



Regarding beasts and humans: A review of taphonomic works with living carnivores



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ABSTRACT

Understanding how fossil assemblages were formed and which species modified the bones recovered in archaeological sites is no easy task. Nevertheless, during recent decades taphonomists have been working on the study of living carnivores in order to have a framework available for comparing fossil assemblages. In this paper we provide an overview of the results obtained from taphonomic work with living carnivores, the limitations of the results in relation to the variety of procedures implemented, and the application of the results obtained from the fossil record. The experimental conditions, i.e., wild versus captive carnivores, the prey size of the carcasses, etc., in large part determine the validity of the results obtained from taphonomic observations. For this reason we must be cautious when comparing the data with the fossil record. More studies on carnivores, especially on wild species, are necessary for us to increase our knowledge of the role of carnivores in the fossil record.

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1. Introduction

The history and evolution of hominins has been inexorably linked to carnivores. Just like hominins, some carnivores accumulate carcasses in cave dens, and both compete for the same prey, shelter (caves and rock-shelters), territories, and resources. Furthermore, hominins were occasional prey of the carnivores, and vice versa. For these reasons, taphonomic research has been focused on the study of living carnivores as taphonomic agents with the purpose of interpreting the archaeological record for decades. To make more accurate hypotheses regarding past processes, it is crucial to understand present dynamics and processes. Thus, research into the role of carnivores in bone modification and accumulation has been based on the Principle of Uniformitarianism, which assumes that natural laws and processes that operate in the present are the same as those that operated in the past. Among this research, Professor G. Haynes's work is notable. In the words of Prof. G. Haynes (1981): "while fossil bone assemblages may misrepresent aspects of extinct animal communities, the nature and extent of biasing factors may be better evaluated by the study

of possibly analogous agencies of modification to modern bone assemblages. Since the past cannot be directly observed, the present must serve as a model". After Prof. Haynes' doctoral dissertation about the skeletal disturbances by natural agencies in North America (Haynes, 1981) and other publications about this issue (Haynes, 1980a, 1982, 1983a, 1983b, 1985, 1991), more researchers followed with experimental work on living carnivores, improving our knowledge of the role of carnivores in the archaeological record. Although there is still much work to do, the results have proven to be great tools for interpreting faunal remains in archaeological sites. The aim of this paper is to update the taphonomic works with large living carnivores (bears, wolves, lions, leopards and hyenas) and their applications to the fossil record.

2. Carnivores as accumulation agents

With the aim of making consistent taphonomic interpretations, it is essential to acquire knowledge about the behavior of large carnivores as accumulation agents of bones. Brain (1981) argued that some carnivores (especially hyenas and leopards) used caves as places of consumption and breeding. Under certain circumstances, the preservation of prey may occur. Several previous works, most notably including those by Domínguez-Rodrigo (1994a, 1994b, 1994c), have shown that although most of the predators are able to move carcasses to nearby places in relation to the collection

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points, only a few species make significant bone accumulation. Stiner (1999) divided the carnivore species into bone collectors and non-collectors. In this section we describe the observable behavior of various carnivore species in relation to the use of dens and places of bone accumulations.

Current ursid species display differences regarding feeding behavior, as some species are more herbivorous than others (Christiansen, 2007). Although the diet of living brown bear (*Ursus arctos*) is mainly herbivorous, meat appears in the diet in varying amounts, particularly in spring, usually as a result of scavenging carcasses and rarely as a direct result of predation (Clevenger and Purroy, 1991). Stable isotope studies on extinct species of bears indicate that some were also mainly vegetarian. This is indicated by Bocherens et al. (2006, 1994), who state that the diet of the cave bear (*U. spelaeus*) was essentially herbivorous. Moreover, isotopic analyses conducted on Middle Pleistocene bear fossils (*U. deningeri*) from the Sima de los Huesos indicate a basically herbivorous diet (García et al., 2009). Nevertheless, some evidence of cannibalism among Pleistocene bears has been reported, indicating that the extinct bears were also able to include meat in their diet, depending on nutritional stress (Pinto and Andrews, 2002; Rabal-Garcés et al., 2012; Sala et al., 2014b).

Experiments with wild bears in the North of Spain demonstrate that brown bears can transport large-sized ungulates hundreds of meters from the point of initial deposition before they begin to consume the carcass. Nevertheless, it was reported that wild brown bears do not take carcasses (partial or whole) to their dens and, therefore, did not generate skeletal accumulations in caves (Sala and Arsuaga, 2013). The same observation was made in the case of North American black and brown bears, demonstrating that these species under modern conditions do not normally carry food to dens (Rogers, 1987; Stiner, 1999). Thus, ursids must be considered non-collectors, and we do not have any reason to believe that this behavior was different in the past.

There is a lack of clear evidence in experimental studies that wolves generate bone accumulations (Binford, 1981; Castel, 2004; Yravedra et al., 2011; Fosse et al., 2012), mainly because wolves usually consume their prey where they are killed or scavenged so they do not usually transport carcasses (Joslin, 1967; Mech, 1970; Fox, 1971). Based on field observations, Haynes (1981) describes different possible scenarios in which bones of carcasses can be found: i) Kill sites; ii) Consumption sites where parts of the prey can be carried up to 30 m away from the kill site to be eaten; iii) Den and rendezvous sites that are used during denning season. The dens may be burrows in the ground, rock cavities, etc., which are used until pups have been weaned. Rendezvous sites, used after dens, are places where subadults remain while adults hunt; and iv) Scavenging sites, where wolves gnaw bones discarded by humans or other species. Nevertheless, none of these places are characterized by large accumulations of bones.

During the breeding season adults may provision pups by the regurgitation of meat, and this behavior does not usually generate large bone accumulations (Domínguez-Rodrigo, 1994b). Living wolves are not currently accumulation agents of bone remains, but we are not sure about the behavior of these canids in the past (Yravedra et al., 2011). Nevertheless, canids can become major taphonomic agents (through secondary access to carcasses) in relation to modification of bone assemblages (Castel, 2004). Although wolves may not have created the bone accumulations in Pleistocene sites, they could have been major bone modifiers in archaeological and paleontological contexts (Sala et al., 2014a).

Regarding felids, different species display different behavior regarding the transport and accumulation of carcasses. Lions are social felids and are the best example of predation. Their diet is strictly carnivorous and they are able to access a high variety of prey,

from rhinos to porcupines, including all kinds of ungulates and carnivores (including other lions) (Schaller, 1972). Although up to 16% of living lions' diet comes from scavenging (Schaller, 1972), their trophic choice usually represents large ungulates of a weight range of 190–550 kg, though the optimal weight of their prey is 350 kg (Hayward and Kerley, 2005). Their advantage as the most significant predator lies not only in their strength and size, but also in their gregarious behavior (Curio, 1976; Domínguez-Rodrigo, 1994b, c, 1999; Pusey and Packer, 1997). Usually after hunting, lions typically eat the carcass directly near the kill site, consuming large part of the viscera, muscles, skin and soft tissues, including fine bones of face and the end of the ribs (Schaller, 1972). Although lions are able to transport the prey a few hundred meters if the conditions are not comfortable for them (Domínguez-Rodrigo, 1994c), they do not preferentially transport the carcass far from the kill site. Instead, they usually feed until they are satiated, leaving behind food (especially bones) for scavengers (Schaller, 1972). Lions do not carry meat in the breeding season either, since lion cubs tend to move with the group when the hunting occurs (Schaller, 1972; Bertram, 1978; Domínguez-Rodrigo, 1994c). This behavior does not generate bone accumulations caused by lions.

In contrast to lion, leopards consume protein derived from any source, from beetles to antelopes (Estes, 1992). Studies of food preferences conducted in different regions show that leopards usually consume ungulates, preferably small-medium sized, with weights ranging from 10 to 40 kg (Hayward et al., 2006). However, leopards often prefer prey whose weight is within their own range of body weight (23–25 kg), which are found in small groups, and present minimal risk during the hunt. This is because, unlike lions, leopards are not social felines, and they hunt alone (Hayward et al., 2006). The pressure other large carnivores put on these solitary felines often compels them to transport prey carcasses to the upper branches of trees, for example, where they can be consumed in peace (Brain, 1981; Cavallo and Blumenschine, 1989; Estes, 1992). This behavior allows leopards to keep prey away from other predators and keep the meat available for longer than the case for other carnivores. Nevertheless, studies carried out in South Africa reported that this behavior has been observed rarely, and instead, transport and accumulation of bones occurs more frequently in caves, when available (Ruiter and Berger, 2000, 2001).

There are three species of hyena that can potentially generate bone accumulations and/or bone modifications: the striped hyena (*Hyaena hyaena*), the brown hyena (*Hyaena brunnea*), and the spotted hyena (*Crocuta crocuta*). Differences in these species' behavior are described in Lansing et al. (2009) and references therein. In this paper, we will focus on the spotted hyena since this species has traditionally been the most studied in past literature due to their abundance in the European Pleistocene fossil record. The spotted hyena is a social carnivore, both an opportunistic scavenger and an effective hunter that includes in the diet whatever resources can be found, from termites, turtles, ungulates, to other carnivores (including hyenas) and elephants (Kruuk, 1972; Kingdon, 1997). Hyenas preferably consume ungulates weighing between 20 and 250 kg, although for scavenging activities, these weights may be higher, including carcasses of hippopotamus and giraffes (Cooper et al., 1999). The behavior of the spotted hyena changes drastically compared with other species of carnivores since they are specialized in the systematic transport and accumulation of carcasses to their dens (Sutcliffe, 1970; Kruuk, 1972; Mills and Mills, 1977; Henschel et al., 1979; Skinner et al., 1986; Hill, 1989; Lam, 1992). Spotted hyenas consume their prey or carrion *in situ* but also transport carcasses to their dens to feed young individuals of their groups, and that is where the accumulation of bones occurs (Domínguez-Rodrigo, 1994b). Although ecological behavioral studies on modern spotted hyenas reported that bone

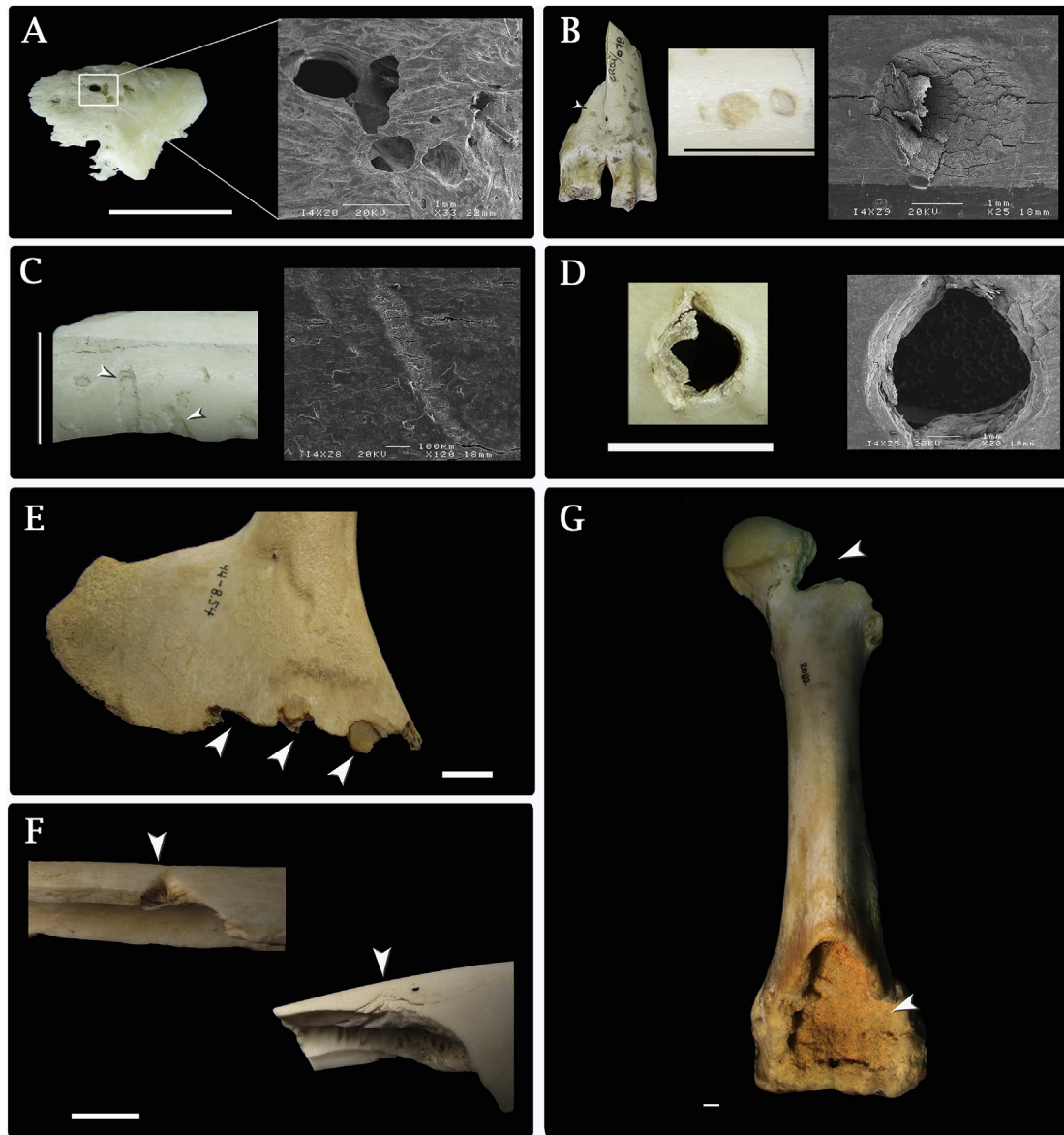


Fig. 1. Photographs and SEM images showing some examples of bones modified by living carnivores and tooth marks considered in this study. A) Bone fragment with traces of dissolution due to gastric acid recovered from wolf excrement. B) Tooth pits on an ovicaprid metacarpal caused by wolves. C) Scores on a long bone diaphysis caused by wolves; D) Puncture produced by a lion on a humerus diaphysis of *Capra hircus*. E) Crenulated edges produced by hyenas on an innominate bone of a sheep; F) Comparison of marks associated with a long bone fracture caused by carnivore activity (upper image) and humans (lower image); G) Furrowing and scooping out on a femur of *Bos taurus* caused by hyenas. A, B, C and D bones from the taphonomic collection of Sala and Arsuaga (Centro Mixto UCM-ISCIII, Madrid-Spain); E and F bones from the taphonomic collection of Curtis Marean (Arizona State University, Tempe-USA); G bone from the taphonomic collection of Gary Haynes (University of Nevada, Reno-USA). Scale bar 1 cm.

accumulation rates are highly variable and depend on several factors (Lansing et al., 2009), it is well accepted that extant hyenids accumulate bones (Hughes, 1954, 1958; Brain, 1981; Bunn, 1983). Actually, hyenas have been studied since the early nineteenth century when Buckland (1822) concluded that the large accumulation of fossils of large-sized herbivores in Kirkdale Cave (Yorkshire, U.K.) was transported by hyenas. Their extraordinary behavior has turned this taxon into one of the best studied in taphonomic literature (Hughes, 1954; Sutcliffe, 1970; Bunn, 1983; Binford et al., 1988; Hill, 1989; Cruz-Urbe, 1991; Skinner and van Aarde, 1991; Marean et al., 1992; Lam, 1992; Selvaggio, 1994; Pickering, 2002; Brink, 2004; Faith, 2007; Faith et al., 2007; Pokines and Peterhans, 2007; Egeland et al., 2008; Prendergast and Domínguez-Rodrigo, 2008; Kuhn et al., 2009, 2010; Lansing et al., 2009; Domínguez-Rodrigo and Pickering, 2010; among others). Hyena den

sites have been recognized and studied, especially in the European record from the Early to Late Pleistocene (Stiner, 1991; Palmqvist et al., 1996; Marra et al., 2004; Diedrich, 2009; Villa et al., 2010; Blasco et al., 2011; Palmqvist et al., 2011; Arsuaga et al., 2012; Sala et al., 2012), to mention some.

In sum, and following Stiner's (1999) classification, carnivore species can be divided between bone collectors (mainly hyenas) and non-collectors (e.g., bears and lions). Nevertheless, other species, such as wolves and leopards, under specific circumstances may generate isolated bone remains but rarely generate large bone accumulations. It is important to note that carnivore behavior depends on several factors (availability of caves, competition with other carnivore species, accessibility to ungulates, nutritional stress, etc.) that are difficult to control for in current ecosystems. Therefore, it is more difficult – or impossible – to make detailed

inferences about the past. For this reason, it is crucial to have a framework of bone modification patterns to approach the role of carnivores in archaeological assemblages.

3. Methods for approaching bone modification by carnivores

In addition to the studies about the ethology of the carnivore species regarding the diet and accumulation of carcasses, for decades the studies regarding taphonomy of carnivores have been focused on bone modification patterns, especially tooth mark types and dimensions, as well as breakage capacity. Different methodologies of study and different experimental conditions have been developed since the more descriptive analyses from older publications, including the multivariate approaches proposed by Domínguez Rodrigo et al. (2012) and Domínguez Rodrigo and Pickering (2010) up to the use of GIS techniques (Parkinson et al., 2014, 2015).

3.1. Tooth marks

While consuming carcasses, carnivores may leave tooth imprints on bone surfaces. There is great heterogeneity in the terminology of tooth marks in the literature. Here we utilize terminology for those tooth mark types generally used in the bibliography (Fig. 1). Tooth marks on bone surfaces are usually classified as pits, punctures, furrowing, and scores (Maguire et al., 1980; Haynes, 1980a; Binford, 1981). Pits and punctures are marks generated by the pressure of a tooth on the cortical surface of a bone. Their difference lies in whether the mark penetrates the cortical bone (puncture) or not (pit) (Sala et al., 2014b). Scores are elongated marks with a U-shaped cross-section and a flat bottom that are produced by tooth cusp movement over the bone surface. Furrowing is the result of carnivore gnawing and involves the extraction or absence of portions of the cancellous bone tissue. Furrowing can be light, moderate, or heavy depending on the portion of cancellous tissue removed (Haynes, 1982).

In addition to the conspicuous marks, there are also other traces of carnivore activity on bone surfaces. One example is the dissolution caused by gastric acids produced during the consumption of bone fragments. Some carnivores (and also birds) are able to swallow bone fragments. These splinters can be recovered from feces and they are also the product of regurgitation. Bones affected by acid-etching usually display characteristic features described previously by Sutcliffe (1970), such as scalloping of the bone surface, presence of holes, and/or fine and sharp edges (Fig. 1).

Measurements of tooth marks may be useful to at least determine the size of the carnivore that caused them. Different methodologies by different authors have been used over time. Haynes (1983b) recorded different morphologies of dental impressions in trabecular tissue that differentiate canids, hyenas, bears, and felids. Thus, square or rectangular holes are typical of bears, conical holes are characteristic of canids and hyenas and, finally, elongated V shape morphologies would be typical of felids (Haynes, 1983b).

Later, Selvaggio and Wilder (2001) performed research based on metric data of tooth pits to differentiate carnivore species (hyenas, leopards, lions, jackals, and cheetahs). They observed that the size of the marks is not only related to the size of the carnivore, but also to bone density. Therefore, they focused on differentiating marks in cancellous bone, thin cortical and cortical bone. Their results show that the area of the markings substantially overlaps among the carnivores. Subsequent work by Domínguez-Rodrigo and Piqueras (2003) is based on Selvaggio and Wilder (2001), but increased

the sample of carnivores (lions, dogs, hyenas, jackals, baboons, and bears). This paper concluded that tooth pit measures are useful for interpreting the size of the carnivore involved in the modification of bones, but are not diagnostic for differentiating specific taxa. Metric data should be combined with other aspects of bone modification to identify the carnivore taxa responsible for the bone damage.

Delaney-Rivera et al. (2009) conducted a study on tooth mark dimensions, which provided new experimental data and concluded that there is considerable overlap of values in pit dimensions, considering size, type, and species of carnivore involved.

A more recent study (Andrés et al., 2012) shows that small and large carnivores can be clearly differentiated when using tooth pit size, especially in dense shafts. These authors argue that the overlapping detected in previous studies of tooth mark sizes probably was caused by the use of a small sample as well as by the small-sized carcasses used.

In addition to the previous work regarding tooth mark analyses of several taxa, different papers also provide metric data as the result of experimental studies on specific carnivores, especially bears (Sala and Arsuaga, 2013; Saladié et al., 2013; Arilla et al., 2014) and wolves (Campmas and Beauval, 2008; Yravedra et al., 2011; Sala et al., 2014a).

As can be seen in Table 1, the tooth mark values provided by different authors differ substantially, mainly depending on the experimental conditions as discussed in Andrés et al. (2012). Additionally, we must consider that each author used different methodologies in quantifying the tooth mark dimensions in terms of tooth mark type and also when statistically processing data. For example, to carry out metrical comparisons, some authors grouped pits and punctures together since they correspond to the same mechanical effect (Pobiner, 2007; Sala and Arsuaga, 2013; Saladié et al., 2013). However, other authors considered only pits (Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003; Delaney-Rivera et al., 2009; Andrés et al., 2012). On the other hand, some authors preferred size ranges (Andrews and Fernández-Jalvo, 1997; Pinto et al., 2005; Rabal-Garcés et al., 2012), while others preferred a Mean plus 1 Standard Deviation (Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003; Delaney-Rivera et al., 2009; Saladié et al., 2013), and some preferred 95% confidence intervals, since this represents the variation of the majority of each sample (Andrés et al., 2012; Sala et al., 2014a). These differences make it difficult to compare samples to apply metric data to the archaeological record.

Table 1
Carnivore tooth marks size.

	n	Mean	SD	Min.	Max.
<i>U.a.</i> pit cortical Length*	214	3.04	1.50	0.5	8.46
<i>U.a.</i> pit cortical Breadth*	214	2.03	1.07	0.12	5.79
<i>U.a.</i> pit trabecular Length**	21	5.24	1.91	2.36	10.13
<i>U.a.</i> pit trabecular Breadth**	21	3.68	1.02	1.79	5.85
<i>U.a.</i> scores trabecular Breadth**	9	2.14	1.03	1.06	4.7
<i>P.leo</i> pit cortical Length*	28	2.87	1.8	1.29	9.2
<i>P.leo</i> pit cortical Breadth*	28	1.7	1.41	0.6	7.25
<i>P.leo</i> pit trabecular Length*	178	4.05	2.37	0.74	15
<i>P.leo</i> pit trabecular Breadth*	178	6.17	3.51	0.98	23.3
<i>P.leo</i> scores trabecular Breadth*	76	2.7	2.59	0.5	18.8
<i>P.leo</i> pit cortical Length**	22	5.97	1.59	3.37	9.64
<i>P.leo</i> pit cortical Breadth**	22	4.7	1.40	2.59	8.40
<i>P.leo</i> pit trabecular Length**	61	3.72	1.08	1.97	6.25
<i>P.leo</i> pit trabecular Breadth**	61	2.51	0.72	1.07	4.15
<i>P.leo</i> scores trabecular Breadth**	24	1.26	0.33	0.79	2.0
<i>C.c.</i> pit cortical Length*	46	2.71	3.11	0.33	9.1
<i>C.c.</i> pit cortical Breadth*	46	1.55	1.2	0.21	8.7
<i>C.c.</i> pit trabecular Length*	17	5.4	5.1	0.3	25.6

Table 1 (continued)

	n	Mean	SD	Min.	Max.
C.c. pit trabecular Breadth ^ˆ	17	2.9	2.73	0.11	14.0
C.c. scores trabecular Breadth ^ˆ	542	0.66	0.73	0.11	9.0
C.c. pit cortical Length ^ˆ	456	1.57	0.98	0.17	11.3
C.c. pit cortical Breadth ^ˆ	456	1.19	0.75	0.15	6.52
C.c. pit trabecular Length ^ˆ	260	2.39	1.64	0.31	20.8
C.c. pit trabecular Breadth ^ˆ	260	1.64	1.24	0.23	11
C.c. pit cortical Length [‡]	17	2.42	0.82	11.21	4.10
C.c. pit cortical Breadth [‡]	11	2.04	0.72	0.84	3.27
C.c. pit trabecular Length [‡]	7	3.04	0.33	2.60	3.50
C.c. pit trabecular Breadth [‡]	3	2.07	0.38	1.12	3.02
C.c. scores trabecular Breadth [‡]	26	1.78	0.57	0.83	3.73
C.l. pit cortical Length ^ˆ	236	2.39	1.15	0.4	9.41
C.l. pit cortical Breadth ^ˆ	236	1.8	0.87	0.16	7.48
C.l. pit trabecular Length ^ˆ	129	3.61	1.63	1.04	9.95
C.l. pit trabecular Breadth ^ˆ	129	2.7	1.25	0.83	7.41
C.l. scores trabecular Breadth ^ˆ	78	2.92	1.63	1.0	7.91
C.l. pit cortical Length [‡]	218	2.11	0.64	0.82	3.70
C.l. pit cortical Breadth [‡]	151	1.65	0.53	0.66	3.07
C.l. pit trabecular Length [‡]	54	2.81	0.68	1.24	4.45
C.l. pit trabecular Breadth [‡]	37	2.31	0.59	11.23	3.90
C.l. scores trabecular Breadth [‡]	33	2.35	1.38	0.80	7.41
V.v. pit cortical Length ^ˆ	67	1.54	1.18	0.36	6.52
V.v. pit cortical Breadth ^ˆ	67	0.99	0.87	0.19	5.91
V.v. pit trabecular Length ^ˆ	41	2.56	1.5	0.99	9.07
V.v. pit trabecular Breadth ^ˆ	41	1.88	1.08	0.8	5.26
V.v. scores trabecular Breadth ^ˆ	7	0.65	0.4	0.32	1.23

SD = Standard deviation; Max = Maximum; Min: Minimum; U.a. = *Ursus arctos*; P.leo = *Panthera leo*; C.c. = *Crocota crocuta dens*; C.l. = *Canis lupus*; V.v. = *Vulpes vulpes*. Data from: *Saladié et al. (2013); **Sala and Arsuaga (2013); ^ˆAndrés et al. (2012); ^{ˆˆ} Sala (2012); [‡]Sala et al. (2012); ^{‡‡}Sala et al. (2014).

3.2. Breakage analyses

Bones broken by carnivore activity follow the pattern of fresh-bone breakage. To analyze this pattern, the criteria for long bones must be explicit (Bunn, 1982, 1983; Haynes, 1983a; Morlan, 1984; Johnson, 1985; Gifford-González, 1989; Villa and Mahieu, 1991; Sala et al., 2015). These features are: Fracture outline (longitudinal, transverse, or oblique/curved), Fracture angle (right or oblique), Fracture edge (smooth or jagged), Shaft circumference (1: Less than half of the circumference; 2: more than half of the circumference; 3: complete circumference) and Shaft fragment (1: Less than 1/4 of the total diaphysis; 2: between 1/4 and 1/2 of the total diaphysis; 3: between 1/2 to 3/4 of the diaphysis; 4: more than 3/4 of the diaphysis). Fresh-bone breakage is characterized by curved or spiral outlines, oblique angles of the fracture plane, and smooth edges (Sala et al., 2015). Nevertheless, fresh-bone fractures are not necessarily caused by carnivore activity, so other features are necessary to identify the causes of the breakage.

First, tooth marks (e.g., crenulated edges, crushing, tooth pits associated with the fracture plane) associated with the fractures are

useful in identifying fractures caused by carnivores (Fig. 1). On the other hand, some authors argue that carnivores usually consume the long bone ends, leaving behind bone-cylinders (Cruz-Urbe, 1991). Although this is typical when carnivores chew bones, it is not a common pattern when taking into account the different carnivore taxa and contexts.

During carcass consumption, some carnivores can break bones, usually to access marrow. Different carnivore taxa are divided between durophagous (i.e. hyenas and canids) and non-durophagous species (i.e. ursids, felids).

3.3. Stages of bone damage by carnivores

In addition to the analysis of tooth marks and fracture patterns, carnivore damage can be examined according to different stages of consumption. It has been noted throughout experimental studies (Sala, 2012) that carnivores follow a certain order of consumption of carcasses. Usually, they start consuming regions with a high content of spongy tissue, lower density and with meat associated (e.g., proximal femora). Subsequently, if consumption continues and, depending on the carnivore taxa and experimental conditions, bones from other less productive regions can also be modified (e.g., carpal, tarsal or phalanges). Haynes (1981, 1982) defined four degrees of modification of the carcasses: 1–2 indicate light to moderate, 3 means full, and 4 denotes heavy damage specific to each bone type. Saladié et al. (2013) created five stages of consumption by bears following the guidelines described by Haynes (1981, 1982), although without separating the different skeletal portions. Campmas and Beauval (2008) used seven stages of modification in femora of large bovids gnawed by wolves. Similar methods are used by Fourvel et al. (2012) to describe the consumption of long bones by hyenas, and by Domínguez-Rodrigo et al. (2015) where different stages of bone modification or so called “taphotypes” are used. Most of these models consider the modification patterns taking both bone and soft tissues into account. Because soft tissues are rarely preserved in the fossil record, it is difficult to apply these results to fossil assemblages. For this reason, a new model was proposed (Sala, 2012; Sala et al., 2014a) according to five stages of consumption (from light to heavy: I, II, III, IV and V), specific to each bone type (Table 2). This revision of the Haynes (1981, 1982) method is based on the exclusion of the soft tissue modification to compare the results with archaeological assemblages where no meat is conserved (Sala et al., 2014a). It has been noted that the use of this modification stage is a useful tool to differentiate carnivore taxa responsible for bone modification. In this sense, hyenas and wolves are characterized by reaching higher stages of modification when compared with ursids or felids (Sala, 2012). Nevertheless, as explained below, the degree of modification depends on the experimental conditions (Sala, 2012; Domínguez-Rodrigo et al., 2015).

Table 2

Definition of bone modification stages, after Sala et al. (2014) and modified from Haynes (1980a, 1980b, 1981).

	Low modification	Moderate modification		Heavy modification	
	I	II	III	IV	V
Skull	Scores in horns	Nasal bones and horns tooth scratched	Nasal bones ragged at ends. Premaxillaries broken.	—	—
Maxilar	Maxilla articulated. Preserves molar series. Crenulated edges and/or perforations	Isolated maxilla. It can conserve alveolar process and the palate partial or totally. Punctures.	Complete molar series but with a little bone associated	Incomplete molar series.	Isolated teeth
Mandibles	Complete hemimandible. Furrowing in the angular process and/or symphysis	Mandibular corpus and diastema broken	Complete molar series but with a little bone associated	Incomplete molar series.	Isolated teeth

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Table 2 (continued)

	Low modification	Moderate modification		Heavy modification	
	I	II	III	IV	V
Scapula	Furrowing in the vertebral border	Vertebral border broken with sawtoothed edges	Scapular body broken. Furrowing on the scapular spine	Furrowing in the glenoid articulation.	Isolated fragment
Humerus	Greater tuberosities furrowed	Tuberosities gone. Furrowing in the head	Proximal epiphysis gone. Distal epiphysis intact	About 1/3 shaft gone. Furrowing in the distal condyles	Shaft cylinder or isolated shaft fragment
Radius	Furrowing in distal end	Distal end gone	Furrowing in proximal epiphysis	Shaft cylinder	Isolated fragment
Ulna	Furrowing in olecranon process	Olecranon process gone	Disarticulated of radii	Shaft fragment	—
Pelvis	Iliac crest and ischial tuberosity furrowed. Cancellous tissue exposed	Scooping out of cancellous tissue of ilium and ischium	Ilium and ischium totally gone. Only acetabulum remains	Fragment	—
Femur	Furrowing in great trochanter. Scores in femur head	Furrowing in medial and lateral condyles	Great trochanter gone	Distal epiphysis gone. Femur head nearly gone	Shaft cylinder or isolated fragment
Tibia	Furrowing in proximal lateral border	Tibial tuberosity gone	Furrowing in proximal medial border	Proximal epiphysis gone. Distal end intact	Shaft broken, only distal end remains
Metapodial	Maxilla articulated. Preserves molar arcade. Crenulated edges and/or perforations	Distal end gone	Proximal end furrowed	Shaft cylinder	Isolated shaft fragment
Talus	Scores, pitting and furrowing	Fractured	—	—	—
Calcaneus	Furrowing in calcaneal tuberosity	Punctures in lateral surface	Furrowing in articular surfaces	Fragment	—
Phalanges	Scores and pitting	Furrowed	Fractured	Stomach dissolution evidences	—

4. A guide for differentiating carnivore taxa responsible for gnaw damage

In 1983, G. Haynes published a paper entitled “A guide for differentiating mammalian carnivore taxa responsible for gnaw damage to herbivore limb bones”, and the results have been used for decades. After 32 years, new experimental studies with living carnivores have been developed in North America (Stiner et al., 2012; Burke, 2013), South America (Borrero et al., 2005; Montalvo et al., 2007; Mondini and Muñoz, 2008; Muñoz et al., 2008), Europe (Fosse et al., 2004; Fosse et al., 2011, 2012; Yravedra et al., 2011; Sala, 2012; Yravedra et al., 2012; Sala and Arsuaga, 2013; Saladié et al., 2013; Arilla et al., 2014; Sala et al., 2014a), and Africa (Domínguez-Rodrigo, 1999; Faith and Behrensmeyer, 2006; Faith, 2007; Egeland et al., 2008; Prendergast and Domínguez-Rodrigo, 2008; Domínguez-Rodrigo et al., 2012; Gidna et al., 2013, 2014, 2015), among others.

According to Haynes (1983b) “Most bears will usually not gnaw heavily on [large bovid] bones after the soft tissue has been removed” (Haynes, 1983b: 168), an observation compatible with later taphonomic studies on wild bears (Sala and Arsuaga, 2013; Arilla et al., 2014). Bears are able to imprint tooth marks on bones during consumption, mainly furrowing on long bone ends and spongy tissues from axial skeletons (Sala and Arsuaga, 2013; Saladié et al., 2013; Arilla et al., 2014). The tooth mark dimensions can be diagnostic because of their large size (Table 1).

Field studies show bears do not fracture long bones of large ungulates when consuming them in the wild (Sala and Arsuaga, 2013). Compact bones (carpal, tarsal, and phalanges) were not fractured during consumption by bears. Flat bones of the axial skeleton (ribs, vertebrae, and scapulae) showed fractures, especially at the ends (e.g., spinous processes of the vertebrae) or in areas associated with cartilage, e.g., the vertebral border of the scapula or distal ribs (Sala and Arsuaga, 2013). Similar results were obtained with small and medium-sized carcasses in Arilla et al. (2014), who maintain that fractures caused by bears resulted primarily from evisceration-related activities. One interesting observation is the presence of peeling in the fractured ribs as diagnostic criteria for recognizing bear activity (Arilla et al., 2014).

Differences in bone modification patterns were noted when comparing wild and captive bears, and carcass size. Nevertheless, the intensity of bone modification rarely surpasses the light to moderate stages (Sala, 2012; Saladié et al., 2013). Usually bone modification is more pronounced with captive animals and medium to small-sized carcasses (Sala and Arsuaga, 2013). Because bears do not transport carcasses to cave dens, the most usual context of bear-caused bone modifications in the fossil record is expected to be the scavenging of bones of other bears that died during hibernation or in natural traps (Pinto and Andrews, 2002; Pinto et al., 2005; Rabal-Garcés et al., 2012; Sala et al., 2014b).

Wolves can modify animal carcasses into advanced stages including fracturing the bones in order to consume the marrow; nevertheless, as in the case of bears, captive wolves often reach greater degrees of modification than wild ones (Sala et al., 2014a). Wolves can create numerous tooth marks (mainly pits and scores) when consuming prey, especially on the cortical areas of long and flat bones. The spongy tissue can be completely removed or consumed (Sala et al., 2014a). The high frequency of tooth marked bones could be related to the mastication force; the wolf does not have as much mastication power as other large carnivores, such as bears, hyenas, or lions (Christiansen and Adolfssen, 2005). Comparison of wolf tooth mark dimensions with other large carnivores reveals that wolves differ significantly from large felids and ursids, and they have more in common with hyenids (Sala et al., 2014a).

Wolves have a significant ability to fracture bones of ungulates of all sizes to obtain marrow (Sala et al., 2014a). The abundant bone fractures observed in experimental works are characterized by high percentages of bone splinters (incomplete circumferences and small shaft portions), as the shaft cylinders of long bones are restricted to large-sized ungulates (Yravedra et al., 2011; Sala et al., 2014a). These observations are consistent with data from other authors (Binford, 1981; Haynes, 1982; Nadal I Lorenzo, 1996). Nevertheless, Fosse et al. (2012) reported lower proportions of long bone fractures during observation of kill sites in Poland. In addition to the wolves' high capacity to break bones, an analysis of feces indicates that wolves are also able to swallow relatively large amounts of bone fragments (Esteban-Nadal et al., 2010; Fosse et al., 2012).

In archaeological contexts, the identification of bone modification caused by wolves can be problematic due to both their limited capacity to generate large bone accumulations and their similarities to the effects of hyena bone modification. Fortunately accumulations caused by hyenas tend to have other diagnostic features that allow their identification, as explained below. The modification of some fossil assemblages has been proposed as caused by wolves, mainly as the result of secondary access to carcasses (Díez, 1993; Huguet et al., 2001; Castel, 2004).

As Haynes (1983b) noted, hyenas modify bones of any size until the most advanced stages of consumption. The carcasses consumed by captive and wild hyenas are characterized by the high percentage of tooth marks, as well as by a high proportion of bone breakage (Sutcliffe, 1970; Maguire et al., 1980; Brain, 1981; Hill, 1989; Marean and Spencer, 1991; Marean et al., 1992; Sala, 2012). Hyenas show greater destructive behavior than wolves (Domínguez-Rodrigo et al., 2015). Furthermore, hyenas are capable of swallowing bone fragments that usually are preserved with signs of dissolution by gastric acid. In addition to the analysis of bone modification, there are other criteria that can be used to identify accumulations created by hyenas in the archaeological record (Cruz-Urbe, 1991; Pickering, 2002; Kuhn et al., 2010). After reviewing all these criteria, Kuhn et al. (2010) suggested that the best discriminatory factors for the identification of hyena accumulations are the presence of coprolites as well as the occurrence of hyena immature remains at the sites.

The application of data provided in taphonomic works with living hyenas allows for hyena activity to be discerned in the archaeological and paleontological European hyena den sites, including Pinilla del Valle (Arsuaga et al., 2012) and Valle del Tejadilla (Sala et al., 2012), and others in Italy (Stiner, 1994), France (Villa et al., 2010; Fourvel, 2012), and of course in Africa (Binford et al., 1988; Marean et al., 1992; Faith et al., 2007; Prendergast and Domínguez-Rodrigo, 2008), among others.

The observation by Haynes (1983b) that the large cats “lions, tigers and jaguars will not often sustain gnawing on large bones” is compatible with later experimental work with large felids. Particularly relevant are the investigations with wild lions as taphonomic agents, developed by Domínguez-Rodrigo (1999) and Gidna et al. (2013, 2014). Lions are able to imprint a significant proportion of tooth marks during the consumption of carcasses (Sala, 2012; Gidna et al., 2013, 2014), but differences in the tooth mark intensity were noted between wild and captive lions (Gidna et al., 2013). Similarly, captive animals are able to break long bones (Sala, 2012), but this is unusual behavior in the wild (Domínguez-Rodrigo, 1999), especially in regard to large-sized prey. Lions do not usually reach advanced stages of bone modification, even in captivity (Sala, 2012). It is notable that the size of lion tooth marks can be statistically distinguished from hyenas, wolves, and other smaller carnivores, but it is difficult to make this distinction using the bear tooth marks dimensions (Sala and Arsuaga, 2013). One of the diagnostic features used to differentiate the activity of lions, proposed by Gidna et al. (2014), is the ratio between scores and pits. For these authors, the abundance of scores and the underrepresentation of pits in lion-affected assemblages contrasts with hyenas or wolves, where pits are always more frequent than scores (Egeland et al., 2008; Yravedra et al., 2011). An interesting observation we can add here is that large felids are able to create large isolated punctures on dense cortical bone (e.g., diaphysis of long bones) from ungulates of several size classes (Sala, 2012).

Due to the limited ability of lions to generate accumulations, in the fossil record it is difficult to recognize bone modifications made by this taxon. An example of this interpretive problem is the Sima de los Huesos hominins, whose bone modifications were first interpreted as lion activity by Andrews and Fernández-Jalvo (1997), and which later the tooth marks were confidently ascribed to bear (Sala et al., 2014b).

Recent observations of wild leopards point out that the assemblages consumed by this carnivore are characterized by high proportions of complete or almost complete skeletons, with better preserved axial elements if compared with hyena assemblages. The higher proportion of complete skeletal elements is remarkable (Domínguez Rodrigo and Pickering, 2010). As in the case of bears and lions, experimental studies on leopards under different environmental conditions (wild versus captive) demonstrated that captive leopards modify with more intense bone damage and higher tooth mark frequencies than the wild leopards (Gidna et al., 2015). In the fossil record, there are some examples of assemblages interpreted as accumulated or modified by leopards, e.g., Swartkrans (Brain, 1980, 1981; Pickering et al., 2004b), probably also in the Sterkfontein Member 4 (Brain, 1981; Pickering et al., 2004a), La Caune de l'Arago (Testú et al., 2011), Amalda cave (Yravedra, 2006), and Los Rincones cave (Sauqué et al., 2014a, 2014b).

5. Concluding discussion

During recent decades, taphonomic research has been focused on interpreting the processes of bone modification of the archaeological record to understand hominin and carnivore interaction in the past. In this sense, the work of Prof. Haynes is remarkable. Numerous studies on living carnivores have been conducted using different taxa and contexts, including those of Haynes. The results derived from the experimental works with living carnivores are essential tools for the interpretation of archaeological sites.

First, it is important to take into account the behavior of the different carnivore species regarding bone accumulations, as a framework to make coherent hypotheses in the archaeological record. Captive carnivores usually generate greater bone alteration than wild carnivores (Sala, 2012; Gidna et al., 2013; Sala and Arsuaga, 2013; Sala et al., 2014a; Gidna et al., 2015). This could be related not only to the behavior of carnivores in different contexts (e.g., feeding competition, boredom, etc.) but also to longer exposure, which allows carnivores more time to modify the bone remains. For this reason, we must be cautious when applying to the archaeological record the data provided by taphonomic work with captive carnivores. We must also take into consideration the size of the prey selected in our experiments because this is also an important factor when analyzing bone modification by carnivores (Sala, 2012; Domínguez-Rodrigo et al., 2015). There is a broader range of analytical methodologies, especially regarding the metric parameters of tooth marks that sometimes make it difficult to compare the archaeological material with the published data available.

Notwithstanding these limitations, experimental works with living carnivores are crucial to being able to approach the role of carnivores in the archaeological and paleontological records. For this reason, clearly more research on wild carnivores are needed.

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