



Hyaenids, felids and canids as bone accumulators: Does the natural history of extant species support zooarchaeological inferences?

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ABSTRACT

Mammalian carnivores may be important agents of prehistoric bone accumulations. Taphonomic analyses of bone assemblages used for specific assignment usually include information on feeding, breeding, denning and even defecating ecology of extant species. Here, we review literature for the Hyaenidae, Felidae and Canidae families of carnivores, focusing on the ecological and behavioural traits that are commonly used as criteria to assign bone accumulations to specific carnivores, and whether these correspond to the present behaviour and ecology of extant species. We found a total of 93 records where 12 species (9 extant species) of these families were considered as bone accumulators in archaeozoological sites. Hyaenidae was the group most often cited, followed by Felidae and Canidae. *Crocuta crocuta* was by far the species most often cited as a bone accumulator. Most bone deposits assigned to carnivores (84.9%) were found in underground cavities, and to a lesser extent in non-cave deposits (15.1%). The use assigned to the sites was mainly as a den (29.5%) or breeding den (29.5%), followed by prey depot (16.2%), feeding shelter (12.4%), and to a lesser extent a hunting place (7.6%), with some remarkable differences among families. Coprolites were also found in 53.8% of cases.

The behaviour of present hyenas may be similar to that of prehistoric ones as they commonly use underground dens, defecate inside of them and frequently accumulate prey remains. On the other hand, even though present canids are more often recorded than felids using underground dens and accumulating prey, the latter are more often recorded as prehistoric bone accumulators than the former. The behaviour of only one present species of canid (*V. vulpes*) and other a felid (*P. pardus*) matches the one presumed for prehistoric individuals of such species in relation to bone and scat accumulation. The role of the remaining species as bone and scat accumulator agents in prehistoric sites remains questionable due to differences in their present behaviour. Therefore, many assignments of bone accumulation to specific carnivores are based on assumptions, which did not coincide with the present natural history of the species. Our review also highlights the absence of records of small species as prehistoric bone accumulators.

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1. Introduction

Many studies identify mammalian carnivores (hereafter carnivores) as important agents of bone accumulations in zooarchaeological sites. This is not rare since many carnivore species feed upon other animal species that are either hunted or scavenged (Ewer,

1998, Van Valkenburgh, 1989; Gutiérrez et al., 2018). If they repetitively carry prey or part of a prey to specific sites to feed on it themselves or provide it to their cubs, the accumulation of bones may occur (e.g. Domínguez-Rodrigo, 1993; Badenhorst et al., 2021; Box 1). In this regard, the taphonomic features of bone assemblages (mainly bone surface modifications, bone fragmentation patterns and profiles of skeletal parts), have been some of the main criteria used for assigning bone accumulations in archaeological sites to different species of carnivores (e.g. Cruz-Urbe, 1991; Kuhn et al., 2010; Pickering et al., 2004; Domínguez-Rodrigo and Piqueras,

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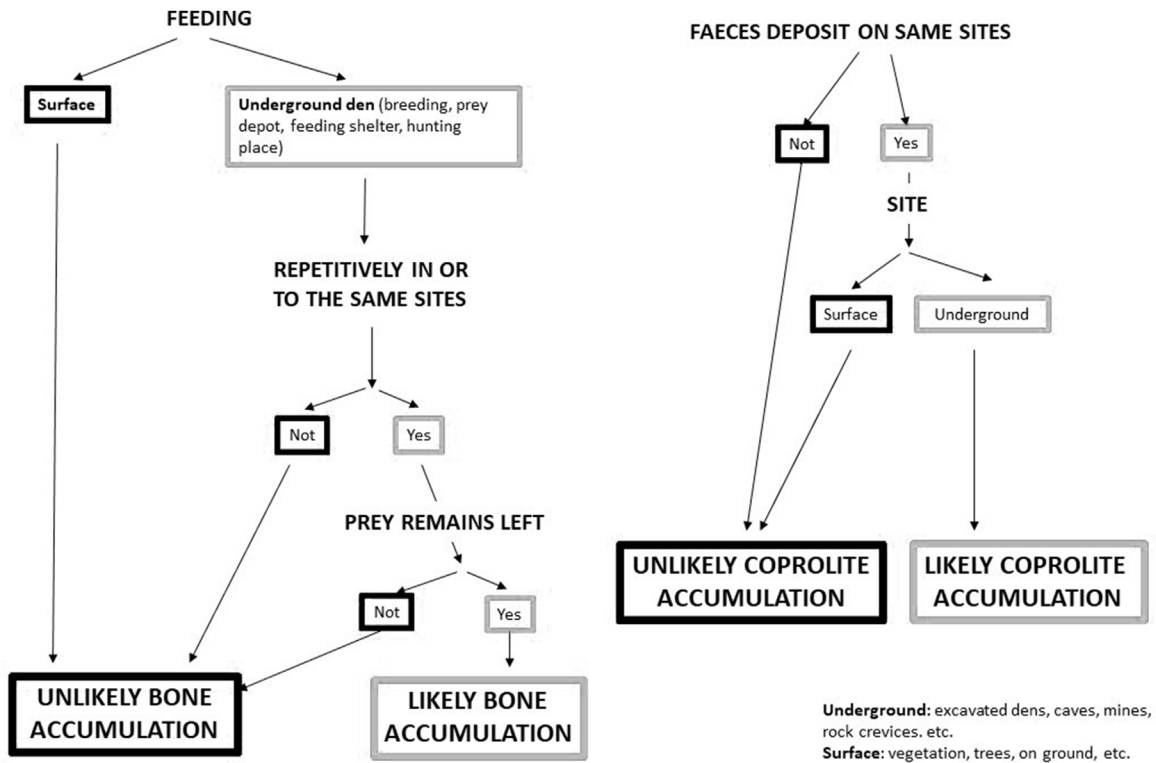
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2003; Thompson et al., 2017; Sala and Arsuaga, 2018).

Additional information about feeding, breeding, denning and even defecating ecology of extant carnivore species is also used to support the assignment of prehistoric bone accumulations to a given carnivore species, frequently after making certain assumptions. For instance, prehistoric carnivores are assumed to produce latrines close to feeding sites, and coprolites are assumed to proceed from former latrines (here we refer to a latrine as any accumulation of scats regardless of the ecological function of this accumulation) located at the bone accumulation site or in the close surroundings (e.g. Horwitz and Goldberg, 1989; Larkin et al., 2000; Sanz et al., 2016). Similarly, the transport of prey or prey remains to

carnivores in the formation of zooarchaeological bone assemblages. We focus on the Hyaenidae, Felidae and Canidae families of carnivores, since most species of these families mainly consume animal prey large enough to provide perdurable bone remains. As ecologists, our review focuses on the ecological and behavioural traits that were used as criteria (see above and Box 1) to assign bone accumulations to carnivores rather than bone assemblage features or carnivore signatures on bones, of which there already exist excellent reviews (e.g. Domínguez-Rodrigo and Barba, 2006; Thompson et al., 2017; Sala and Arsuaga, 2018). In particular, we discuss whether such assignments are supported by current knowledge on the natural history of extant species.

Box 1
Conditions for zooarchaeological bone and coprolite accumulations from carnivores



underground dens or caves used as a depot, shelter or for feeding themselves and/or their weaning cubs, is assumed to be common and systematic (e.g. Horwitz and Goldberg, 1989; Domínguez-Rodrigo, 1993; Krajcarz and Krajcarz, 2012).

Here, we review the literature on bone accumulations by carnivores at prehistoric sites to record the location of such deposits, the function assigned to the site, and the presence of coprolites. Additionally, we review literature on the natural history of extant carnivores related to breeding, feeding, defecating and denning ecology and behaviour. The specific aims of this review are 1) to provide an overview of the current knowledge regarding prehistoric bone deposits assigned to carnivores, and 2) to examine both at the family and the specific level whether there is concordance between the natural history traits observed in extant carnivores and those often used to support the implication of specific

Zooarchaeological bone accumulations made by carnivores derive from hunting and feeding events, either occurring in the same spot or after carrying prey to a specific place. There is a larger likelihood that the skeletal remains will be preserved if feeding occurs in underground conditions. Otherwise, if feeding occurs on the surface, the potential bone accumulation will be more unlikely to persist over time and thus, harder to find. Therefore, several steps related to hunting, feeding and denning ecology must account for a carnivore being able to yield a bone accumulation that lasts through time: 1. Hunting and feeding in underground cavities might favour prey remains to accumulate in such places. This is not unusual since many small carnivores hunt their prey inside underground dens, but prey are small and hunted in very small cavities. Otherwise, prey hunted or scavenged on the surface should be carried to underground cavities for feeding. Species that den in

surface sites such as among vegetation, trees or just on the ground might be unlikely to yield bone accumulations. 2. Prey should be repetitively carried to the same underground sites. For instance, several species use underground sites for breeding, but they change dens continuously so a bone accumulation is unlikely to be yielded by carrying prey for cub feeding unless the site is repeatedly used across many generations. 3. Finally, prey remains should be left on the site; when prey are medium or small, carnivores often ingest the prey completely. Similarly, to find coprolites in areas of bone accumulation carnivores should defecate in underground structures. With both bone and scats, the behaviour should be repetitive and located in the same places to yield accumulations.

2. Methods

2.1. Bibliographical search

We conducted a systematic review of literature on prehistoric and extant Felidae, Canidae and Hyaenidae species, particularly regarding den use, prey accumulations and latrine formation. We located prehistoric studies by using Elsevier's Scopus database and a series of terms associated with the purpose of our review. We combined the following terms: ("deposit" OR "accumulation" OR "taphonomic" OR "zooarchaeological" OR "den" OR "latrine" OR "fecal marking" OR "middens" OR "pile" OR "prehistoric" OR "coprolite" OR "cave") with ("felid" OR "felidae" OR "Acinonyx" OR "Caracal" OR "Catopuma" OR "Felis" OR "Leopardus" OR "Lep-tailurus" OR "Lynx" OR "Otocolobus" OR "Pardofelis" OR "Prionailurus" OR "Puma" OR "Neofelis" OR "Panthera") for felids; with ("hyaena" OR "hyaenidae" OR "crocuta") for hyaenids; and with ("canid" OR "canidae" OR "Atelocynus" OR "Canis" OR "Cerdocyon" OR "Chrysocyon" OR "Cuon" OR "Lycalopex" OR "Lycaon" OR "Nyctereutes" OR "Otocyon" OR "Speothos" OR "Urocyon" OR "Vulpes") for canids. The search was done for title, keywords and abstract of articles in English without date restrictions. The last search was carried out in May 2020. We are aware that some publications were not included, but rather than doing an exhaustive review, our aim was to describe and compare the main patterns found in prehistoric and extant carnivores of these families for the mentioned natural history traits.

2.2. Overview of prehistoric bone accumulations by carnivores

From the articles referring to prehistoric times, we extracted information on the main assigned accumulator species (hereafter referred to as AS), if remains of the AS (including juveniles) were found at the archaeological site, datation of the deposit, location of the bone prey deposit, main accumulated prey species, presence of coprolites and the locality of the site. We discarded descriptive papers where: authors did not make reference to the AS (including when many species were mentioned but none were assigned as AS); authors did not provide any justification for the assignment of the AS; and when the carnivore was assumed to act as a scavenger on the site of the bone accumulation but was not the AS.

When two or more species were cited as AS, we considered the site as many times as the number of species cited as AS. In the same way, when there was information on more than one bone deposit in a unique paper, it was considered as many times as different bone deposits were described. For simplicity, data are presented for species and families, and we did not consider subspecies.

Places for bone deposits were subdivided into two categories:

- 1) Caves: caves and rocky shelters.
- 2) Non-cave deposits: open-air sites such as fluvial-paludal, fan deltas, cliffs, and even dolines.

The use of the bone accumulation site was classified as:

- 1) Den: We included refuge or resting places, bear hibernation caves, and cases where authors used the word "den" without specifying the den type (there was no way to know if the authors referred to breeding dens, as might be the case).
- 2) Breeding den: We included natal, breeding, maternity or communal dens. The classification was not totally clear in all papers, but as a rule, natal and maternity dens referred to places where females give birth, and breeding dens referred to both natal dens and successive dens where females carry and continue rearing the cubs.
- 3) Feeding shelter: Locations where carnivores move prey to safely feed upon it.
- 4) Prey depot: Locations where carnivores move prey to store and feed over hours or days.
- 5) Hunting place: Specific places where carnivores hunt and presumably eat certain prey species.

Note that the same bone deposit can have different uses.

2.3. Overview of natural history traits of extant carnivores

From the articles referring to present times we extracted information on studied species (AS when applicable), location of the bone prey deposit, frequency of prey-accumulating behaviour, use and function of dens, frequency of den-use, and formation, location and size of latrines (here we considered as a latrine any accumulation >2 scats).

When a paper presented data for more than one species, it was considered as many times as the number of species studied. Similarly, when there was information for a given species for clearly different study areas in the same paper, the paper was considered as many times as study areas included.

For extant species reported as prehistoric accumulators in our literature review, we reviewed every step indicated in [Box 1](#) to evaluate their potential as accumulator species according to their present ecology and behaviour. Specifically, we extracted information on the use of underground dens (for breeding, prey depot, feeding shelter or as a hunting place), if they consumed medium or large prey (>1 kg), if they repetitively took prey to the same underground sites, and if they commonly left prey remains at the underground sites. All of these points must be true for a species to potentially be a bone accumulator ([Box 1](#)). Additionally, we also obtained information on scat accumulation by the species, and if scats could be deposited in underground conditions. For all cases, we considered behaviour as possible for the species when the behaviour has been reported at least once. By doing so, we simulated behaviours that although rarely repeated over time, could yield detectable bone accumulations.

3. Results and discussion

3.1. Prehistoric bone accumulations by carnivores

We found a total of 86 useful papers on prehistoric (from Early Pleistocene to Middle Holocene) bone accumulation sites where species of Hyaenidae, Felidae and Canidae were considered, at least partially, as accumulating agents ([Supplementary Table 1](#)). These papers, published between 1981 and 2020, yielded a total of 93 records on one or more of the topics reviewed here. Most records were from sites in Europe (n = 71), followed by Africa (n = 15), America (n = 4) and Asia (n = 3).

Despite the low number of species included in the family Hyaenidae, it was the group most often cited as a bone accumulator,

Table 1
Number of cases reported for each bone accumulator species (AS) of Hyaenidae, Felidae and Canidae families.

Hyaenidae		Felidae		Canidae	
Species	Cases	Species	Cases	Species	Cases
<i>Crocota crocuta</i>	48	<i>Homotherium serum</i>	1	<i>Canis lupus</i>	5
<i>Hyaena brunnea</i>	5	<i>Lynx pardinus</i>	2	<i>Protocyon troglodytes</i>	1
<i>Hyaena hyaena</i>	1	<i>Panthera leo</i>	4	<i>Vulpes vulpes</i>	1
<i>Pachycrocuta brevirostris</i>	2	<i>Panthera onca</i>	2	Unknown sp.	2
Unknown sp.	6	<i>Panthera pardus</i>	9		
		Unknown sp.	4		
TOTAL	62	TOTAL	22	TOTAL	9

followed by Felidae and Canidae (Table 1). *Crocota crocuta* was the species by far the most often cited as a bone accumulator in Hyaenidae, and *Panthera pardus* and *Canis lupus* in Felidae and Canidae, respectively (Table 1).

Most bone deposits assigned to carnivores (84.9% out of 93 sites) were found in underground cavities of different sizes and structures (all caves except two in rock shelters), and to a lesser extent in non-cave deposits (15.1%). The use of the sites (n = 105) was mainly as a den (29.5%) or breeding den (29.5%), followed by prey depot (16.2%), feeding shelter (12.4%), and to a lesser extent as a hunting place (7.6%) such as in the case of *Panthera leo* or *C. lupus* entering bear caves for hunting (Table 2). Bone accumulations assigned to hyaenids were generally located in breeding dens (37.0%) or dens (34.2%); deposits assigned to felids were mainly found in feeding shelters (36.4%), followed by hunting places (27.3%); finally, canids mainly accumulated bones inside dens (40%; Table 2).

On most occasions, the body remains of accumulator species were present in the deposit (91.4%, n = 93); but in three cases of *Canis lupus*, one of *Panthera onca*, one of *Crocota crocuta* and two unidentified species of Hyaenidae, no remains of AS were found; in one additional case of Canidae there was no available information. On the other hand, in 53.8% of cases (n = 93) coprolites were also found at the site, in 20.4% coprolites were not found, and in the other 25.8% of cases, there was no available information. Where coprolites were found, 41 cases (66.1% out of 62) were from Hyaenidae, four cases (18.2% out of 22) from Felidae, and three cases (33.3% of 9) from Canidae.

3.2. Natural history traits of extant carnivores

3.2.1. Den use

We found a total of 101 papers on the use of dens by extant carnivores published between 1979 and 2020, which yielded a total of 151 cases on den use by Canidae (90), Felidae (29) and Hyaenidae (32) for 14 of the 34 extant species of canids; 10 of the 37 species of felids, and for all the 4 species of hyaenas (Supplementary Table 2). *Vulpes vulpes* (28), *Vulpes lagopus* (17) and *Canis lupus* (16) were the Canidae with the most articles documenting den use. *Puma concolor* (5), two *Lynx* species (5 each), *Otocolobus manul* (5) and

Table 2
Function of the sites where bone accumulations assigned to Hyaenidae, Felidae and Canidae were found. More than one function may be assigned to the same den.

Function	Hyaenidae	Felidae	Canidae	Total Cases
Den	25	2	4	31
Breeding den	27	3	1	31
Feeding shelter	4	8	1	13
Prey depot	15	1	1	17
Hunting place	1	6	1	8
No Info	1	2	2	5
Total	73	22	10	105

Crocota crocuta (17) were the Felidae and Hyaenidae species, respectively, for which we found the most articles studying den use (Supplementary Table 2).

Canidae and Hyaenidae mainly used excavated dens (either self-excavated or excavated by other species) for denning, whereas Felidae preferred vegetation (surface) and rock dens (Table 3). Hyaenidae (particularly *Hyaena hyaena* and *Hyaena brunnea*) was the only group for which the use of caves was regularly reported, particularly for breeding and resting. Although the European lynx (*Lynx lynx*) has also been documented to use caves as natal and maternal dens, felids, in general, do not apparently select caves for denning; instead, they prefer vegetation on the surface (i.e. empty logs, or cover under bushes) and secondarily rock crevices. We found no evidence of canids using caves for denning, although a fox was recorded using a mine, which may resemble cave-like conditions.

Most Hyaenidae, Canidae and Felidae used dens mainly during the breeding period (from birth to independence of juveniles; Table 4). Shelter/resting was the second most common function of dens. We only found one case when a den was used exclusively as a prey depot.

The reutilization of dens in different years was recorded particularly for Canidae (25 out of 30 cases with re-use information) and Hyaenidae (9 out of 9 cases with re-use information). Proportionally, Felidae more rarely re-used previous dens (3 out of 15 cases with re-use information). Information on den reutilization was missing for the majority of cases (60 in Canidae, 14 in Felidae and 23 in Hyaenidae).

3.2.2. Prey accumulations

We found a total of 28 papers published between 1979 and 2018 on prey accumulations by extant carnivores, which yielded a total of 31 cases by 4 species of Canidae (n = 8 cases), 3 of Felidae (n = 3 cases) and 3 of Hyaenidae (n = 20 cases) (Supplementary Table 3). *Crocota crocuta* was the species for which the most cases of prey accumulation were documented (n = 10), followed by *Hyaena hyaena* and *Hyaena brunnea* (n = 5 cases each), and *Vulpes vulpes*

Table 3
Number of cases documenting the use of different types of refuges for Hyaenidae, Canidae and Felidae. Others include anthropic refuges such as cars, houses and culverts under roads.

Type	Hyaenidae	Canidae	Felidae	Total
Excavated den	13	59	4	76
Mine	0	1	0	1
Rock den	6	8	8	22
Cave	8	0	1	9
Vegetation	0	6	12	18
Others	1	2	0	3
No info	4	14	4	22
Total	32	90	29	151

Table 4

Number of cases documenting the different functions of each den type in Hyaenidae, Canidae and Felidae. UD: underground dens including excavated dens, rock dens, caves and mines; SD: surface dens including vegetation refuges and anthropic refuges such as cars and houses. Refuges whose type was not known were not included in the table, and some refuges had several functions and thus appeared simultaneously in more than one category.

Function	Hyaenidae		Felidae		Canidae		Total
	UD	SD	UD	SD	UD	SD	
Breeding	22	0	9	12	52	8	103
Shelter	6	0	4	0	22	1	33
Prey depot	0	0	0	0	1	0	1
No info	4	0	0	0	10	0	14
Total	32	0	13	12	85	9	151

(n = 4); the other 6 cases corresponded to *Vulpes velox*, *Otocyon megalotis*, *Panthera pardus*, *Lynx lynx* and *Lynx pardinus* (Supplementary Table 3).

The location of the prey accumulations was named simply as a den for 10 cases; the other 21 cases yielded more precise site descriptions (Supplementary Table 3). Canidae accumulated prey mainly in excavated dens (n = 3) and in one case inside a mine; Felidae accumulated prey among vegetation (n = 2) and in a cave (n = 1); and Hyaenidae accumulated prey in rock dens (n = 6) followed by excavated dens (n = 5) and caves (n = 4). The function of the prey accumulation site was unspecified for 19 cases, whereas it corresponded to breeding and feeding shelters for 11 cases and one case, respectively (Supplementary Table 3).

A total of 20 cases yielded information on the number of specimens (i.e., number of prey remains found), the number of identified specimens (NISP) and the minimum number of individuals (MNI; i.e. the estimated minimum number of individuals for each species based on analysis of remains) per prey accumulation depot (Table 5). The number of specimens ranged from 1 to 6553 for the three species of Hyaenidae (n = 41 depots, 13 cases), and was 1266 for one depot (one case) from a Canidae species, *Lycalopex gymnocercus*. The NISP ranged from 7 to 3227 for the three species of Hyaenidae (n = 38 depots, 16 cases), and was 466 for one depot (one case) from a Canidae species, *Vulpes vulpes*. The MNI ranged from 2 to 539 for the three species of Hyaenidae (n = 32 depots, 15 cases). The MNI was 102 for one depot (one case) by a Canidae species, *Vulpes vulpes*. The MNI was 11 for one case reported in *Panthera pardus*. In addition, *Lynx lynx* and *Lynx pardinus* accumulated 6 and 9 carcasses in a total of 14 and 15 examined dens, respectively (see Supplementary Table 3). Some studies observed *Vulpes velox* and *Otocyon megalotis* bringing prey items to dens but prey depots were not quantified (see Supplementary Table 3).

3.2.3. Latrine formation

We found a total of 29 papers published between 1978 and 2020 on latrines by extant carnivores, which yielded a total of 35 cases

Table 5

Number of specimens (i.e., prey remains), number of identified specimens (NISP), and minimum number of individuals (MNI) per prey accumulation depot found for a total of 20 cases by extant Hyaenidae, Canidae and Felidae. Blank cells indicate no information available. d and c indicate the number of prey accumulation depots and the number of cases, respectively.

	Hyaenidae			Canidae		Felidae
	<i>H. hyaena</i>	<i>H. brunnea</i>	<i>C. crocuta</i>	<i>L. gymnocercus</i>	<i>V. vulpes</i>	<i>P. pardus</i>
No. specimens	466–1792	7–5955	1–6553	1266	–	–
	6d, 2c	13d, 3c	22d, 8c	1d, 1c		
NISP	16–3143	7–2387	37–3227	–	466	–
	14d, 5c	13d, 3c	11d, 8c		1d, 1c	
MNI	6–340	2–51	8–539	–	102	11
	8d, 4c	13d, 3c	11d, 8c		1d, 1c	1d, 1c

with useful information on latrine formation (Supplementary Table 4): 15 from Canidae (11 species), 9 from Felidae (5 species) and 11 from Hyaenidae (3 species). Unfortunately, it was difficult to obtain information on latrine size, since this was recorded in only a few cases. For canids, a maximum of 6 scats was cited for *Canis latrans*, 30 for *Vulpes macrotis* and 105 for *Canis aureus* (Macdonald, 1979; Ralls and Smith, 2004). For felids, Soler et al. (2009) found a mean of 6.1 scats per latrine for *Leopardus geofroyii* and Fernández et al. (2002) found several kitten scats in secondary dens for *Lynx pardinus*. Regarding hyaenids, a maximum of 18 scats was recorded for *Crocuta crocuta* (Tilson and Henschel, 1986), 13 for *Hyaena hyaena* (Macdonald, 1978), and 34–50 and > 194 in outdoor and cave latrines, respectively, for *Hyaena brunnea* (Gorman and Mills, 1984; Berger et al., 2009; Hulsman et al., 2010).

Regarding the location of latrines, all families and species mostly used open-air conditions, either directly on the ground (26 cases) or on trees (3 cases). The exceptions were *Hyaena hyaena*, whose latrines were located inside caves in three out of the four cases reported, and *Hyaena brunnea* that may also form latrines inside caves (Supplementary Table 4). For the rest of the species, there was only one case inside a mine for the canid *Vulpes vulpes*, and another in a rocky shelter for the felid *Leopardus geoffroyi* (Supplementary Table 4).

3.3. Specific information for assigned accumulator species

3.3.1. *Crocuta crocuta*

Crocuta crocuta was considered the main bone accumulating carnivore species at most Late Pleistocene prehistoric sites (48 sites in our literature review), particularly across Europe (e.g. Fourvel et al. 2014; Diedrich, 2011; Álvarez-Lao et al., 2013). The assignment of this species as a bone accumulator is based on the presence of one or more of the following facts at the sites: 1) remains from adult and/or young *Crocuta crocuta*; 2) remains from either hunted or scavenged hyaena prey (mainly large artiodactyls including mammoth (*C. primigenius*) or woolly rhinoceros (*Coelodonta antiquitatis*)) with very characteristic taphonomic clues such as tooth gnawing marks in the joints or irregular margins in bone shafts (Tsoukala, 1992; Fourvel et al., 2014; Diedrich, 2011; Simon et al., 2007); and 3) hyaena coprolites (Tsoukala, 1992; Fourvel et al., 2014; Diedrich, 2011, Villa et al., 2004). Bone accumulation by prehistoric *Crocuta crocuta* occurred mainly in breeding dens where hyaenas were thought to carry prey remains to their cubs, but also in unspecified dens, prey depots with no breeding purposes and hunting sites (e.g., cave bear hibernation sites where hyaenas hunted this species (Fourvel et al., 2014; Diedrich, 2009)). Most prehistoric bone accumulations assigned to *Crocuta crocuta* were found inside caves (e.g. Fourvel et al., 2014; Diedrich, 2011), although a few cases were found in non-cave deposit sites, potentially resulting from excavated dens (Diedrich, 2012; Daschek and Mester, 2020; Pineda et al., 2017; Rosado-Méndez et al., 2015).

In present times, spotted hyaenas regularly use (and sometimes re-use) underground dens mainly for breeding purposes, particularly excavated dens in soft sediment and, more rarely, rock dens and caves (e.g. East et al., 1989; Fourvel et al., 2015). Spotted hyaena pups are born in isolated natal dens and move into larger communal dens after some days where the pups of several females may be reared simultaneously (Kruuk, 1972; East et al., 1989). Although scavenging hyaenas (striped hyaena (*Hyaena hyaena*) and brown hyaena (*Hyaena brunnea*)) are acknowledged as important bone accumulators (Kruuk, 1976; Skinner, 1976, 2006; Mills and Mills 1977), it has not always been clear whether such behaviour is common for spotted hyaenas (Skinner, 2006), which is a more active hunter species. However, Skinner et al. (1986) described spotted hyaenas sometimes carrying and accumulating prey remains inside dens in South Africa. Particularly, larger bone accumulations were found in rock dens and caves than in excavated dens. Moreover, East et al. (1989) showed that spotted hyaena females carried prey remains to the natal dens for their own consumption, as they rarely feed cubs with meat (Kruuk, 1972). Therefore, spotted hyaenas can generate bone assemblages around and inside dens (Kruuk, 1970, 1972; Sutcliffe, 1970; Scott and Klein, 1981; Cooper, 1993). Spotted hyaenas accumulate faeces in communal latrines, but those are always located in the surface and never underground (Tilson and Henschel, 1986; Lam, 1992; Henschel and Skinner, 1990). To our knowledge, no spotted hyaena faeces have been found either underground or inside natal or communal dens.

According to the available information, spotted hyaenas can be important bone accumulators inside underground dens (Table 6), particularly if we consider the re-use of dens over time. However, it is interesting that although no spotted hyaena scats have been reported inside underground dens, the presence of coprolites was generally considered as a fundamental clue to assign bone accumulation in prehistoric sites to spotted hyaenas.

3.3.2. *Hyaena brunnea*

In our review on prehistoric bone accumulators, we found 5 sites from South Africa where the brown hyaena was considered the accumulator species. The main criteria followed to assign the bone deposits to brown hyaena were: 1) the high carnivore/ungulate ratio of bone remains; 2) the presence of coprolites assigned to this species; and 3) the presence of diverse small carnivore species (Grine and Klein, 1993; Klein et al., 1999; Ruiter et al., 2008; Val et al., 2014; Fourvel et al., 2018). Two more works not detected in our review were found where the brown hyaena was considered as the accumulator species (Swartklip I, Klein, 1986, Equus Cave, Klein et al., 1991; and recently in Sterkfontein, Arriaza et al., 2021; all them in South Africa). Authors assume that hyaenas carry prey remains to dens for cub feeding (Klein et al. 1991, 1999; Grine and Klein, 1993; Ruiter et al., 2008, Arriaza et al., 2021).

The brown hyaena is a scavenger that feeds on a wide spectrum of vertebrate remains (Mills and Mills, 1978; Owens and Owens, 1978). They breed communally or solitarily in excavated dens or caves (Skinner, 1976; Owens and Owens, 1979; Mills, 1983) and the adults carry abundant food for cubs, leaving prey remains both inside and outside dens (Mills, 1983, 1984; Owens and Owens, 1979; Skinner and van Aarde, 1991; Skinner et al., 1998, Fourvel et al. 2015). The dens can be reused over several years (Owens and Owens, 1979). In addition, they usually make latrines well distributed throughout their territory in prominent places (Owens and Owens, 1978; Gorman and Mills, 1984; Hulsman et al., 2010), although they have also been described inside caves (Berger et al., 2009). Latrines in caves can contain a high number of excrements (>194).

According to present behaviour, it is very likely that the brown hyaena is an important bone and scat accumulator (Table 6). However, the restricted distribution of the species may explain why it has not been identified as a bone accumulator agent in more prehistoric sites.

Table 6

Ecology and behaviour of present-day Hyaenidae, Canidae and Felidae species reported as bone accumulators in zooarchaeological sites. Columns represent the necessary requirements (outlined in Box 1) for a given species to act as a bone or scat accumulator in underground conditions. Shaded cells highlight species that according to the current information on their natural history are likely to accumulate prey remains or form latrines in underground conditions. The number of cases where each species was reported as a bone accumulator in zooarchaeological sites is shown in brackets. UD: underground den; LF: latrine formation; ULF: underground latrine formation; Yes: the species exhibits the correspondent behaviour/trait; Unreported (Unrep): the behaviour/trait is not known for the species.

Species	Bone accumulations							Coprolite accumulations	
	Use of UD				Medium and/or large prey	Repetitively prey carried to the same UD sites	Prey remains left in UD sites	LF	ULF
	Breeding	Prey depot	Feeding shelter	Hunting places					
<i>C. crocuta</i> (48)	Yes	Unrep	Yes	Unrep	Yes	Yes	Yes	Yes	Unrep
<i>H. hyena</i> (1)	Yes	Unrep	Unrep	Unrep	Yes	Yes	Yes	Yes	Yes
<i>H. brunnea</i> (5)	Yes	Unrep	Unrep	Unrep	Yes	Yes	Yes	Yes	Yes
<i>P. leo</i> (4)	Unrep	Unrep	Unrep	Unrep	Yes	Unrep	Unrep	Unrep	Unrep
<i>P. pardus</i> (11)	Yes	Unrep	Yes	Unrep	Yes	Yes	Yes	Unrep	Unrep
<i>P. onca</i> (2)	Unrep	Unrep	Unrep	Unrep	Yes	Unrep	Unrep	Yes	Unrep
<i>L. pardinus</i> (5)	Yes	Unrep	Unrep	Unrep	Yes	Unrep	Unrep	Yes	Unrep
<i>C. lupus</i> (5)	Yes	Unrep	Unrep	Unrep	Yes	Unrep	Unrep	Yes	Unrep
<i>V. vulpes</i> (1)	Yes	Unrep	Unrep	Unrep	Yes	Yes	Yes	Yes	Yes

3.3.3. *Hyaena hyaena*

The striped hyaena was considered as a bone accumulator in the archaeological site of Kromdraai (South Africa; [Fourvel et al., 2018](#)). This conclusion arose after examining carnivore marks in bones from prey potentially scavenged by this species, and after finding body remains and coprolites compatible with this species. The conclusion was also supported by the argument that modern striped hyaenas act as important bone collectors and defecate inside dens. In an additional paper not detected during our literature review, the striped hyaena is hypothesized as the potential bone accumulator in Makapansgat (South Africa, [Maguire et al., 1980](#)).

Nowadays, the use of cavities (caves, excavated dens or rock shelters) for breeding in striped hyaena is well documented ([Leakey et al., 1999](#); [Kerbis-Peterhans and Horwitz, 1992](#); [Kuhn et al., 2009](#); [Fourvel et al., 2015](#); [Mwebi and Brugal, 2018](#)), as is their behaviour of provisioning remains from large prey to the dens as food for offspring ([Leakey et al., 1999](#), [Kerbis-Peterhans and Horwitz, 1992](#), [Skinner, 2006](#), [Fourvel et al., 2015](#), [Mwebi and Brugal, 2018](#), [Kuhn et al., 2009](#); [Kuhn et al., 2010](#), [Table 6](#)). The species may also re-use dens ([Kerbis-Peterhans and Horwitz, 1992](#)). On the other hand, it is also well known that striped hyaenas deposit scats both inside and outside dens ([Macdonald, 1978](#), [Horwitz and Goldberg, 1989](#), [Kerbis-Peterhans and Horwitz, 1992](#); [Fourvel et al., 2015](#)).

According to present behaviour, the striped hyaena is a very probable bone and scat accumulator ([Table 6](#)), and it is surprising that this species has not been more often reported as responsible for bone and/or coprolite accumulation in zooarchaeological sites. Nevertheless, its likely absence from Europe and parts of Africa during the Pleistocene could at least partially justify these results ([Rohland et al., 2005](#)).

3.3.4. *Panthera leo*

The lion was reported as a bone accumulator in four zooarchaeological deposits in Europe (Bilstein and Zoolithen caves in Germany, and Sloup and Barová caves in Czech Republic). In all cases, lions entered the cave to prey (and occasionally scavenge) upon hibernating bears (e.g. [Diedrich, 2009, 2011, 2012](#); [Roblíčková et al., 2017](#)) and encountered hyaenas. As such, bone remains of lions usually accompany those of bears and hyaenas, as well as bones from hyaena prey.

In present times, lions do not act as bone accumulators despite hunting large prey. Instead, they consume their prey on-site or in the proximity ([Schaller, 1972](#) mentions wildebeests and zebras dragged up to 160 m). However, an intriguing paper describes an accumulation of wildebeest bones on a rocky slope in the Serengeti that could be attributed to lions ([Arriaza et al., 2016](#)), which opens the possibility of lions as bone accumulators in prehistoric times. Furthermore, cubs are born and kept while suckling in secluded thick vegetation or among rocks, but at 6–8 weeks old they begin to follow the mother with no permanent den site ([Kingdon, 1977](#)). Present lions have not been documented hunting in underground cavities. There is also no information on lions having latrines in underground conditions.

According to the available present information, it is unlikely that lions act as bone and scat accumulator agents ([Table 6](#)), since prey remains and latrines or isolated scats are not found in underground dens or their surroundings (but see [Arriaza et al., 2016](#) for lions as exceptional bone accumulators in open-air conditions). Furthermore, there is no information on modern lions entering cave-like environments to hunt or scavenge.

3.3.5. *Panthera onca*

Only two studies, in the Milodón and Las Guanacas caves in Chile, reported the jaguar as a bone accumulator species ([Labarca et al., 2008](#); [Martín, 2018](#)). In both cases, the jaguar was

considered the bone accumulator species based on tooth marks and the distribution of bone remains, and by looking at analogies with prey management of present jaguars, where hunting of large prey and their transport to caves for feeding could take place.

To our knowledge, there is no report of jaguars using underground dens for breeding, but in two cases, individuals were observed entering caves for refuge in the Yucatan peninsula, and at least one of them was used by several individuals (C. Chavez, com. pers.). On the other hand, it is not rare to find groups of 2–3 jaguar scats, but they are always located on the ground in outdoor conditions ([Palomares et al., 2016](#)).

There is insufficient information on the natural history of jaguars to consider the species as a potential bone accumulator in zooarchaeological sites ([Table 6](#)), as it is currently unknown if they take prey for feeding shelter to the same underground sites.

3.3.6. *Panthera pardus*

Leopards were noted as bone accumulators in 11 archaeological sites (Spain: Los Rincones Cave, Imanolen Arrobia, Llonin Cave, Racó del Duc, S'Espasa Cave, Tritons Cave, Amalda and Esquilleu; Italy: Equi; and South Africa: Kromdraai, Wonderwerk and Swatkrans Cave; [Supplementary Table 1](#) and [Yravedra, 2006, 2010](#) and [Brain, 1981](#) found after the review). We did not consider two more sites where leopards were suggested (among other carnivores) as potential bone accumulating agents without certainty ([Bunn et al., 2010](#); [Stewart et al., 2019](#)). Only in one of the sites (Llonin Cave) were some coprolites assigned to probable leopards, and another site was considered a breeding den. Curiously, all records, except this of [Brain \(1981\)](#) were published after 2006, denoting that the attribution of bone assemblages to leopards (and, in general, to felids) is recent. In fact, [Brain \(1981\)](#) was the first hypothesizing that leopards accumulated and/or preyed on australopithecines in Swatkrans cave in South Africa. Furthermore, there is a spatial bias towards Spain, representing 72% of the sites.

As a rule, leopard-made bone assemblages are characterized by: the presence of leopard remains, the abundance of small-medium sized prey from most age-classes (20–100 kg; in Spain, mountain goats and chamois), proportional representation of skeletal parts (suggesting prey were carried whole), scarce modification and teeth marks on bones, and lack of coprolites and digested bones. All authors, except [Ghezze and Rook \(2015\)](#) who considered their site to be a leopard breeding cave, assumed that leopards transported prey to underground refuges for feeding shelter to avoid kleptoparasitism from intraguild competitors.

Today's leopards are well known for their unique habit of caching, storing and consuming prey on trees to avoid kleptoparasitism (e.g. [Stein et al., 2015](#); [Balme et al., 2017](#)). However, by using his own observations and some bibliographic references, [Brain \(1981\)](#) proved that leopards also hide and consume prey inside caves where they are available. Moreover, [Brain \(1981\)](#) reported at least two cases of leopard breeding dens in caves. More recently, [De Ruiter and Berger \(2000, 2001\)](#) described the remains of several ungulates (as big as adult zebras and a female *Taurotragus oryx*) found inside six South African caves where leopards were seen entering, although [Pickering et al. \(2004\)](#) questioned that leopards can drag prey over 100 kg a certain distance. We found no references of leopard scats in underground cavities.

According to these observations, leopards might have been responsible for prehistoric bone deposits in some circumstances, but probably not for coprolites found in caves ([Table 6](#)).

3.3.7. *Lynx pardinus*

The Iberian lynx was considered as the primary agent (or at least participating) of prehistoric bone deposits from four zooarchaeological sites in the Iberian Peninsula: Buraca Escura ([Aubry et al.,](#)

2001), Cueva de Maltravieso (Rodríguez-Hidalgo et al., 2013a, b), Terrasses de la Riera dels Canyars (Daura et al., 2013; Rosado-Méndez et al., 2015), and Cova del Gegant (Rodríguez-Hidalgo et al., 2020). Two of these sites (Cova del Gegant and Terrasses de la Riera dels Canyars) were found in the initial general review, and the other two were obtained in a more detailed bibliographic search. In four of the sites, the deposits consisted of unconsumed prey remains. There is another study (Refugio rocoso de Navalmaillo, Arriaza et al., 2017) where bone remains might come from a latrine of Iberian lynx, but authors recognised great uncertainty. The accumulated bones always belonged to lagomorphs, except for the Buraca Escura site where they belonged to Spanish ibex, *Capra pyrenaica*. Coprolites assigned to the Iberian lynx were found in two sites. The arguments used to assign the Iberian lynx as the accumulator agent were mainly two-fold: the co-occurrence of putative prey and Iberian lynx bones (in four sites Iberian lynx bone remains were found), and the taphonomic patterns of the prey bone remains. Several assumptions about the behaviour and ecology of the Iberian lynx are stated explicitly or implicitly in the studies: 1) lynx fed on Spanish ibex (Aubry et al., 2001) or lagomorphs (Arriaza et al., 2017; Aubry et al., 2001; Daura et al., 2013; Rodríguez-Hidalgo et al., 2020; A. J. Rodríguez-Hidalgo et al., 2013b; Rosado-Méndez et al., 2015) of various ages, including newborns, obtained by digging in rabbit burrows (Arriaza et al., 2017); 2) lynx used caves to breed (Aubry et al., 2001; Rodríguez-Hidalgo et al., 2020), and sometimes transported prey to breeding dens for cub feeding (Rodríguez-Hidalgo et al., 2020; Rosado-Méndez et al., 2015; Aubry et al., 2001), where prey remains may accumulate (Aubry et al., 2001; Rodríguez-Hidalgo et al., 2020; Rosado-Méndez et al., 2015); furthermore, they entered hyaena dens to scavenge food (Daura et al., 2013); 3) young individuals (up to six-months old) were using dens (Rosado-Méndez et al., 2015); 4) skeletal remains of lynx of all ages may be found in the breeding dens (Aubry et al., 2001; Rodríguez-Hidalgo et al., 2020; Rosado-Méndez et al., 2015); and 5) Iberian lynx made latrines (Arriaza et al., 2017), even inside breeding dens (Rodríguez-Hidalgo et al., 2020).

Present-day Iberian lynx have been recorded using large hollow trees, rock hollows, dense bushes, piles of tree branches on the ground as natal dens, or even an abandoned building (Fernández and Palomares, 2000; Garrote et al., 2017; Simón, 2012), where cubs stay until they are 3–4 weeks old. They are then relocated to a series of auxiliary dens where they spend on average 8 days in each one (Fernández et al., 2002) until cubs are 56–66 days old. Subsequently, females and their young roam within their home range showing no fidelity to any den (Fernández et al., 2002; Garrote et al., 2017). In natal dens female Iberian lynx only feed cubs with milk, whereas in auxiliary dens they are fed both with milk and prey carried by their mother (Fernández et al., 2002; Yerga, 2015; Yerga et al., 2016, author pers, obs.). Nevertheless, finding prey remains in auxiliary dens is uncommon. For example, after examining 15 auxiliary dens used by three female lynxes and their young, only some remains of 9 prey (rabbits) were found (i.e., 0.6 rabbits/auxiliary den; Fernández et al., 2002). A dead lynx cub was found in a natal den and another one in an auxiliary den (Fernández et al., 2002), but no dead juvenile (older than three months) or adult individuals have been found in dens (Fernández et al., 2002).

The Iberian lynx is a trophic specialist on European rabbits, *Oryctolagus cuniculus*, accounting for 70–100% of its diet (Aymerich, 1982; Delibes, 1980; Delibes et al., 1975; Gil-Sánchez et al., 2006; Palma, 1980; Palomares et al., 2001). Other prey species never accounted for more than 20% of their diet. Lynx are capable of feeding on all age classes of rabbits (including kittens that they can occasionally dig up from their burrows) (Calzada et al., 2003). There is no evidence of lynx feeding solely or primarily on ungulates, although they may sporadically hunt and feed

upon them over several days (Beltrán et al., 1985). Lynx may drag prey a few metres to a concealment site before eating, but never to specific locations, except to auxiliary dens when breeding (Delibes, 1980; Fernández et al., 2002; Yerga, 2015). In the case of ungulates, there is no record of lynxes transporting them over long distances or carrying them for cub feeding. Similarly, there are no records of lynx scavenging or kleptoparasiting, even in Doñana National Park, where carrion is abundant (Domingo et al., 2020), and where lynx ecology has been monitored by radio-tracking for nearly 40 years (López-Bao et al., 2010; Palomares et al., 2012).

Iberian lynx deposit their faeces both as isolated deposits and in latrines of 2–10 scats (Robinson and Delibes, 1988; Rodríguez et al., 2009). Scats from adult individuals have never been found in natal dens; scats from cubs may appear in auxiliary dens (Fernández et al., 2002).

Therefore, based on its present ecology and behaviour, the Iberian lynx is a species with little capacity to generate prey bone accumulations (particularly from prey such as ungulates) both in open and underground conditions directly from remains of hunted prey or from scat remains (Table 6).

3.3.8. *Canis lupus*

The wolf was considered as responsible for bone accumulations in five zooarchaeological sites: Chagyrskaya and Denisova Caves (Russia), Grand Abri aux Puces of France, and Sewell and Victoria Caves of England (Lord et al., 2007; Vasiliev, 2013; Fourvel et al., 2014; Morley et al., 2019). Fourvel et al. (2014) considered the wolf a potential predator in the Grand Abri aux Puces site based on the skeletal parts and tooth marks on bear remains in the anterior part of a rock shelter. Vasiliev (2013) noted that Chagyrskaya Cave was a comfortable den (for shelter or breeding) for wolves, which was concluded after finding numerous wolf skeletal elements, some traces of fermentation in the digestive tract, and tooth marks in bones. Similarly, Lord et al. (2007) proposed the wolf as one bone accumulator based on tooth marks and gnawing in bones at Victoria and Sewell Caves, where wolves carried prey to dens; 3) hunted or scavenged prey inside caves; and 4) formed latrines in underground cavities.

The review of the present behaviour of wolves revealed that the species may commonly use underground dens for breeding. Of a total of 16 records found in our literature review (see Supplementary Table 2), in at least 10 cases they used excavated dens for breeding, and in at least four cases, wolves re-used dens. Normally these dens are used as natal dens until cubs are 6–8 weeks old (Vià, 1995; Packard, 2003). Afterwards, pups commonly spend several months of dependence (up to 4–5 months) at one or several so-called rendezvous sites, where adults retrieve food for pups. Pups are weaned at 6–10 weeks old (Packard, 2003), so most or all feeding on meat from prey remains retrieved by adults takes place above ground at rendezvous sites (Murie, 1944; Joslin, 1967). Rendezvous sites are commonly located in dense vegetation, shrub undergrowth, and more rarely among boulders in screes, but not in actual caves. Scat accumulations are a common feature of rendezvous sites, where pups spend weeks or even months before they are able to travel with adults (Stenglein et al., 2011). Fragments of large bones can also be present at rendezvous sites after the feeding activities of pups by chewing or gnawing bones attached to pieces of large prey delivered at the sites by adults (Theuerkauf et al.,

2003; authors pers. obser.) Wolves usually hide portions of prey in “food caches” after feeding ad libitum under debris or snow to avoid being encountered by scavengers but never conceal such food caches in caves. We have no information on wolves hunting or scavenging in cave-like environments. Finally, we found a paper (Kowalewski et al., 2009) that recorded wolves forming latrines outdoors on the ground, but not in underground cavities.

Based on currently available information, although wolves repeatedly use subterranean dens for breeding, bring large prey to pups, and may form latrines, they would not be a likely accumulator of bones and scat, as no isolated prey remains, latrines or scat are found in or around subterranean dens (Table 6). Furthermore, there is no information on modern wolves entering cave-like environments to hunt or scavenge.

3.3.9. *Vulpes vulpes*

The red fox was only cited as an accumulator species in the zooarchaeological site of Srbsko Chulum-Komin, a cave used by hyaenas as a den in Czech Republic (Diedrich and Zák, 2006; Diedrich 2010, 2016). These authors mentioned that the site was also used by the red fox for prey storage (mostly fish, frogs, hares *Lepus europaeus/timidus* and grouse *Lagopus lagopus*), also leaving tens of thousands of small mammal bones in their scats.

At present, the species has frequently been recorded using (and re-using) excavated underground dens (and in one case an abandoned mine) mainly for breeding purposes (see Supplementary Table 2 for references). In at least five articles, red foxes were reported accumulating medium-sized prey remains, normally around breeding underground dens (Ruiz-Olmo et al., 2003; Marks and Bloomfield, 2006; Panek, 2009; Krajcarz & Krajcarz, 2010, 2012). The main prey remains were from *Anas platyrhynchos*, *Gallus gallus f. domestica*, and *Lepus europaeus*. In at least one site with many *Gallus gallus* remains, its number was large (Supplementary Table 3). Krajcarz and Krajcarz (2012) also reported three accumulations of scats in the interior of one mine, around 2–3 m from an accumulation of prey remains.

According to the available information, the red fox is very likely a bone and scat accumulator (Table 6). It is surprising that the red fox was not recorded more often as responsible for bone or coprolite accumulation in zooarchaeological sites.

4. Conclusions

Our review aimed to summarize the role of mammalian carnivores as agents of prehistoric bone accumulations and if the known present behaviour and ecology regarding feeding, breeding, denning and even defecating ecology of extant species support assumptions made by archaeologists on these species in the past.

Hyaenidae was the family most often reported as bone accumulators in zooarchaeological sites, followed by Felidae and Canidae. Bone accumulations were mainly found in underground cavities. Coprolites were associated with bone accumulations in approximately seven of every 10 cases reported for Hyaenidae, but more rarely when the presumed bone accumulator was a Canidae or a Felidae (three and two out of 10 cases, respectively).

The behaviour of present-day Hyaenidae species may be similar to their prehistoric counterparts as they commonly use (and reuse) underground cavities as dens, frequently accumulate large prey remains, and defecate inside underground dens. However, the behaviour of present-day Felidae and Canidae species may conflict with the number of records found that identified them as bone accumulators in prehistoric sites. For example, although Felidae are more often cited as bone accumulators than Canidae in prehistoric sites, the latter use (and reuse) underground dens and accumulate large prey more frequently than Felidae, which more often use

surface burrows and rarely accumulate prey remains. Scat accumulations are rare for both Canidae and Felidae in underground cavities.

With the exception of *C. crocuta* for the formation of underground latrines, the known natural history of all extant Hyaenidae species confirms that they may act as bone and scat accumulators in underground conditions. However, the paucity of records for *H. hyaena* and *H. brunnea* is surprising despite the fact that both species have higher rates of bone accumulation and may defecate within underground dens more frequently than *Crocuta crocuta*. This may be explained by the likely Africa-only distribution of both species, whereas *C. crocuta* was also widely distributed in Europe during the Pleistocene, and most prehistoric records (71 of 86) come from Europe.

Present-day behaviour of only one species of Canidae (*V. vulpes*) and one of Felidae (*P. pardus*) matches that presumed for prehistoric individuals of such species in relation to bone and scat accumulation. The role of the remaining species (some of them very well studied such as *C. lupus*, *P. leo* and *L. pardinus*) as bone and scat accumulator agents in prehistoric sites remains questionable due to differences from their present-day behaviour. *P. onca* is the only species with a remarkable lack of information on its natural history, making it difficult reach a reliable conclusion.

Our review also highlights the absence of records of small carnivores of the families included in our review as bone accumulators in zooarchaeological deposits, although recent studies show bone accumulations by present-day small animals (e.g. Laudet and Selva, 2005; Krajcarz and Krajcarz, 2012; Arilla et al., 2020). Two non-exclusive reasons might explain why small carnivores were never cited as accumulating agents: 1. Most archaeological deposits have been studied from a hominid perspective focusing on the strategy of carcass acquisition by humans, interspecific competition with large carnivores, and hominin social behaviour. Therefore, materials not related to these topics may have been overlooked. This can be particularly true for remains of small prey species, those that small canids and felids feed upon. 2. Bone remains of small prey are more difficult to find, detect and study, so the chance of detecting a prehistoric bone accumulation from a small carnivore is lower.

Information on the natural history of different carnivore species is needed to better understand the role of these species as bone accumulating agents in zooarchaeological sites.

Author contributions

Francisco Palomares: Conceptualization, Methodology, Investigation, Data curation, Writing, Writing – review & editing, Supervision, Project administration. **Héctor Ruiz-Villar:** Conceptualization, Methodology, Investigation, Resources, Data curation, Writing, Writing – review & editing; **Ana Morales-González:** Conceptualization, Methodology, Investigation, Resources, Data curation, Writing, Writing – review & editing; **Javier Calzada:** Conceptualization, Methodology, Investigation, Data curation, Writing, Writing – review & editing; **Jacinto Román:** Conceptualization, Methodology, Investigation, Data curation, Writing, Writing – review & editing; **Juan Carlos Rivilla:** Conceptualization, Methodology, Investigation, Data curation; **Eloy Revilla:** Conceptualization, Methodology, Writing – review & editing; **Alberto Fernández-Gil:** Investigation, Data curation, Writing, Writing – review & editing; **Miguel Delibes:** Conceptualization, Methodology, Investigation, Data curation, Writing, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing

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Appendix A. Supplementary data

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