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Deciphering the diet of the Iberian lynx: Insights from taphonomic analysis of Pleistocene coprolites

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ABSTRACT

Pleistocene deposits often result from multiple and overlapping contributions. Carnivores play a significant role as bone accumulators in archaeological sites, but identifying the specific agent responsible for a particular accumulation can be challenging. Referential studies provide valuable insights into bone accumulation patterns, but they are based on modern collections and often fail to account for taphonomic biases associated with site formation processes. Here, we present, for the first time, a taphonomic study focused on fossilised Pleistocene Iberian lynx coprolites within the European context. The assemblage, dated to ca. 33 ky B.P., was recovered from layer III of Cova del Gegant, a site identified as a lynx den likely used for rearing cubs. This study is based on previous research at the site and analyses bone remains consumed by the Iberian lynx (*Lynx pardinus*), recovered from coprolites, to investigate their role in archaeological contexts. The findings are consistent with other lynx accumulations documented in literature, particularly regarding leporid remains. The anatomical proportions in this assemblage are more balanced than other types of accumulations, with a higher representation of cranial elements. Digestive damage is predominant, affecting most bones, especially at moderate and strong degrees. These results enhance our understanding of archaeological accumulation processes and highlight the role of lynxes as bone accumulators. The archaeological evidence from the site indicates that the Iberian lynx inhabited environments and climates that differ significantly from those currently observed. However, the present study suggests that its diet remained relatively consistent with that of contemporary Iberian populations.

1. Introduction

Caves function as a natural strategic features within the landscape, with both humans and carnivores utilising them for habitation and other purposes throughout time (e.g., Binford, 1981; Brugal and Fosse, 2004; Domínguez-Rodrigo et al., 2007; Rosell and Blasco, 2009). During the Palaeolithic period, these spaces often experienced alternating occupations by humans and various carnivorous species, resulting in mixed accumulations within the same area. Thus, these deposits can be challenging to discern. Mammalian carnivores, use caves as dens or refuges (Fosse, 1997; Brugal and Fosse, 2004; Blasco et al., 2011), leading to the accumulation of bones, leftovers, and faeces (also called coprolites when they fossilise). In the same manner, birds of prey may also use these spaces for nesting, accumulating the leftovers of their food in the form of non-ingested bones or pellets that, through the past of time become disaggregated and form palimpsests with other remains (e.g., Laroulandie, 2000; Blasco and Peresani, 2016 and references therein). Each of these predators has specific characteristics in their accumulations, which might be helpful to differentiate occupation events. In this line, extensive scientific literature has explored methods to determine the origins of bone accumulations through zooarchaeological and taphonomic analyses (e.g., Laroulandie, 2000; Cochard, 2004; Lloveras et al., 2008a, 2008b, 2009, 2012a, 2012b, 2018, 2020; Sanchis, 2012; Yravedra, 2004, 2006; Stiner et al., 2012; Rodríguez-Hidalgo et al., 2013, 2016; Krajcarz and Krajcarz, 2014; Marin-Monfort et al., 2019). Most of these works are based on neotaphonomic approaches, which help to better understand the taphonomic signature left by a specific agent. When studying bone accumulations produced by different predators, it is important to differentiate between ingested and non-ingested remains. This is because the patterns and bone surface modifications

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observable on bones would differ depending on what happened to the bones before being abandoned. For example, it is assumed that those body parts that were ingested would be more prone to suffer digestive damage (e.g., Bochenski et al., 1997; Laroulandie, 2000; Lloveras et al., 2008a, 2008b, 2009, 2012a, 2012b; Armstrong, 2016; Rufà and Laroulandie, 2019), while bones accumulated by the same predator that did not suffer any digestive process may not document any kind of dissolution due to digestion but display other bone surface modifications such as pits or punctures because of mechanical or chewing damage (e.g., Bochenski et al., 1997, 1999, 2009; Laroulandie, 2000; Yravedra, 2006; Sanchis, 2012; Lloveras et al., 2012a, 2014a, 2014b, 2018; Rodríguez-Hidalgo et al., 2013, 2015, 2016).

When analysing coprolites, we are examining an accumulation of ingested bones, the presence of these remains within a coprolite indicates that they have passed through the entire digestive system before being excreted and deposited at the site. In addition, coprolite analysis provides a valuable tool for identifying specific predators responsible for an assemblage (Chin, 2002; Yang et al., 2022; Sanz et al., 2016, 2023). The macroscopic inclusions within coprolites—such as animal bones, hair, and feathers—offer insights into the diets of their producers, shedding light on digestive efficiency, feeding strategies, and trophic levels within the food chain. Even if coprolites have a lot of potential for understanding ethologic and archaeologic interactions, coprolite studies mainly focus on paleoenvironmental data (Carrión et al., 2001, 2003, 2007; Gil-Romera et al., 2014; Brönnimann et al., 2017; Zhang et al., 2019; Ochando et al., 2022). Some studies have also tried to correlate specific coprolite sizes and morphologies to predators better to understand the dynamics of occupation in different sites, also in correlation with other taphonomic and zooarchaeological approaches (e.g., Barrios-de Pedro et al., 2018; Cambronero and García, 2024; Sanz and Daura, 2018a; Sanz et al., 2023). In this line, there is an increasing interest in characterising actual faeces assemblages produced by carnivores, to relate them to specific predators. Chame (2003), Jouy-Avantin et al. (2003) and Diedrich (2012) stated some standardised descriptive parameters for coprolites, then also adapted by Sanz (2013) and Sanz et al. (2016), among others. These criteria are mainly based on the state of preservation of coprolites (entire, fragmented, disaggregated), their morphology (considering volume, extremities and number of segments) and measurements (length and width). It is widely accepted that the shape and diameter of faeces are the most reliable indicators for taxonomically characterising coprolites. In Furninha cave (Portugal) and cova del Coll Verdaguer (Spain), for example, morphometric studies of coprolites were carried out, identifying various coprolite carnivore types and describing different categories as follows: (1) morphotype 1—globular, crumbly texture, hard consistency and scarce bone inclusions (hyenids); (2) morphotype 2—cylindrical shape, spiral internal fabric, friable, abundant bone contents (non-hyenid carnivores), and (3) a supposed morphotype 3—larger size, crumblier texture and strong hardness (large carnivore, hypothetically bear) (Brugal, 2010; Sanz et al., 2016). A new category, morphotype 4—cylindrical, homogeneous and porous, hard with no bones— has been recently added, exclusively related to the bearded vulture (Sanz and Daura, 2023; Sanz et al., 2023).

Despite extensive research focusing on the analysis of coprolites, certain taxa originating them are more readily identified than others. This is particularly evident in the case of hyenas (e.g., Pesquero et al., 2011; Linseele et al., 2013; Sanz et al., 2016). Coprolites, which are fossilised masses of desiccated and subsequently mineralised soft tissue, exhibit considerable variability in preservation. Bone-rich tissues are more likely to withstand fossilisation, making hyena coprolites relatively common due to their well-documented behaviour of consuming and digesting bones.

While coprolites from specific taxa can be identified, in other cases distinguishing them poses challenges, especially in the case of carnivores such as wolves, lynxes, or foxes (e.g., Pineda et al., 2017; Rodríguez-Hidalgo et al., 2013; Morales et al., 2016; Lloveras et al., 2020). In such cases, a multidisciplinary approach becomes essential, incorporating additional indirect evidence from the archaeological or paleontological contexts. This includes analysing the taxonomic composition of prey remains found at the site, potentially indicative of predator behaviour, and assessing taphonomic modifications on these bones. Some animals also have specific hunting preferences or might adapt their feeding behaviours according to prey availability. In this line, it is also important to study predators' ethology, which also considers their feeding habits and whether they have any preferred animals to prey on (e.g., Delibes, 1980; Ferreras and Fernández-de-Simón, 2019; Duľa and Krofel, 2020). In this context, neotaphonomic research becomes crucial, as they can provide both ethological and taphonomic information about different carnivorous predators and their feeding habits (Stiner et al., 2012).

The Iberian lynx (*Lynx pardinus*), an endemic species of the Iberian Peninsula, is a predator commonly identified in archaeological sites. Although its population has significantly declined over the past centuries, now confined to areas such as Doñana National Park, the Sistema Central, Montes de Toledo, and the westernmost Sierra Morena Mountain ranges, this species was widely distributed across the peninsula during the Pleistocene (Brugal, 2010; Rodríguez-Hidalgo et al., 2020; Daura et al., 2013). The Iberian lynx's diet is highly specialised, with lagomorphs—primarily rabbits—comprising 80–100 % of its intake, occasionally supplemented by birds and other small prey (Odden et al., 2006; Hanson and Moen, 2008; Morin et al., 2016; Delibes, 1980; Gil-Sánchez et al., 2006; Ferreras et al., 2011). This dietary hyper-specialisation underscores the species' specific ecological requirements. Neo-taphonomic studies examining lynx feeding traces have reinforced these observations, characterising their prey accumulation patterns from zooarchaeological and taphonomic perspectives (Lloveras et al., 2008b; Rodríguez-Hidalgo et al., 2013, 2016). Such research highlights diagnostic traits in bone assemblages attributed to lynxes, providing critical insights into their behaviour, ecological role and the identification of these feeding traits in Pleistocene assemblages (Rodríguez-Hidalgo et al., 2020; Rosado-Méndez et al., 2015).

This study seeks to evaluate the diagnostic potential of bone remains extracted from coprolites recovered at Cova del Gegant (Sitges, Barcelona, Spain) layer III. This site offers a compelling case for such analysis, as prior studies on bone remains from the site and coprolites have mostly attributed this accumulation to lynx activity (Rodríguez-Hidalgo et al., 2020; Sanz, 2013; Sanz et al., 2017). Additionally, it is an exceptional case because it represents a den where parts of carcasses and coprolites have accumulated by the same agent. Building upon this foundation, the present research aims to characterise the bones retrieved from coprolites and assess how their analysis complements the earlier findings. The methodology combines visual examination of coprolites with the identification and detailed analysis of some of the bones they contain. Although advanced techniques such as paleoproteomics and ancient DNA (aDNA) analysis provide promising opportunities, traditional analytical approaches remain essential due to the often variable preservation of coprolitic material. By integrating these methods, this study seeks to refine interpretations of predator-prey relationships and contribute to a deeper understanding of site formation processes within both paleontological and archaeological frameworks. Moreover, the objective is to increase our understanding of the dietary habitats of the Iberian lynx in regions where it is no longer present today.

2. Background

2.1. Cova del Gegant

Cova del Gegant is an archaeological site situated on the Garraf Massif in northeastern Iberia, approximately 40 km from Barcelona (41°13′24.75" N, 1°46′27.33″ E) (Fig. 1A to 1C). The cave is located on the cape of Punta de les Coves, at an elevation of zero meters above sea level (Fig. 1D). The area is primarily composed of Cretaceous limestone, which has facilitated the development of a small karstic system that

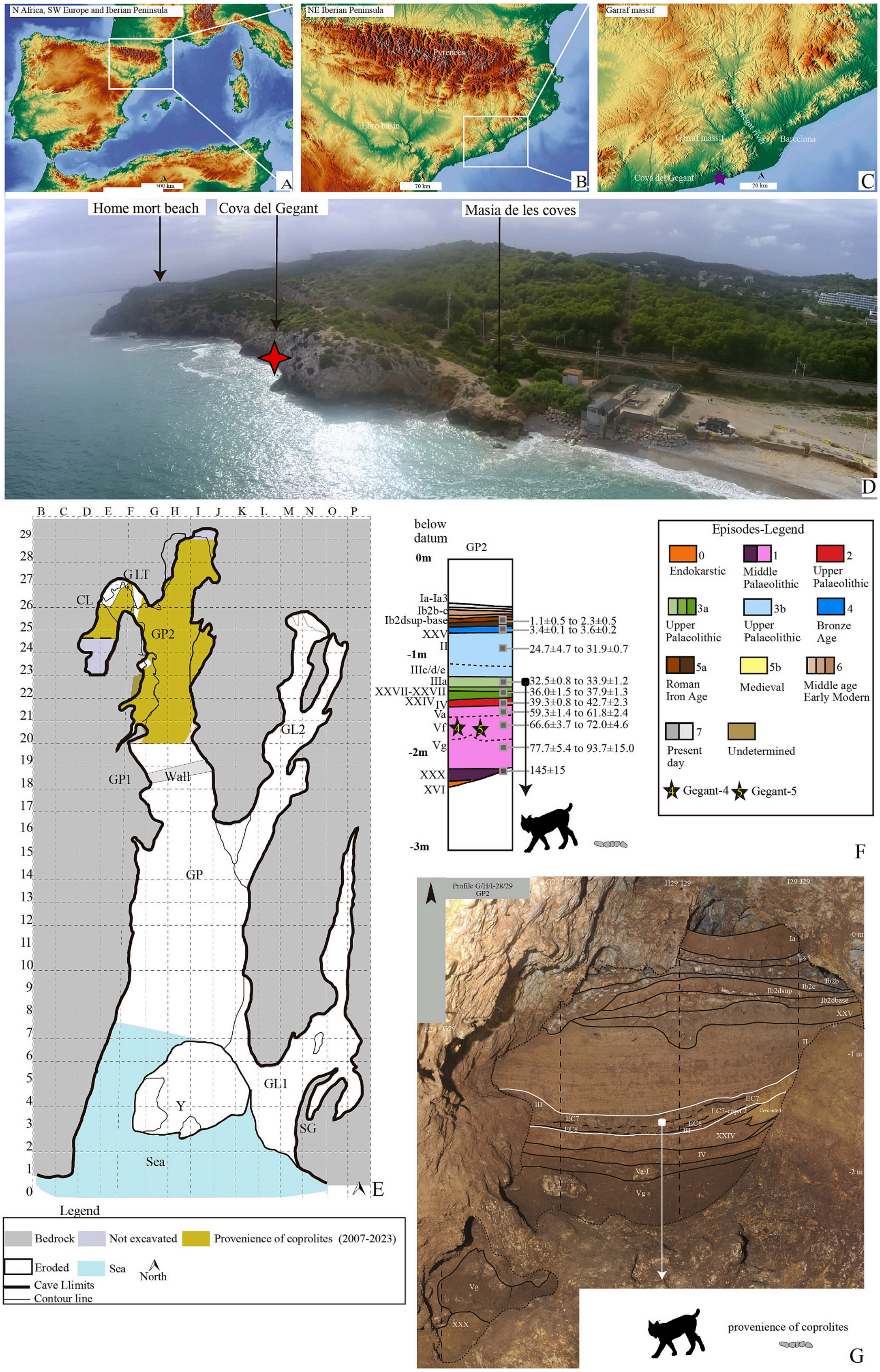


Fig. 1. Cova del Gegant site. A–C: Location of Cova del Gegant within the Iberian Peninsula. D: Drone view of Punta de les Coves and the Cova del Gegant site. E: Site plan indicating the provenience of the bone remains. F–G: Stratigraphic profile and Bayesian modelled ages showing the provenience of the analysed bone remains.

includes a network of caves, such as the Cova del Musclo, Cova del Gegant, and Cova Llarga. Cova Llarga connects with the Cova del Gegant through a narrow passage (GLT).

Cova del Gegant consists of three distinct galleries: the main chamber, which is 22 m long (sections GP1 and GP2), and two nearly parallel galleries (GL1 and GL2) (Fig. 1E). Due to the partial flooding of the cave's main entrance, access is now achieved through a natural shaft at the roof of the cave, which descends 20 m into the system.

The site was first discovered in 1952 and subsequently excavated on multiple occasions until the 1980s (Daura et al., 2022). Since 2007, a research team from the Grup de Recerca del Quaternari (SERP, University of Barcelona) has focused on the excavation of sediments at GL1 and mainly at the back of the main gallery (GP2).

The 2.5-m-thick stratigraphic sequence of the cave at GL2, initially outlined by Daura et al. (2005), has undergone refinement over subsequent years of excavation (Daura et al., 2010; Daura and Sanz, 2011; Daura et al., 2021). The sequence at GP2 encompasses an extensive chronological record spanning approximately 145 ka to 25 ka. Layer XXX represents the basal sedimentation in the main gallery, with an OSL age of 145 ± 14 ka obtained from this deposit. Layer V corresponds to Middle Palaeolithic occupations and was accumulated between the end of MIS 5 and late MIS 4 or early MIS 3 (López-García et al., 2022). The uppermost sublayer of this unit (Va) yields a Bayesian modelled age range of 61.8 ± 2.4 to 59.3 ± 1.4 ka cal BP, while the middle (Vf) and basal (Vg) sublayers were deposited between 72.0 ± 4.6 to 66.6 ± 3.7 ka cal BP, and 93.7 ± 15.0 to 77.7 ± 5.4 ka cal BP, respectively. A Bayesian modelled age range of 42.7 ± 2.3 to 39.3 ± 0.8 ka cal BP was obtained for layer IV, while layers XXIV–XXVII accumulated between 37.9 ± 1.3 and 36.0 ± 1.5 ka cal BP. Layer III was deposited between 33.9 ± 1.2 and 32.5 ± 0.8 ka cal BP, and Layer II formed between 31.9 ± 0.7 and 24.7 ± 4.7 ka cal BP (Fig. 1F).

Among the archaeological record of GP2, basal layer V is particularly notable. Dating to the Mousterian period, this layer contains faunal remains, Neanderthal human fossils (Daura et al., 2005; Arsuaga et al., 2011; Daura and Sanz, 2011; Quam et al., 2015), Mousterian lithic tools, evidence of human activity and coprolites. The accumulation of ungulate bones is primarily attributed to large carnivores, particularly hyenas (Sanz, 2013; Sanz and Daura, 2020; Daura et al., 2021). The overlying layers (IV, XXIV, III and II) correspond to the Upper Palaeolithic. These layers reflect alternating episodes of human and carnivore activity, including combustion structures and fire-related by-products (Sanz et al., 2017), a limited lithic tool assemblage, and carnivore activity, particularly that associated with lynx occupations (Daura et al., 2021).

2.2. Layer III and the coprogenic assemblage

The coprolites discussed in this study come from layer III preserved at the inner part of the main gallery (GP2) (Fig. 1F to 1G) with modelled age between 33.9 ± 1.2 to 32.5 ± 0.8 ka cal. BP. Layer III functioned mainly as a carnivore den or shelter, with very few and occasional visits by humans documented by combustion structure and by-fire products (Rodríguez-Hidalgo et al., 2020; Sanz, 2013; Sanz et al., 2017; Daura et al., 2021) that probably are related to resting or bedding areas. The analysis of the faunal assemblage—mainly composed of leporids (see Supplementary Table 1)—suggests that layer III served as a lynx den (Rodríguez-Hidalgo et al., 2020; Sanz et al., 2017) for rearing cubs (Jiménez et al., 2025).

This study focuses on the faunal remains visible within disaggregated and fragmented coprolites from layer III. These coprolites, characterised by a high proportion of leporid remains, exhibit morphological and taphonomic features distinct from those typically attributed to hyenas. The assemblage is highly fragmented, with 89 % of specimens shapeless, 15.1 % fragmentary, and only 2 % preserved as complete coprolites. Despite this, the preserved morphometry and external characteristics allow clear attribution to morphotype 2 (Sanz, 2013; Sanz et al., 2017; Sanz et al., 2016; Rodríguez-Hidalgo et al., 2020).

Morphotype 2 display a consistent cylindrical shape, spiral internal fabric, friable texture, and uniform surfaces—traits that differ notably from hyena coprolites (morphotype 1). Morphometric analysis of well-preserved specimens yielded diameters averaging 21 mm, consistent with scat sizes of medium-sized carnivores such as lynx, fox, and wolf, and incompatible with those of larger or smaller felids.

Although the coprolites were not fully disaggregated, diagnostic bone and tooth fragments—primarily from leporids—were identifiable externally and in fractured sections. These include isolated teeth, femora, and ulnae (Rodríguez-Hidalgo et al., 2020, Table S9).

Multiple lines of evidence support the interpretation of these coprolites as originating from Iberian lynx activity at Cova del Gegant. These include the cave's use as a natal den, the presence of tooth marks consistent with kittens, a predominance of rabbit remains, the lynx-specific taphonomic pattern on rabbit bones, and the demographic profile of lynx individuals from layer III (Sanz, 2013; Sanz et al., 2017; Rodríguez-Hidalgo et al., 2020; Jiménez et al., 2025).

3. Methods

The material analysed in this study was recovered during fieldwork conducted by the Grup de Recerca del Quaternari (GRQ-SERP) of the University of Barcelona. Processing, storage, and initial identification of the material were carried out at the La Guixera Laboratory (Castelldefels City Council) and at the University of Barcelona.

To identify the potential accumulator agents of the coprolites at Cova del Gegant, we employed a multidisciplinary approach integrating zooarchaeological and taphonomic analyses. In the dataset presented in Supplementary Materials 2, the identified bones are listed according to their corresponding coprolite of origin. The number assigned to each coprolite (Coprolite ID) corresponds to the site inventory number. Coprolites that could not be individually identified are indicated as "n/d" (not determined). The analysis of bones observable within coprolites and the bone surface modifications documented have been performed. In addition, other diagnostic criteria have been applied to the coprolites to get additional information about the predator accumulating them. Given the poor preservation of paleoproteins and ancient DNA at the site, methods relying on morphological, textural, and compositional features were prioritised (Jouy-Avantin et al., 2003; Sanz et al., 2016). Specifically, the analysis focused on four criteria: (1) shape and morphology; (2) size; (3) internal texture; and (4) hardness.

Due to the variable preservation of the coprolites, only those that were naturally fragmented or crumbled were selected for detailed examination, ensuring minimal disruption of intact specimens. That way, only surface-visible bones and those already individualised from disaggregated coprolites were examined. Specimens were sorted and classified according to established zooarchaeological standards.

The recovered faunal remains were identified anatomically and taxonomically, facilitating the differentiation of taxa based on osteological markers (e.g., Callou, 1997; Bochenski and Tomek, 2009; De Marfà, 2009). Age profiles were mainly established by assessing the degree of ossification and epiphyseal fusion in long bones (Cochard, 2004; Jones, 2006; Sanchis, 2012).

Bones were quantified according to the Number of Remains (NR), the Number of Identified Specimens (NISP), the Minimum Number of Elements (MNE), and the Minimum Number of Individuals (MNI), as well as the calculation of their percentage of Relative Abundance (RA). Additionally, differential bone conservation was evaluated through a Pearson's r correlation analysis, using bone density data from *Oryctolagus cuniculus* (Pavao and Stahl, 1999), as leporids are the most abundant taxon in the assemblage. The proportions of skeletal elements for Leporidae remains were evaluated, considering the criteria of Andrews (1990) and adapted by Lloveras et al. (2008a) – expressed as a percentage: limb elements, vertebrae and ribs compared to total numbers of mandibles, maxillae and teeth (PCRT/CR); long bones, scapula, innominate, patella, metapodials, carpals, tarsals and phalanges compared to mandibles, maxillae and teeth (PCRAP/CR); postcranial long bones compared to mandibles and maxillae (PCRLB/CR); autopodium elements compared to zeugopodium and stylopodium (AUT/ZE); zeugopodium elements compared to stylopodium (Z/E); humerus, radius, ulna compared to femur and tibia (AN/PO). Metapodials have not been taken into account for the AN/PO proportion, as it was not possible to classify most of them as metacarpals or metatarsals.

The percentage of bone fragmentation was also calculated. In addition, fragmentation was evaluated by discerning between green and dry fractures (Steadman et al., 2002; Sanchis, 2012; Cochard et al., 2012). Green fractures are characterised by curved or spiral forms with oblique angles and smooth edges, while dry fractures usually display transverse forms with straight and jagged edges.

A Euromex stereomicroscope with magnification ranging from 6× to 45× was employed to identify surface modifications. Carnivore activity was assessed by documenting chewing activities related to pits, punctures, scores, notches, and crenulated edges (Binford, 1981; Lyman, 1994; Fernández-Jalvo and Andrews, 2016). Detailed high-magnification pictures of some of these modifications have been taken by using an Hirox KH8700 3D digital microscope. Digestive damage was also evaluated by using Andrews' (1990) corrosion scale, ranging from no visible alteration (degree 0) to extreme corrosion (degree 4). Other human-related modifications were considered for the analysis, including cut marks (Shipman and Rose, 1983) and burning damage (Stiner et al., 1995), though none were observed. Other post-depositional modifications were documented, following the criteria established in the specialised literature (e.g., Lyman, 1994; Fernández-Jalvo and Andrews, 2016).

4. Results

4.1. Coprolites

The bones analysed originate from at least 113 different coprolites recovered in layer III. Most of these coprolites were either disaggregated or fragmented. Due to this fragmentation, measuring the coprolites has often been challenging, and thus, no systematic analysis in this regard has been conducted for the current study. Further information on this topic can be consulted in Rodríguez-Hidalgo et al. (2020) and Sanz et al. (2017). However, even if most coprolites do not preserve a complete shape, it is sometimes possible to infer their original morphology.

In general, observable coprolites exhibit a tubular or cylindrical shape. Pointed ends are often noted on both complete and fragmented specimens, which are typically composed of multiple segments (see Fig. 2). The coprolites contain identifiable remains, as well as other undetermined fragments. The partial or complete disaggregation of most studied coprolites allows for a detailed taphonomic examination of the bones they enclose.

Of the bones analysed, 40 elements were retrieved from fully disaggregated coprolites, making it impossible to determine whether they originated from multiple faeces or a single specimen. This is also the reason why it has been counted as a minimum number of coprolites. A

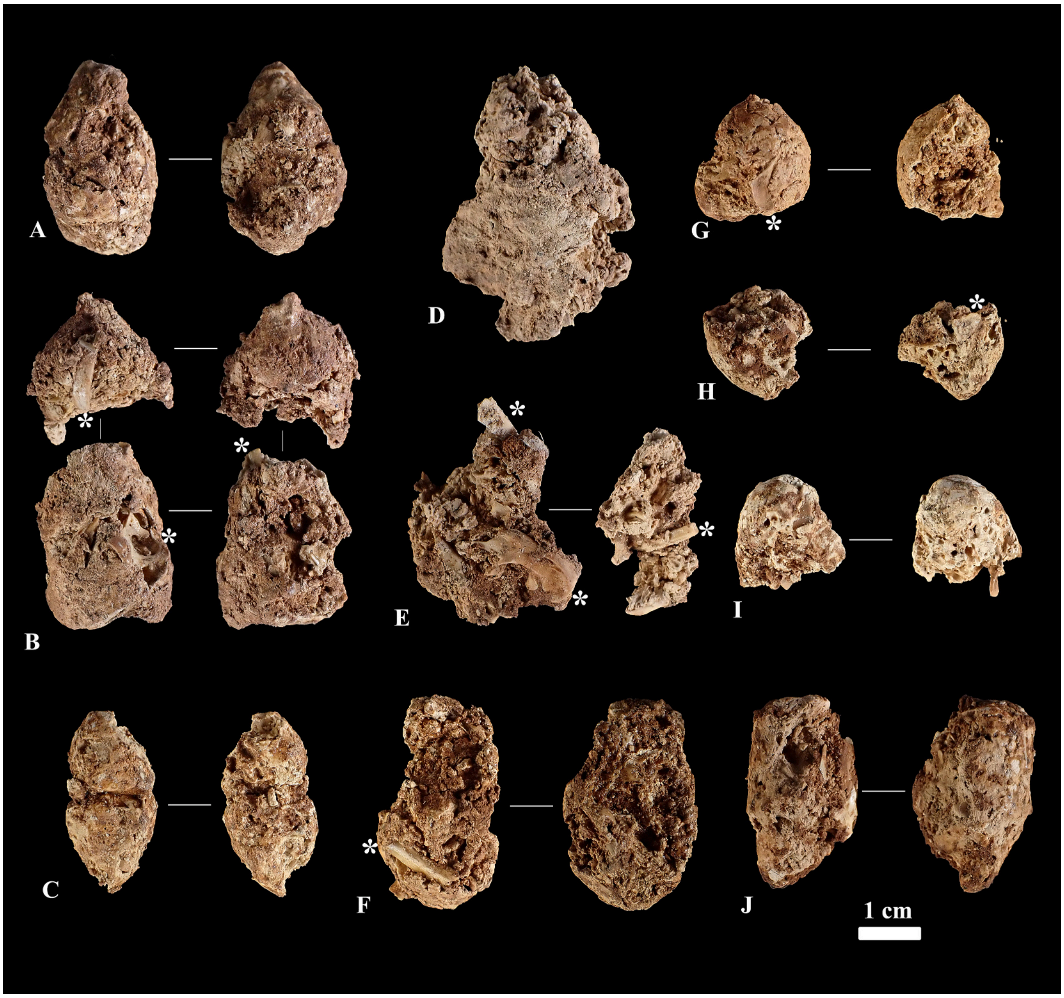


Fig. 2. Fragmented coprolites recovered at Cova del Gegant layer III. Each letter (A–J) corresponds to an individual coprolite specimen.*The asterisks mark the bones observed inside the coprolites.

few coprolites ($n = 10$) contain more than 10 observable bones. However, the majority reveal only one to six bones. Across all the analysed coprolites, the mean number of bones per coprolite is 2.5, which serves as an indicator of the density of visible bones within each specimen.

4.2. Bone contents

A total of 460 bones recovered from the coprolites were analysed (Table 1). Various taxa have been identified within the assemblage, with Leporidae family bones being the most abundant (NISP = 416; 90.4 % of the total layer III assemblage). Although the size of the bones suggests that these remains likely belong to the European rabbit (*Oryctolagus cuniculus*), the broader category of the Leporidae family has been retained. This allows the inclusion of potentially identifiable remains and those that cannot be determined at the species level. These were followed by undetermined micromammal specimens (NISP = 17; 3.7 %), undetermined medium-sized birds (NISP = 4; 0.9 %), and small mammalian carnivore remains (NISP = 4; 0.9 %). Among the carnivore remains, there is a patella that has been confirmed as belonging to a felid. It is possible that the other carnivore elements also belong to this taxonomic group. However, the maturity of the bones, along with fragmentation and damage, prevents more precise identification. In addition, other mesofaunal (NR = 12; 2.8 %) and macrofaunal (NR = 7; 1.5 %) fragments without specific taxonomic attribution have been identified. These fragments may partially complement some of the previously mentioned taxonomic groups.

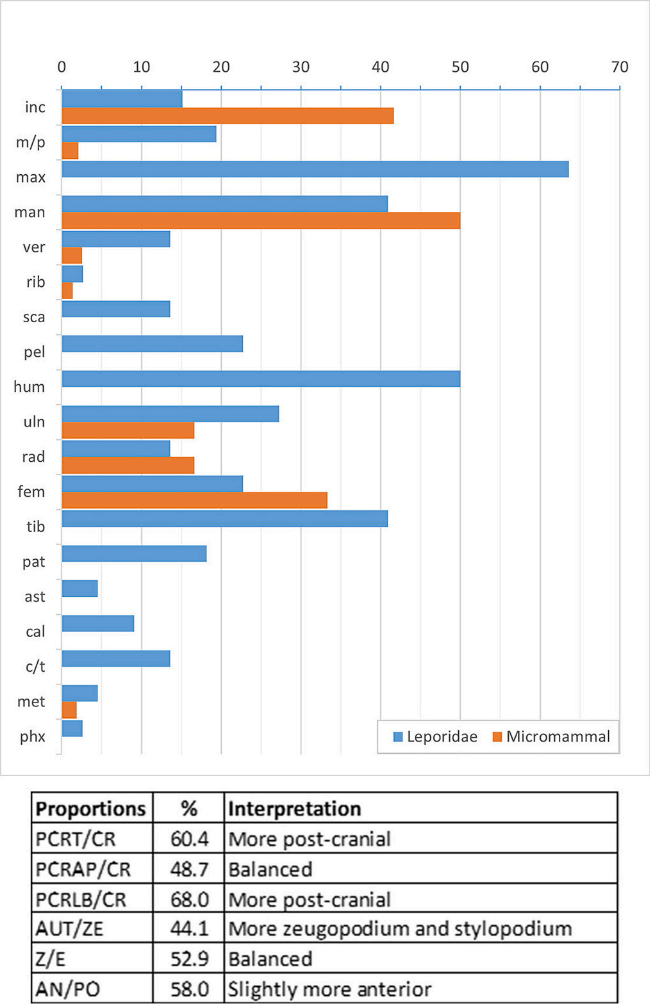
Using the repetition of specific anatomical parts and their laterality, a minimum of 17 individuals (MNI) has been recorded. Leporids are the most abundant (MNI = 11; 65 % of the assemblage), followed by micromammals (MNI = 3; 17 %). Among the Leporidae MNI, three immature and one neonatal individuals were recorded (36.4 % of the total leporid individuals). Similarly, one immature individual was documented within the micromammals (see Table 1). Only one individual was documented for both birds and felids. An additional individual was identified within the undetermined carnivore group, corresponding to an immature specimen, which could not be included in the Felidae family in this assemblage.

Considering the skeletal representation leporids are well-represented in all the skeletal categories. If we consider the percentage of relative abundance of these remains (Fig. 3), maxilla (63.6 %), and mandibles (40.9 %) stand out among cranial remains. Some long bones are also well represented, humeri having 50 % of representation, and 41 % for tibias. Ulnas (27 %), femora (22.7 %) and pelvis bones (22.7 %) followed with moderate percentages of representation. Other skeletal elements, even if less represented are also found such as isolated molars/premolars (19.4 %), incisors (15.2 %), patellas (18.2 %), vertebras (13.6 %), scapulas (13.6 %), radii (13.6 %) or carpal/tarsal bones (13.6 %).

If we consider the proportion of skeletal elements reported by Lloveras et al. (2008a) for leporids, there is a slight prevalence of post-cranial remains over cranial remains. This is reflected in the PCRT/CR (60.4 %) and the PCRLB/CR (68 %). However, the proportions appear balanced when considering the PCRAP/CR (48.7 %). Additionally, there are slightly more zeugopodium and stylopodium elements relative to the autopodium (AUT/ZE = 44.1 %), a balanced proportion of zeugopodium relative to stylopodium (Z/E = 52.9 %) and a modest predominance of anterior limb elements compared to posterior limb elements (AN/PO = 58.8 %).

Table 1
Frequencies of Number of Remains (NR) or Number of Identified Specimens (NISP), Minimum Number of Elements (MNE), Total Minimum Number of Individuals (MNI), and the separation of individuals by age categories. Neo: neonatal (<3 months); Imm: immature (adult size but still not fused areas and porous tissue); Ad: adult.

	NR/NISP	MNE	MNI	MNI Neo	MNI Imm	MNI Ad
Aves	4	4	1	0	0	1
Carnivora	3	3	1	0	1	0
Felidae	1	1	1	0	0	1
Leporidae	416	202	11	1	3	7
Micromammal	7	1	3	0	1	2
Macrofauna	12	1	–	–	–	–
Mesofauna	17	17	–	–	–	–
TOTAL	460	229	17	1	5	11



Proportions	%	Interpretation
PCRT/CR	60.4	More post-cranial
PCRAP/CR	48.7	Balanced
PCRLB/CR	68.0	More post-cranial
AUT/ZE	44.1	More zeugopodium and stylopodium
Z/E	52.9	Balanced
AN/PO	58.0	Slightly more anterior

Fig. 3. Percentage of Relative Abundance for the main represented taxonomic groups. The proportions of skeletal elements were calculated for leporids. Inc.: incisive; m/p: molar/premolar; max; maxilla; man: mandible; ver: vertebra; sca: scapula; pel: pelvis; hum: humerus; uln: ulna; rad: radius; fem: femur; tib: tibia; pat: patella; ast: astragalus; cal: calcaneus; c/t: carpal/tarsal; met: metapodial; phx: phalanx.

Micromammal specimens are primarily represented by teeth (35.3 % of the total micromammal remains) and mandibles (17.6 %). These percentages increase when analysed based on the Minimum Number of Individuals (MNI). For instance, incisors account for 41.7 % of the representation, mandibles for 50 %, and femora for 33.3 %. However, due to the low number of individuals identified in this category, these values should be interpreted with caution (Fig. 3). For carnivores and birds, relative abundance was not calculated, as they are represented by only a few remains (Table 2). In addition, elements grouped into larger taxonomic categories (macrofauna and mesofauna) are mostly rib fragments, flat bone fragments, and undetermined elements. These remains are small and highly fragmented, making it impossible to discern any trends in skeletal representation.

To evaluate the relationship between bone density and relative abundance in the assemblage, the Pearson-*r* correlation coefficient was

Table 2
Frequencies of skeletal representation by taxonomic groups.

	Aves	Carnivora	Felidae	Leporidae	Micromammal	Macrofauna	Mesofauna	TOTAL
incisive	0	0	0	17	5	0	0	22
molar/premolar	0	0	0	47	1	0	0	48
skull	0	0	0	26	0	0	0	26
maxilla	0	0	0	16	0	0	0	16
mandible	0	0	0	22	3	0	0	25
vertebra	1	0	0	46	2	0	0	49
rib	0	0	0	7	1	1	1	10
scapula	0	0	0	5	0	0	0	5
pelvis	0	0	0	12	0	0	0	12
humerus	0	0	0	11	0	0	0	11
ulna	1	0	0	6	1	0	0	8
radius	1	1	0	4	1	0	0	7
femur	0	0	0	15	2	0	0	17
tibia	0	0	0	25	0	0	0	25
patella	0	0	1	4	0	0	0	5
astragalus	0	0	0	1	0	0	0	1
calcaneus	0	0	0	2	0	0	0	2
carpal/tarsal	0	0	0	3	0	0	0	3
metapodial	0	1	0	14	1	0	0	16
phalanx	1	1	0	15	0	0	0	17
long bone	0	0	0	116	0	0	0	116
flat bone	0	0	0	2	0	2	3	7
undetermined	0	0	0	0	0	4	8	12
TOTAL	4	3	1	416	17	7	12	460

Fig. 4. Example of bones presenting carnivore damage. All bones present digestive damage: moderate (C, I), heavy (A, B, E, F, G) and extreme (D, H). Picture I shows a proximal femur with a pit. A: molar. B: premolar. C: proximal humerus. D: scapula. E: proximal ulna. F: calcaneus. G & H: vertebras. I: femur.

calculated. This analysis was performed exclusively for leporids (r = 0.7220336), as they represent the most abundant taxa in the assemblage and provide a sufficient sample size for meaningful calculations. The results indicate a positive and moderate/strong correlation, suggesting that denser bones are more likely to be preserved. Therefore, there does not appear to be a process suggesting biases in skeletal representation that would require an explanation based on external factors.

The assemblage shows a high degree of fragmentation, with 78.9 % of the total remains being fragmented. Micromammal remains are an exception, where over 82.4 % of the elements are complete; only a femur and a mandible are fragmented. Additionally, a bird phalanx and a felid patella are complete. Among leporids, the most representative taxon, complete bones account for less than 19.5 %. These are limited to isolated teeth and small, compact elements such as the patella, astragalus, carpal and tarsal bones, and phalanges, typically found intact. In contrast, other skeletal elements are consistently fragmented, with only a small proportion of complete vertebras (4.3 %), humeri (9.1 %), and metapodials (7.1 %) observed. If only considering long bone completeness, the values are even lower, with a mean value of 1.8 % of complete long bones.

For long bones, fracture analysis was conducted when possible. However, in most cases, digestive damage, and concretions around fracture edges—likely due to the coprolite component—obscured observations. Only 28 fractures were sufficiently visible for analysis, all of which were determined to be in a fresh state. This subset represents 43.8 % of the total broken long bones.

4.3. Bone surface modifications

Bone surface modifications observed in the assemblage are predominantly associated with carnivore activity, specifically digestive damage. Mechanical chewing damage is rare, with only two leporid bone elements displaying visible alterations. These include a tibia shaft featuring a notch and a proximal femur with a pit (Fig. 4I). Digestive damage is observed across all taxonomic groups in similar proportions. Overall, nearly 92 % of the examined bones exhibit clear signs of digestive alterations (Fig. 4). Of these, the majority show moderate (33.3 %) or heavy digestion (29.1 %). Light digestive damage is identified in 23.7 % of the cases, while extreme digestion is present in 6.4 % of the sample. For the Leporidae taxonomic group, these percentages are similar (Fig. 5).

Apart from that, 82 bones present post-depositional modifications. Manganese coating is dominant, affecting 77 of the remains in the coprolite assemblage (17.8 %). Four bones present superficial fissures as a consequence of humidity changes (0.9 %) and six bones present concretions that do not seem to be directly associated with the coprolites itself (1.3 %). In addition, one bone presents chemical corrosion associated with root etching (0.2 %).

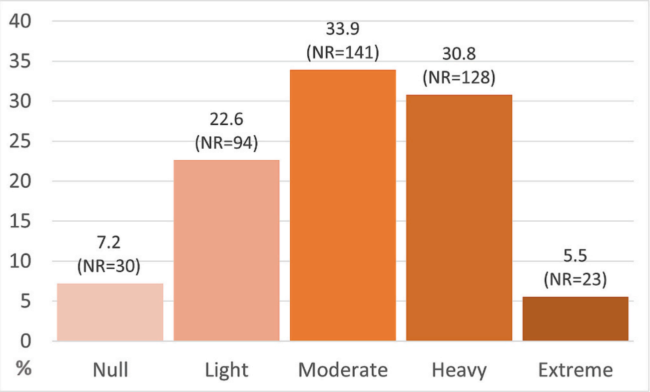


Fig. 5. Percentage of digestive damage on Leporid remains at Cova del Gegant layer III.

5. Discussion

5.1. Lynx coprolites

The analysis of the coprolite bone assemblage from layer III of Cova del Gegant aligns with characteristics commonly associated with lynx activity. In previous studies (Rodríguez-Hidalgo et al., 2020; Sanz et al., 2017), a general revision of the complete coprolites recovered at the site was performed, confirming that they were associated with morphotype 2 typology (Brugal, 2010; Sanz et al., 2016). The coprolites exhibit cylindrical shapes—described by Chame (2003) as "sausage-shaped"—with visible sub-divisions and tapered extremities. Thus, they are more likely to be associated with felines or canids (Brugal, 2010; Sanz et al., 2016; Cambronero and García, 2024). Importantly, these coprolites differ in morphology from those typically attributed to hyenas. The coprolites analysed in the current study lack any noticeable texture differences between the inner and outer areas, the internal texture is not lumpy, and, when perceptible, their morphology is cylindrical rather than spherical. However, canids tend to consume more bones, facilitating better coprolite preservation. Additionally, the existence of elongated vacuums within the coprolites could indicate the decomposition of organic material, providing further insight into their formation processes.

5.2. Feeding traits of the Iberian lynx

Beyond the information directly obtained from coprolites, the bones within them also provide significant insights into the potential predator generating them. Notably, over 90 % of the bones found in these coprolites belong to leporids, likely the European rabbit (*Oryctolagus cuniculus*), a species abundant on the Iberian Peninsula. This abundance in southern European areas has made rabbits a critical dietary component for various small predators, including birds of prey, foxes, and felids (Sanchis, 2012). Among these predators, the genus *Lynx* has a pronounced reliance on rabbits and other lagomorphs as primary food sources (e.g., Werdelin, 1981; Palomares et al., 2001). This finding is analogous to the data obtained from the holistic analysis of the level based on the skeletal elements recovered during the excavation, with the exception of the coprolite contents not analysed (Rodríguez-Hidalgo et al., 2020). However, in the present study, as the remains were exclusively and directly digested by lynxes, the MNI data is more precise because it eliminates the bias introduced by other agents. The data highlight that the lynx's diet in areas where it is no longer present (northeastern Iberian Peninsula) and in environments with colder and more arid conditions follows a pattern similar to its current diet (Delibes, 1980; Palomares et al., 2001; Miguel and Ayanz, 2006; Gil-Sánchez et al., 2006; Hanson and Moen, 2008; Parrish, 2021).

The Iberian lynx (*Lynx pardinus*) has a highly specialised diet. According to Delibes (1980), over 88 % of the prey remains in its diet consists of rabbits. Birds, such as the mallard (*Anas platyrhynchos*) and red-legged partridge (*Alectoris rufa*), contribute an additional 19 % of its dietary intake. This specialisation has been corroborated by subsequent studies (Palomares et al., 2001; Miguel and Ayanz, 2006). For instance, Gil-Sánchez et al. (2006) reported that the diet of the Iberian lynx in southern Spain comprises over 90.8 % rabbits, with red-legged partridges contributing 4.5 %. These values can reach even higher values if considering previous studies (Palomares et al., 2001), where rabbits compose 99.3 % of the Iberian lynx diet.

Other lynx species worldwide also exhibit a preference for leporid prey. For example, the Canada lynx (*Lynx canadensis*) relies heavily on the snowshoe hare (*Lepus americanus*), which constitutes over 76 % of its diet (Hanson and Moen, 2008; Parrish, 2021). Similarly, the Eurasian lynx (*Lynx lynx*) frequently preys on hares, though its diet can include a higher percentage of ungulates in boreal regions of Europe, reflecting prey availability and accessibility in these habitats (Odden et al., 2006). This evidence highlights the ecological importance of lagomorphs as a dietary cornerstone for lynx species, with variations influenced by regional prey abundance and predator adaptation. Thus, the accumulation of leporid remains at Cova del Gegant could align with the dietary profile of lynxes.

5.3. Zooarchaeological and taphonomic characteristics of lynx accumulations

From a zooarchaeological and taphonomic perspective and, in comparison with other neotaphonomic studies on leporid accumulations produced by lynx (Lloveras et al., 2008b; Rodríguez-Hidalgo et al., 2013, 2015), both similarities and differences can be observed. It is important to note that some of these studies were conducted on non-ingested lynx accumulations, which may explain most of these differences.

According to Lloveras et al. (2008b), leporid accumulations in scats show a high representation of cranial elements, with mandibles, skulls (primarily maxillae), and isolated teeth. Additionally, long bones such as the femur, ulna, humerus, and pelvis, exhibit relative abundances exceeding 50 %, while other skeletal elements are less represented. In the case of the Cova del Gegant assemblage, skull fragments (mainly maxillae) are similarly prominent, with the representation values exceeding 60 %. Other elements, such as humeri, mandibles, and tibias, also show relatively high representation, with values exceeding 40 %, comparable to those observed in the study by Lloveras et al. (2008b). However, isolated teeth, pelvises, and other long bones are less represented in the Cova del Gegant assemblage compared to the referential assemblage. Despite these differences, when Spearman's correlation coefficient is calculated between the anatomical representation observed in the present study and that reported by Lloveras et al. (2008b), a positive correlation is evident ($r = 0.7$, $p < 0.01$). This statistical result aligns with the nature of the accumulation in both cases, as both represent leporid remains processed and deposited in scats. By contrast, the study of fossils and actualism exhibits a slight divergence, introducing a certain bias when compared to collections not originating from materials digested in coprolites. This discrepancy can be attributed to the potential influence of other factors on archaeological sites. This pattern differs from the studies published by Rodríguez-Hidalgo et al. (2013, 2015), where lower hindlimb elements predominate in the assemblages. It is important to note, however, that these studies analysed non-ingested lynx accumulations. Thus, differences with the assemblage analysed at Cova del Gegant, primarily composed of ingested remains, were expected.

The faunal assemblage at Cova del Gegant also exhibits a high degree of fragmentation. Analysis reveals that only 21.1 % of the total skeletal elements are complete. This fragmentation is particularly pronounced among leporids, with complete elements representing only 19.5 % of their remains. This value is lower than that reported by Lloveras et al. (2008b). However, when considering the mean value for leporid long bones, the results align with those observed in previous literature. This extensive fragmentation is likely attributable to the ingestion and mastication processes experienced by the bones. Despite the relatively small size of most animals in the assemblage, complete ingestion was not feasible. Consequently, bone breakage during mastication was prevalent. This observation contrasts with other non-ingested bone accumulations (Rodríguez-Hidalgo et al., 2013, 2015), where fragmentation is typically less pronounced. When comparing these results with other actualistic studies on carnivore-ingested remains, we also observe values closely resembling those produced by wildcat scats (Lloveras et al., 2018) and remains ingested by small canids such as foxes and coyotes (e.g., Schmitt and Juell, 1994; Cochard, 2004; Sanchis, 2012; Lloveras et al., 2012a; Armstrong, 2016).

The patterns of digestive alterations at Cova del Gegant also exhibit strong similarities to those observed in previous referential studies. Notably, the higher percentage of moderate and heavy digestion aligns with the findings of Lloveras et al. (2008b) for scat-recovered remains from lynx and other canid-ingested material (e.g., Lloveras et al., 2012a; Armstrong, 2016). Conversely, these results differ from those associated with larger canids and wildcats, which typically exhibit higher frequencies of extreme digestion (Lloveras et al., 2018, 2020). While the observed levels of digestive damage could also be consistent with those produced by some diurnal birds of prey on ingested prey, such as Imperial and Bonelli's eagles (Lloveras et al., 2012b; 2014a), these taxonomic groups were excluded from consideration given the exclusive presence of bone remains within coprolites in this assemblage and the absence of potential pellets in the layer.

5.4. Iberian lynx role in Pleistocene deposits

Given the nature of the accumulation at Cova del Gegant layer III, and according to a previous study conducted at the site (Jiménez et al., 2025; Rodríguez-Hidalgo et al., 2020; Sanz et al., 2017), the coprolites analysed are consistent with an origin in lynx activity. Rodríguez-Hidalgo et al. (2020) reported that leporids are the most abundant taxon in the faunal accumulation unrelated to coprolites, comprising over 84 % of the NISP. Similarly, leporids dominate the faunal remains analysed from coprolites, representing over 90 % of the total NISP and exhibiting a comparable proportion of adult individuals (c.63 %). The high prevalence of complete lynx remains in the assemblage, as previously documented, further supports the interpretation of the site as a lynx den. The anatomical proportions calculated for leporid bones in the current study show less pronounced differences than those reported by Rodríguez-Hidalgo et al. (2020), where cranial elements were notably underrepresented. In general, the anatomical parts in the current analysis appear relatively balanced, with a slight predominance of specific elements. This interpretation is supported by the mortality profile, which suggests that the cave was used as a natal den by Iberian lynx (Jiménez et al., 2025).

When comparing these results to other archaeological sites interpreted as lynx accumulations, some differences emerge. For instance, at the Navalmaíllo Rock Shelter (Arriaza et al., 2017), the anatomical representation of lagomorph remains closely aligned with Rodríguez-Hidalgo et al.'s (2020) findings. Although fragmentation is comparable to the results presented in the current study, digested bones are rare and, when observed, digestions are typically light or moderate. However, the proportion of adult and immature individuals is similar to the results presented here.

Another comparable site to Cova del Gegant layer III is the Sala del Llop chamber Unit 3 of Cova del Coll Verdaguer. This site was interpreted as primarily used by lynxes and sporadically by foxes (Gabucio et al., 2024; Sanz and Daura, 2018b). In terms of anatomical and taxonomic representation, as well as fragmentation, the results are comparable to those obtained by Rodríguez-Hidalgo et al. (2020) for accumulations interpreted predominantly as non-ingested. At another Iberian site interpreted as a lynx accumulation, Terrasses de la Riera dels Canyars (Rosado-Méndez et al., 2015), the anatomical representation of rabbit remains resembles the results obtained from coprolite analysis at Cova del Gegant. The proportion of adult individuals is also consistent with the findings of the current study. Nevertheless, as with Navalmaíllo and Cova del Coll Verdaguer, the percentage of digested elements is low, and mechanical modifications are more prevalent. Similar results were obtained at Escoural Cave, in Portugal (Cobo-Sánchez et al., 2024). All these assemblages, although interpreted as lynx accumulations, appear to result from a combination of ingested and non-ingested remains or entirely non-ingested origins. Their formation may have been influenced by multiple factors, and examining the diverse taphonomic indicators within these assemblages is particularly challenging, as their manifestation is susceptible to numerous variables, including the environmental context, prey availability, and the functional use of the space by the lynxes themselves, such as the den of a solitary individual or the den of cubs. Additionally, the potential involvement of other accumulating agents, which might not have been recognised, should also be considered.

In addition to the previous aspects discussed, another significant feature of the present study is the attempt to determine the temporality of the predator occupation at Cova del Gegant. According to actualistic studies, an adult lynx of average size (approximately 12 kg), resting for 10 h and travelling 7 km per day, would require around 747 kcal daily. This is equivalent to 729 g of rabbit meat per day, or approximately 308 rabbits per year. Consequently, it can be deduced that an average adult lynx would require the consumption of approximately one rabbit per day (Aldama and Delibes, 1991; Aldama et al., 1991). In comparison to the MNI of rabbits obtained from coprolites (11) and the MNI of fauna from level III (56), it can be concluded that layer III corresponds to a short-duration occupation. This idea is consistent with current studies conducted on Iberian lynx populations in the southern Iberian Peninsula, which indicate that approximately one month after birth, female lynxes tend to move their kittens to auxiliary dens, where they remain for a short period until they move to other lairs (Fernández et al., 2002). The ecologic studies made on the Iberian lynx also confirm that, around four weeks after birth, cubs are already capable of consuming meat, meaning they could potentially produce coprolites containing bone fragments. Moreover, the brief use of these spaces as dens could be linked to sanitation concerns, such as the growth of parasites that would make prolonged occupancy of the cavity unhealthy, as well as other disruptions caused by animals or humans occasionally entering the space. Also, after two months, the kittens have already developed sufficient motor capabilities to begin venturing out of the den (Fernández et al., 2002), which may also suggest that faeces become less frequent inside, as they are likely to defecate during their excursion.

The accumulation at Cova dels Gegant layer III represents a prime example of an archaeological lynx den. The advanced excavation techniques employed – allowing the recovery of any item –, and the excellent preservation of remains at the site facilitated the documentation and recovery of coprolites, providing an ideal scenario for analysing this type of assemblage, which is rarely studied from a taphonomic perspective. The combined analytical approach used to study the faunal remains supports the previously stated conclusion that the cave functioned as a lynx den. The limited evidence of human activity at the site, coupled with the intense activity of small carnivores, further underscores the interpretation that human occupations were sporadic.

6. Conclusions

The faunal accumulation at Cova dels Gegant layer III offers a rare and valuable example for interpreting archaeological assemblages potentially produced by lynxes. While previous studies had already identified the site as primarily the result of lynx activity, this study is the first to undertake a detailed analysis of bones derived from disaggregated coprolites. These findings demonstrate the critical importance of such analyses in complementing broader faunal studies at archaeological sites. Furthermore, they enrich referential studies, which often lack the post-depositional alterations that affect archaeological assemblages, thereby providing a more nuanced understanding of taphonomic processes.

The results of this study align with previous observations regarding lynx-ingested accumulations. Specifically, these accumulations tend to exhibit more balanced anatomical representations due to the ingestion of whole bones that remain preserved within coprolites. This process also mitigates the presence of mechanical modifications by carnivores, as the digestive process itself obscures potential evidence of such interactions. As anticipated, most bones recovered from coprolites exhibit clear signs of digestion, with moderate and heavy digestion being predominant, although light and extreme digestion are also present.

When preservation conditions and excavation methods allow, integrating bone analysis of faunal remains within coprolites can offer unique insights into the formation processes of faunal assemblages and the behaviours of small carnivores like lynxes. By providing a more realistic view of how archaeological remains are altered over time, studies like this contribute significantly to the understanding of taphonomic processes and the dynamics of past ecosystems.

The analysis of coprolite content from Cova del Gegant, in combination with existing data, suggests that the Iberian lynx formerly inhabited environments significantly distinct from its contemporary habitats. Furthermore, it is evident that the species inhabited a significantly cold climate, approximately ca. 33 ka BP. However, its diet was based on prey consumption patterns and ingestion rates that were very similar to those observed today. This is a significant finding for understanding this species, which is considered vulnerable, and for future reintroduction programs.

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CRediT authorship contribution statement

Anna Rufà: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Montserrat Sanz:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Joan Daura:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors report there are no competing interests to declare.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2025.113086.

Data availability

All data supporting the findings of this study are included in the manuscript and in the supplementary materials. Additional information is available from the corresponding author upon request.

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