |
| II Phalanx | 1 | / | / | / |
| Indet. | | 9 | | |
| Tot. | | 64 | | |

all'Onda (Molara, 2012), Grotta La Fabbrica 1 (Pitti et al., 1977), Grotta Breuil (Alhaique and Tagliacozzo, 2000), Grotta Guattari (Petronio et al., 2021), Grotta di Torre Nave (Mangano, 2007), Ingarano (Petronio and Sardella 1998); Fig. 1]. Evidence of living alternation within the same site is scarce [i.e., Buca della Iena (Pitti and Tozzi, 1971), Grotta Reali (Peretto, 2012); Fig. 1]. The radiocarbon dating dataset produced suggests a possible coexistence between the two species within La Sassa. It should be considered that radiocarbon dating of Pleistocene contexts presents a significant sigma range, therefore this data should be carefully considered. Moreover, the concomitance of cave hyenas and bears within the same cave is highly unlikely, albeit is attested in several sites in Europe (Diedrich, 2006, 2014, 2015). However, coexistence in Italy seems so far to have never been documented, therefore La Sassa provides an unusual case study. Interestingly, hyena coprolites are extremely numerous in communal dens within large cave systems shared with bears, wolves and cave lions (Diedrich, 2012a, 2014, 2015). These were most probably used to mark the boundaries of their areas and keep other predators away. Their abundance within a well delimited area close to the prehistoric entrance at La Sassa could set the perimeter of the den, which in other shared caves is often placed near the entrance (Diedrich, 2014, 2015).

Human subsistence as an accumulation agent of the faunal assemblage has also been discussed. Interactions and cave alternations between humans and bears (Bona et al., 2007; Romandini et al., 2018, 2020; Viranta and Grandal-d'Anglade, 2012), as well as humans and hyenas (Daujeard et al., 2019; Enloe et al., 2000; Fourvel, 2012; Stiner, 1992, 2004), are attested throughout the Middle and Upper Pleistocene in Italy and Europe. Three Aurignacian lithic artifacts have been discovered in Room 1 at La Sassa, near the prehistoric entrance of the cave (Fig. 10). Nonetheless, cut marks or anthropic manipulation of the bones are absent and the spatial distribution of these few artifacts suggests transportation through soil sediments from the outside. Therefore, an active anthropic role in the bone accumulation can be excluded but it seems humans occasionally attended the surrounding area. This evidence is extremely interesting since Late Pleistocene human sites on the slopes of the Monti Ausoni are lacking at present. Further studies will clarify if this absentee is due to the scarcity of archaeological investigations carried out in the area or to a subsistence choice of prehistoric groups that preferred the occupation of the coastal zone around the Monte Circeo, about 30 km far from La Sassa Cave, over the hinterland.

### 5.2. The palaeoecological perspective

The ecological requirements of the taxa from La Sassa cave, although there has been a selection of the prey by the hyenas, and possibly by other occasional predators, provide some useful indications to preliminary reconstruct the environmental landscape of the Rio Sassa valley and surrounding Ausoni Mountains during the final stages of MIS 3.

Among artiodactyls, the most abundant order of the assemblage, the wild boar prefers woods and wetlands; the red deer is particularly common in open woods with large grassy clearings; the fallow deer preferably lives in sparse woods/Mediterranean scrub and the roe deer is a typically woody species preferring hardwood forests rich of brushwood and clearings (Boitani et al., 2003). The chamois attend coniferous and hardwood woody areas with rich brushwood spaced by rocky walls and stony zones, alpine prairies, bare patches and grassy ledges (Boitani et al., 2003; Salari et al., 2014). The aurochs, *B. primigenius*, preferred open forest or grasslands with woods rich of glades (Petronio et al., 2008 and references therein).

*Equus ferus* and *E. hydruntinus* were quite common during the Late Pleistocene, preferring open environments like steppes and grassland (Conti et al., 2010; Salari and Masseti, 2016). The Italic hare is a species adapted to live in several environments but seems to prefer shrubby dry areas and prairie alternated to hardwood forest with large grassy clearings. Instead, the European hare has rather open habitats like prairie and steppe (Amori et al., 2008). Beaver and water vole live on river embankments (Amori et al., 2008; Salari et al., 2020). About the carnivores, wild cat, brown bear and mustelids prefer woodland areas near water sources, while wolves and foxes are animals adapted to a variety of environments generally settling the den in woodlands with gorges and stony zones (Boitani et al., 2003). Cave lion and cave hyena seem to have frequented different environments, with a predilection for open spaces, like the lion and spotted hyena extant of the savannah (Dorst and Dandelot, 1972; Mills and Hofer, 1998; Bauer et al., 2016).

The Ausoni Mountains slopes were probably covered by forests with clearings and sparse woods frequented by cervids, brown bears and other small carnivores and aurochs. Rocky surroundings and stony zones were frequented by chamois, while the Rio Sassa valley was covered by grasslands that may have evolved into steppe inhabited by hare and
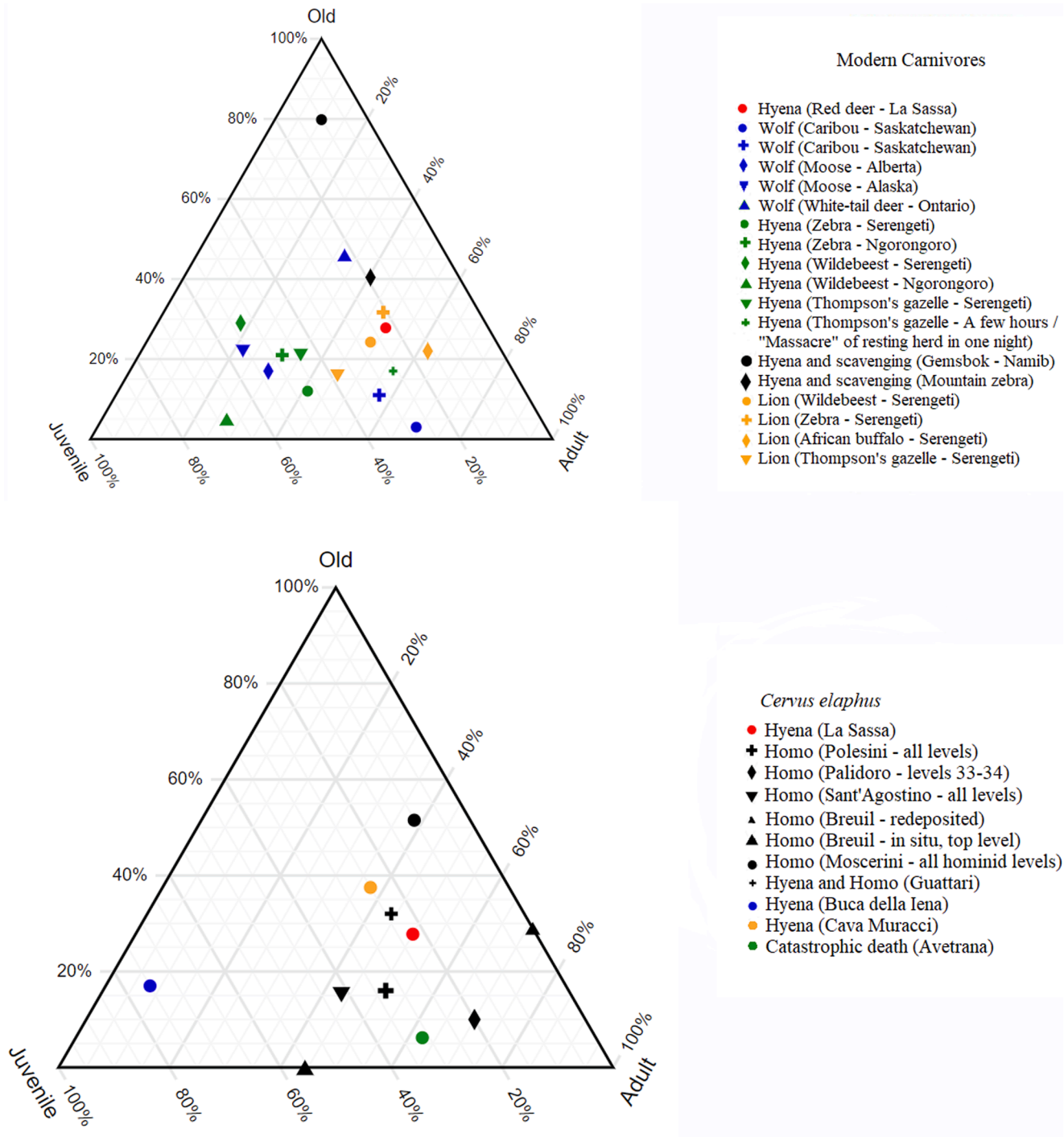
**Fig. 9.** Ternary diagrams showing mortality profile of *Cervus elaphus* from La Sassa cave compared with mortality profiles of main preys of extant large carnivores (up) and others Late Pleistocene sites of central and southern Italy (down) (data by Stiner 1990, Pandolfi et al. 2013; Gatta et al. 2019).

equids and grazed by aurochs. Moreover, the embankments rich in vegetation provided sustenance to wild boars, beavers and water voles. Finally, the presence of the chamois and the greater percentage of *C. elaphus* compared to *D. dama* suggest that the area investigated was cooler during MIS 3 than today (see Gatta et al., 2019; Salari et al., 2011, 2019 and references therein).

## 6. Conclusions

The Late Pleistocene faunal deposit of La Sassa cave consists of 4739 macromammal remains of which 21 % have been taxonomically

identified allowing to recognise over 20 different taxa. The study of the assemblage, which comprised a detailed taphonomic analysis, NISP and MNI counts and determination of age at death, together with stratigraphic observations and coprolites morphometry identified the cave hyena as the main agent of accumulation during a very short timeframe of the Late Pleistocene between 33 and 31 ka BP. Interestingly, the preservation of the record also permitted to interpret La Sassa as a communal den established in the outer rooms of the cave, while the inner area (i.e., Room 6) was used as a winter shelter by at least one brown bear. On the other hand, evidence suggests anatomically modern humans did not occupy the cave during the time-span analysed in this
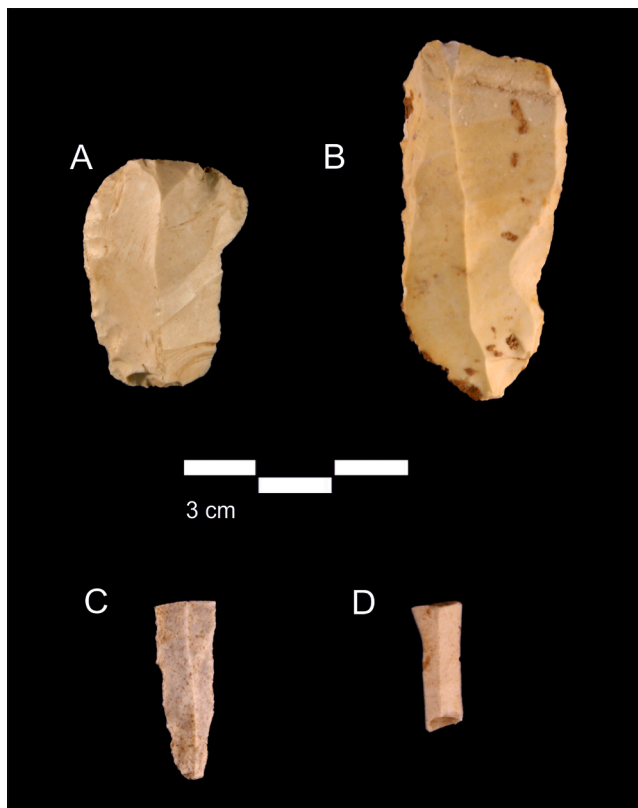
**Fig. 10.** Aurignacian lithic artifacts. A) Rep. 4590 – Retouched end-scraper short frontal (G4); B) Rep. 2295 – Retouched blade (L2); C) Rep. 3760 – bladelet with marginal retouch (L1); D) Rep. 2041 – Fragment of unretouched bladelet.

paper but possibly frequented the surrounding area, while sporadic/occasional attendances by fox and perhaps cave lion are recorded, perhaps during times of absence or infrequent presence of cave hyena.

A palaeoecological perspective on taxa identified and their abundance gave us the opportunity to provide a first environmental description of the Ausoni Mountains during the final stages of MIS 3. Nevertheless, it should be interpreted bearing in mind that: i) the faunal assemblage is affected by the hunting behaviour of cave hyenas, therefore, additional data could improve the results of paleontological analysis. Indeed, further studies, among which the pollen from coprolites, are ongoing to provide detailed flora data on a local scale; ii) modern spotted hyenas usually hunt within 15 km from their den (Scott, 1987; Argant and Dimitrijevic, 2007), assuming it was the same for the cave hyena, the analysed faunal assemblage reflect local habitats.

The environmental reconstruction shows a wooded area with some open areas and surprisingly mild conditions for MIS 3. Further excavations of the numerous Middle and Upper Palaeolithic sites of the area will reveal the context of the La Sassa cave fauna both in terms of the local variation in the landscape as in the climatic changes that affected the region in the final stages of the last glacial.

## CRediT authorship contribution statement

**Maurizio Gatta:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Funding acquisition. **Angelica Fiorillo:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Leonardo Salari:** Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Supervision. **Katia Francesca Achino:** Formal analysis, Investigation, Writing – review &

editing. **Mario Federico Rolfo:** Investigation, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Luca Alessandri:** Investigation, Resources, Writing – review & editing, Project administration, Funding acquisition.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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