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Hyena as a predator of small mammals? Taphonomic analysis from the site of Bois Roche, France

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Abstract.—Feeding behaviors may differ between past and current predators due to differences in the environments inhabited by these species at different times. We provide an example of this behavioral variability in spotted hyena (*Crocuta crocuta*), for which our analysis of a late Pleistocene micromammal assemblage indicates that hyenas preyed upon small rodents, a feeding habit that is rarely observed today among hyenas.

The Bois Roche cave site is situated at the edge of a low bluff overlooking the floodplain of a small stream in Cherves-Richemont (Charente, France). The deposits are dated by electron spin resonance (ESR) to about 69.7 ± 4.1 Ka. Excavations at the site recovered fossil bones and teeth of large and small mammals, together with hyena coprolites. Water screening of the sediments produced large accumulations of rodent remains with low taxonomic diversity. Small mammal bones were recovered from hyena coprolites as well. Descriptions of small mammal bone modification, both from the sediments and coprolites, are reported here. The analysis yielded a distinct taphonomic pattern representative of large carnivores (over 30 kg), which differs from any other modern or fossil predator-accumulated microfaunal assemblage taphonomically analyzed to date. To our knowledge, previous studies of hyena diet have not recorded high concentrations of a single-rodent prey species. We conclude that the low species diversity of this small mammal assemblage most likely relates to a local abundance of the prey species due to an outbreak in the rodent population, rather than from specialist predator behavior and hunting technique.

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Introduction

Hominins, Hyenas, and Rodents.—The relationship between hyenas and hominins has been considered by several authors as an important aspect of mutual evolution in the use of space, hunting resources, or scavenging strategies (Stiner 1991, 1994, 2004; Brantingham 1998). There are also descriptions of frequent hominid–hyena associations during the Plio-Pleistocene (e.g., Bunn et al. 1980; Binford 1981; Brain 1981; Potts 1989; Shipman and Walker 1989; Blumenschine et al. 1994). Stiner et al. (2000) postulated that humans could not have fed solely on large animals, given the high cost to obtain this food source, but must also have fed on small game and other animal protein sources (such as small mammals), which must have had an important role in their daily subsistence activity. We have found evidence of hyenas preying upon rodents in the Bois Roche Pleistocene site, as humans did in the past and even do today (Lupo and Schmitt 2005; Sealy 2006; Rodríguez-Hidalgo et al. 2011; Medina et al. 2012; Fernández-Jalvo and Andrews 2016). The initial interpretation of Bois Roche was as a site where humans and hyenas coexisted due to the presence of stone artifacts and putative bone tools and ornaments. Microscopic analyses of the bone

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tools and stone artifacts showed that the former were modified by hyenas and the latter were carried into the site by gravity and slope wash (Villa and Bartram 1996; d'Errico and Villa 1997; Villa and Soressi 2000; Villa and d'Errico 2001).

Foraging habits have definitively changed in the human lineage (Diamond 2002). Evidence from the cave site of Bois Roche indicates that a change also occurred in hyenas, due in part to the environmental context and the nature of this hyena den. Pokines and Kerbis Peterhans (2007) showed strong differences between bone accumulations in burrows versus caves in African environments, due mainly to the small size and impermanence of the burrows. According to these authors, cave dens allow higher numbers of individuals to occupy a site with longer periods of occupation. Dens also lead to improved rates of bone preservation when compared with open-air sites. Bois Roche has been interpreted as a hyena den that functioned as a maternity cave site (Marra et al. 2004; Villa et al. 2004).

Excavations at Bois Roche, (see map, Fig. 1) in 1995, 1997, and 1998 by P. Villa and L. Bartram and in 1999 and 2000 by Villa yielded high quantities of small mammal bones. The history of the excavations of the site and the general cave morphology are documented elsewhere by Bartram and Villa (1998), Marra et al. (2004), and Villa et al. (2004, 2010). Two major stratigraphic units have been distinguished in the site (units 1 and 2), with four subdivisions of the upper unit 1 (Goldberg 2001; Marra et al. 2004). The electron spin resonance (ESR) averaged value of six samples from units 1c and 2 is 69.7 ± 4.1 Ka, placing the site at the beginning of MIS 4, that is, in the upper Pleistocene during a period of cold climate (Villa et al. 2010). With the exception of a high concentration of amphibians and squamate reptiles (minimum number of individuals [MNI] = 4,851) from all levels (Blain and Villa 2006), most small vertebrate bones were the remains of small mammals. These authors noted: "Herpetofauna suggests a very open environment, with damp meadows and small grove areas of broadleaved trees and conifers" (Blain and Villa 2006: p. 30).

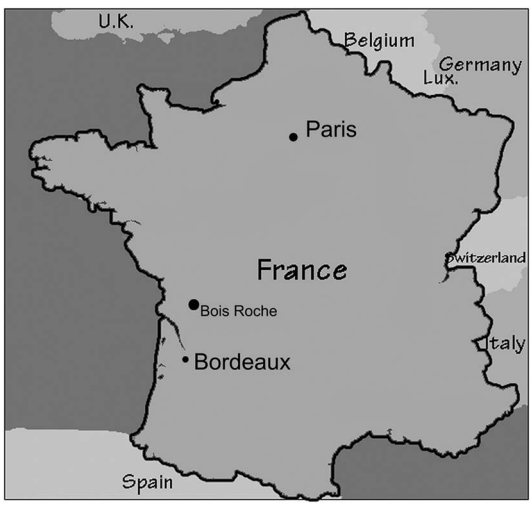

FIGURE 1. Location map of the site of Bois Roche in France.

Taxonomic analysis of the small mammals of the 1995 material was undertaken by C. Sesé at the Museo Nacional de Ciencias Naturales, Madrid (Sesé and Villa 2008). Villa et al. (2010) analyzed subsequent material obtained from the site during the 1997 through 2000. Sesé and Villa (2008) and G. Cuenca Bescós (in Villa et al. 2010) described an assemblage dominated by *Microtus gregalis* (94% and ~80 %, respectively), with *Arvicola terrestris* present in much lower abundance. In terms of paleoenvironmental reconstruction, the northern water vole, *A. terrestris*, is known to inhabit waterside environments and thus represents locally moist conditions, and *M. gregalis* is a typical inhabitant of the cold steppe, living today in arctic areas (Sesé and Villa 2008).

Preliminary taphonomic results were provided in the above-cited studies, suggesting the contribution of hyenas in introducing the small mammals to the site. Villa et al. (2010) also suggested that nocturnal birds of prey were involved in the predation and deposition of small vertebrates in the cave. In this paper, we present a detailed taphonomic analysis of the small mammal fossil assemblage of Bois Roche in order to understand the action of predators and "any" natural forces involved in the deposition of the microfossil assemblage. Having identified the predator (or predators), it is then possible to consider how predation or other taphonomic bias might influence the reconstruction of past environments.

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Small mammal Taphonomy.—Bones and teeth of small mammals are regularly recovered from caves (Andrews 1990; Bramwell et al. 1990; Avery 1992; Fernández-Jalvo 1995) and open-air sites spanning wide geological and archaeological time periods (Buckland 1976; Mayhew 1977; Andrews 1983; Wesselman 1984; Maas 1985; Denys 1986; Dobney et al. 1996; Fernández-Jalvo et al. 1998; Murphey et al. 2001). At cave sites, the relative lack of active transportation and protection from aerial weathering processes combine to increase the possibility of deposited material being recovered during excavation. Caves also provide excellent locations for habitation and shelter for many birds and mammals (including humans), and over time, large deposits of dietary waste (and cultural material) can accumulate at these sites.

Taphonomic analysis of specific patterns of modification (such as breakage and digestion) of the small mammal bones and teeth from these sites can aid in the identification of the accumulation agent (e.g., Andrews 1990; Fernández-Jalvo and Andrews 2016). These patterns are compared with those from actualistic studies of pellets or coprolites of modern avian and mammalian predators. The purpose of conducting a taphonomic analysis of small mammal deposits is to investigate how the fossil community represents the community from which it was originally drawn. Small mammals are sensitive to climatic and environmental constraints and are therefore good proxy indicators of past environments. Taphonomic analysis of small mammal accumulations increases the potential information on climate and environment by: (1) identifying a predator and its habits, (2) recognizing possible biases due to hunting methods and prey preferences (Andrews 1990; Fernández-Jalvo et al. 1998), (3) detecting postdepositional hydrodynamic sorting and transport (Dodson and Wexlar 1979; Korth 1979), and (4) by taking into account bone breakage or mixtures due to reworking processes (Fernández-Jalvo et al. 2014).

Identifying Specific Predators.—One of the most valuable pieces of information provided by taphonomic analyses of microfauna is the detection and identification of predators as sources of a bone assemblage. Analysis of actualistic data from dietary waste from avian and mammalian predators of small mammals was carried out by Andrews (1990). Data were collected for breakage of long and cranial bones and digestion of molars, incisors, and some long-bone epiphyses. At a general level, Andrews showed that taphonomic differences exist among owls, diurnal raptors, and mammalian predators, and for the molar and incisor digestion data, it is possible to group specific species based on similarities in results. These groups and the respective levels of digestion are shown in Table 1. Statistical analysis of these data has been carried out, and it has been demonstrated that there is significantly more variation between these groups than within them (Williams 2003).

There are not many small mammal taphonomic analyses from scats of modern large carnivores (above 30 kg), with some notable exceptions (Gómez 2003; Montalvo et al. 2007). Gómez's (2003) work was based on an experimental study of pumas fed on rodents in a zoo, but the sample of rodents recovered from the scats was too small for the taphonomic methodology to be fully applied. Montalvo et al. (2007) collected 76 scats of pumas from the wild; they recovered enough small mammals to apply the methodology used in this paper (Andrews 1990). Montalvo et al. (2012) also studied 179 scats of Geoffroy's cat (*Leopardus geoffroyi*), but the taphonomic results are similar to those of other small mammalian carnivores such as wild cats (López et al. 2017), coyotes, and foxes (Andrews 1990), which are much more destructive than large carnivores.

The macrofaunal fossil bone assemblage at Bois Roche has been shown to have been accumulated by hyenas (Villa et al. 2004, 2010; Blain and Villa 2006). More specifically, it is suggested that the site functioned as a hyena maternity den (Marra et al. 2004; Sesé and Villa 2008). The interior of Bois Roche Cave should have been dry enough to allow the preservation of hundreds of complete or almost complete coprolites and their content. Among the bones, coprolites and fragments of coprolites have been recovered and plotted, although many were disintegrated into 1 cm or smaller pieces or can only be seen in

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TABLE 1. Summary of digestion category on molars (1st molar and in situ molars in jaws) and incisors (both isolated and preserved in jaws) of small-mammal prey (Fernández-Jalvo et al. [2016], modified from Andrews [1990] and Demirel et al. [2011]).

Predator category	Digestion category	1st molar digestion	In situ molar digestion	Incisor digestion	In situ incisor digestion
Category 1	Absent or minimal Molars <2% Incisors 5–13%	*Tyto alba*, *Asio flammeus*, *Asio otus*, *Bubo lacteus*	*Tyto alba*, *Asio flammeus*, *Asio otus*, *Bubo lacteus*	*Tyto alba*, *Asio flammeus*	*Tyto alba*, *Asio flammeus*
Category 2	Light digestion Molars 0–5% Incisors 10–30% (tips only)	*Nyctea scandiaca*	*Nyctea scandiaca*	*Asio otus*, *Nyctea scandiaca*	*Asio otus*, *Bubo lacteus*, *Nyctea scandiaca*
	Moderate digestion Molars 4–6% Incisors 20–30%	*Bubo africanus*, *Strix nebulosa*	*Bubo africanus*, *Strix nebulosa*	*Strix nebulosa*, *Bubo lacteus*	*Strix nebulosa*
Category 3	Heavy (low-level) digestion Molars 11–22% Incisors 50–70%	*Bubo bubo*	*Bubo bubo*, *Strix aluco*	*Strix aluco*, *Bubo africanus*, *Bubo bubo*, *Athene noctua*	*Bubo africanus*, *Bubo bubo*, *Strix aluco*, *Athene noctua*
Category 4	Heavy (high-level) digestion Molars 50–70% Incisors 60–80%	*Strix aluco*, *Athene noctua*, *Circus cyaneus*, *Falco tinnunculus*, *F. peregrinus*	*Athene noctua*, *Circus cyaneus*, *Falco tinnunculus*, *F. peregrinus*	*Falco tinnunculus*, *F. peregrinus*	*Falco tinnunculus*, *F. peregrinus*
Category 5	Extreme digestion Molars 50–100% Incisors 100%	*Buteo buteo*, *Milvus milvus*, mammalian carnivore	*Buteo buteo*, *Milvus milvus*, mammalian carnivore	*Buteo buteo*, *Circus cyaneus*, *Milvus milvus*, mammalian carnivore	*Buteo buteo*, *Circus cyaneus*, *Milvus milvus*, mammalian carnivore

micromorphological sections (Villa et al. 2004). One of the complete coprolites from Bois Roche is illustrated in Villa et al. (2010: Supplementary Fig. 5) and shows a microtine molar embedded within the coprolite.

It is unusual to find well-preserved coprolites or pellets of small mammal predators in the fossil record. Most degrade, and only the bones are left behind. Hyena coprolites survive at higher frequency than those of other mammalian predators (Horwitz and Goldberg 1989; Harrison 2011; Bennett et al. 2016) due to the high mineral (calcium phosphate) content after bone digestion. However, we have not found any record of fossil hyena coprolites containing small mammal bones so far, other than from Bois Roche.

Most zoologists studying the ethology of modern hyenas have not observed them feeding on, or even being interested in, small mammals (I. Wiesel personal communication 2010; K. E. Holekamp personal communication 2011), although hungry hyena cubs may hunt insects or any other appropriately sized animals (K. E. Holekamp personal communication 2011). Apart from some rare cases of rodent remains recorded in modern hyena scats in South Africa (G. Avery personal communication 2015), there is little published information on this topic. Korb (2000), an ecologist and entomologist who studied the hyenas (*C. crocuta*) of the Comoe National Park (CNP, Ivory Coast), mentions that "it was rare to observe hunts, because faecal analysis demonstrated that small mammals such as rodents account for more than 60% of hyena diet in CNP" (Korb 2000: p. 9). She described the rare solitary and shy behavior of these hyenas, which caused difficulties in applying standard methods used to locate and observe these populations. This solitary and shy behavior may account for the presence of rodents in their diet, which is absent in other communities (I. Wiesel personal communication 2010; K. E. Holekamp personal communication 2011). Unfortunately, the author did not report the number of scats analyzed, what taxa formed the other 40% nonrodent content (e.g., insects, worms, birds), or the procedure to calculate the percentage of each type of prey. No taphonomic analysis has been carried out on this modern reference collection yet. With the

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exception of the Ivory Coast hyenas, predation of microfauna by modern hyenas appears to be an irregular activity, which makes the high number of rodent individuals present in Bois Roche more outstanding.

Hyenas.—Hyenas have a wide diet range, and they are considered one of the most generalist carnivores in the African ecosystems (Mills and Hofer 1998). Hyenas have been studied extensively in terms of their feeding and social habits for ecological purposes (Kruuk 1972; Holekamp and Smale 1990; Mills 1990; Wiesel 2006; Holekamp 2007). Paleontological investigations have also been carried out to distinguish between the role of hyenas (especially in their maternity dens) and hominins as bone collectors in fossil sites (e.g., Brain 1969; Sutcliffe 1970; Haynes 1983; Hill 1984; Skinner et al. 1998; Villa et al. 2004, 2010; Pokines and Kerbis Peterhans 2007; Prendergast and Dominguez-Rodrigo 2008; Kuhn 2011).

The spotted hyena (*C. crocuta*) is the largest extant hyaenid, with a weight ranging between 45 and 85 kg. They are good hunters, versatile in their choice of prey (from large-sized [wildebeest and zebra] to small-sized [warthog and impala] mammals). They practice a diversity of hunting techniques and strategies (both solitary and in groups), usually hunting at night. Their roaming area varies greatly according to habitat and climatic region, from 28 to 80 km (Hofer 1998).

A close evolutionary relationship between Eurasian Pleistocene hyenas (*Crocuta crocuta spelaea*) and modern *Crocuta* has been established based on nuclear genes, while the limited genetic diversity in striped and brown hyenas indicates population bottlenecks in these species during the Pleistocene (Bon et al. 2012). An African origin during the Pleistocene has been established genetically, and dispersal to Eurasia of both spotted and striped hyenas must have been rapid during subsequent migration waves (Rohland et al. 2005). Some Plio-Pleistocene European fossil representatives (i.e., *Pliocrocuta*) have been proposed to be taxonomically conspecific with brown hyenas (Kurten 1968; Turner 1990; Turner and Anton 1996), although this is not a universally held view (Werdelin and Solounias 1991; Jenks and Werdelin 1998).

Hyenas mark their territory by leaving a secretion from the anal gland. Mills and Hofer (1998) record scat territory marking, like canids, with defecation at latrine sites. Chemical analysis by X-ray diffraction of hyena coprolites (Lewis 2011; Pesquero et al. 2011) and modern scats (Horwitz and Goldberg 1989; Larkin et al. 2000) yields a high abundance of hydroxylapatite, the mineral com ponent of bones, compared with organic content. The enrichment in calcite phosphates is the result of the large amount of bone cracked and ingested by hyenas. The high mineral content in fresh hyena scats produces a sticky coating on the brown scats, which becomes white and hardened a few hours after exposure to the sun in an open environment. The high calcite phosphate content in hyena coprolites thus favors their preservation and high abundance in fossil sites, both in caves and open-air sites. By comparison, herbivore coprolites are more friable and less common in the fossil record (Harrison 2011).

Materials and Methods

The taphonomic analysis reported here was undertaken on samples recovered in the 1995 season, referred to in Table 2. The material was received already sorted into cranial and postcranial elements. All of the sediment from the 1995 excavation had been sieved through 5 mm and 2 mm mesh screens. The smallest-sized mesh was decreased in size to 1.4 mm in the 1997 and subsequent field seasons. From the 1998 season's material, subsamples from the first 5 liters of sediment from each new 5 cm spit of each square were sieved through the 1.4 mm mesh. The remainder of the deposit was sieved through the 5 mm mesh and then a 2 mm mesh to ensure recovery of all coprolite fragments smaller than 5 mm. All mandibular first molars were removed for taxonomic analysis. The taphonomic analysis reported here was undertaken on the rest of the small mammal material. The taxonomic analysis of the 1995 season small mammal assemblages was carried out by Sesé and Villa (2008), and material recovered from 1997 to 2000 was analyzed by Cuenca Bescós (Villa et al. 2010).

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The Bois Roche site has two distinct areas, the so-called Vestibule (about 5 m^2), giving access to the cave from the entrance, and the Grande Salle, a larger chamber (9 × 4 m) in the caves's interior. The cave deposits slope away from the entrance toward the rear of the inner chamber (Villa et al. 2010). Samples come from two levels, unit 1, with at least three subunits (1a, 1b, and 1c), and a more massive unit 2. In this paper, we compare material from the two different areas of the cave and also from the two different stratigraphic units (Fig. 2).

Our taphonomic analysis followed the methodology set out by Andrews (1990) and Fernández-Jalvo and Andrews (1992). Twenty-five different samples containing both cranial and postcranial elements were analyzed from seven different squares of the two distinct areas (Vestibule and Grande Salle) (Table 2, Fig. 2). The samples were spatially distributed in different areas of the site and also from different depths within specific squares corresponding to the two stratigraphic units (11 samples from unit 1 and 14 from unit 2). Samples with large numbers of small mammals were preferentially selected to ensure that the information from the taphonomic analysis would be sufficiently reliable. In addition, a total of 135 coprolites from both units and areas were also studied. Eighty-three of these contained osseous remains (micromammal bones and small bone flakes of larger mammals) (see Table 3).

Cranial and postcranial material was analyzed using binocular light microscopes with variable magnification. Selected bones were also studied under an environmental scanning electron microscope (FEI-Quanta 200) hosted at the Museo Nacional de Ciencias Naturales (Madrid) using secondary and backscattered electron detectors.

A *G*-test of independence using R (R Core Team 2017) was applied to the results, with a significance level of 0.05. The tests compared anatomical representations (taking into consideration cranial vs. postcranial remains), bone breakage (considering broken vs. complete), and digestion (with digestion vs. without digestion).

This test compared unit 1 and unit 2 to investigate differences between the two time periods. The Grande Salle and Vestibule areas were compared separately, as was a single sample named "total" (which was the sum of data from either the Vestibule and Grande Salle or units 1 and 2). The total sample results were also compared with results obtained from the coprolites.

Results

Abundance, Completeness, and Distribution.—The taphonomically studied samples of small mammal anatomical elements from the 1995 excavations are displayed in Table 4. Samples having high abundance of both cranial and postcranial elements were primarily chosen for this study. Figure 2 shows the squares from which samples were selected. Unit 2 has a higher fossil content than unit 1, and the Vestibule is richer than the Grande Salle (Table 2). Figure 2 also shows the squares from which coprolites studied here were recovered. The coprolites come from the 1995, 1998, 1999, and 2000 excavation seasons, as shown in Table 3.

The completeness of the small mammal samples (and thus the anatomical representation, see following section) is difficult to assess, because there have been a number of taphonomic biases acting on this material. First, all elements that can pass through a 2 mm sieve may be underrepresented. For the postcranial material, the major limb bones are recorded, although small items such as ribs and bones of the extremities would not have been retained by the 2 mm sieve (Williams 1997). The most common limb bones are the femur and the humerus. Small and fragile bones such as the radius, scapula, and pelvis are particularly underrepresented, as are distal portions of the ulna, which as a narrow bone is likely to have been lost through sieving.

Anatomical Representation.—The mandibular first molars (2592 in total) had been removed for taxonomic analysis and were not physically available at the time when the taphonomic analysis took place. Thus, evidence of digestion on the M1 teeth could not be studied, but the database of excavated M1 teeth was provided by C. Sesé and the number of M1s was included in the analysis of skeletal element abundance (Table 4).

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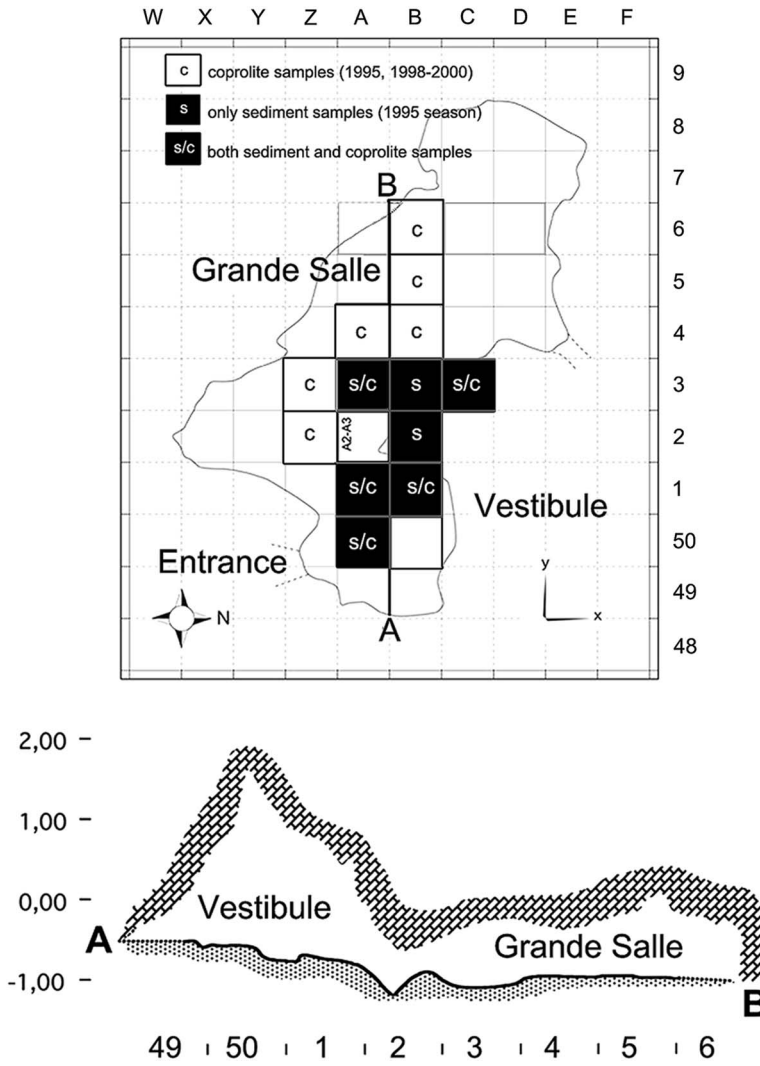

FIGURE 2. Bois Roche map. Top, map of the excavation. Letters at the top and numbers on the right correspond to the grid system used to label squares. The black squares refer to sediment (s) sieved during the 1995 season that contained sufficient cranial and postcranial small mammal skeletal elements to undertake the taphonomic analysis (25 samples). The white squares refer to squares that yielded coprolites (c); five of the black squares also yielded coprolites (s/c), making a total of 135 coprolites studied in this paper. Bottom, profile of the cave along the line A–B; numbers at the bottom refer to the square labels. The cross section indicates the Vestibule and the Grande Salle areas distinguished during excavations and described in this paper.

Around 30,000 skeletal elements (minimum number of elements [MNE]) were available for taphonomic analysis. No postcranial material was available from samples labeled as B2/1c, 96–106, and A50/1c, 91–96, in Table 2. There are lower numbers of calcanei, astragali, ribs, metapodials, and phalanges observed in all samples relative to the MNI calculated on the number of the most common element (incisors). Larger skeletal elements, such as pelvises, scapulae, radii, or vertebrae also have a reduced relative abundance (Table 4). The most abundant postcranial elements are usually femurs and humeri, with a lower MNE of tibiae and ulnae.

Indices.—The postcranial/cranial indices, isolated teeth, and incisor and molar loss are shown in Table 5. Postcranial/cranial indices are usually below 100% when isolated teeth are included (pc/c) and slightly above

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TABLE 2. Samples from the Bois Roche 1995 season taphonomically analyzed. The labels indicate the square (letter and number), followed by the stratigraphic unit (unit 1a, 1b, 1c, or 2), and then the depth range. MNE, minimum number of elements.

Grande Salle (12)	MNE Grande Salle	Vestibule (13)	MNE Vestibule
B2 1c 96-106	325	A50 1c 91-96	1038
A3 2 145-150	449	A50 1c 96-98	957
A3 2 150-155	582	A50 1c 105-110	2223
A3 2 155-160	406	A50 2 95-100	757
A3 1b 111-116	225	A50 2 98-103	4420
A3 1c 126-131	417	A50 2 100-105	813
A31c 131-136	157	A50 2 103-108	3042
B3 1a 124-132	67	A1 2 115-120	581
C3 2 150-155	103	B1 2 90-96	776
C3 1a 109-116	140	B1 2 95-102	779
C3 1a 116-120	395	B1 2 102-107	1994
C3 1c 120-124	158	B1 2 107-110	3448
		B1 2 110-115	5553
Total Grande Salle	3,424	Total Vestibule	26,381

100% when isolated molars are not included (e.g., see the femur + humerus/mandible + maxilla index in Table 5). Femurs and humeri are always more common than distal long bones (tibiae and radii). The index of isolated molars (which indicates jaw destruction when values are above 100%) yielded 113%. This would indicate that mandibles and maxillae are not highly destroyed. However, the isolated incisor indices reach values around 241%, indicating there are more incisors present in the sample than jaws from which they have been lost. In situ teeth are rare, as is also indicated by high tooth-loss indices (rate of empty alveoli), mostly above 90%, sometimes 100%. The most commonly retained tooth is the mandibular incisor, which is retained in about half of the mandibles recovered. The value of this index, together with the difference between indices of isolated molars (below 100%) and incisors (well above 100%) suggests a relatively high loss of molars during sieving.

Breakage.—Cranial breakage is high (Table 6), with almost no intact skulls found. Very few skull fragments have a zygomatic process still attached. Mandible breakage is also high, and almost all samples contain more than 60% frequency of breakage of the inferior border. Teeth are broken but most of this breakage appears to have occurred after deposition, as teeth that are broken and then digested are found in lower frequency to the total proportion of digested teeth; less than 20% of broken incisors have evidence of digestion, and less than 7% of broken molars had been digested (Table 7). Fragments of mandibles and maxillae are present in all samples, with many empty molar alveoli (above 90% in almost all samples). The number of incisors removed from jaws is more variable, with values between 55% in mandibles and around 90% in maxillae.

Breakage of limb bones is relatively low, with several long-bone categories containing more than 20% complete bones. The most commonly recorded elements are distal humerus, proximal ulna, and proximal femur. Tibia breakage appears to be more random, with variable recovery of both proximal and distal ends. Breakage in radii is the most variable across the different parts and depths of the cave (Table 6).

Digestion.—Digestion was analyzed for molars, incisors, distal humeri, and proximal femurs. The frequency of digestion for incisors corresponds to around 75% (Table 7), most frequently affecting the tip of the incisor. The low values of breakage before digestion indicate that small mammal individuals were not heavily broken during ingestion and were most probably swallowed complete. Molar digestion is similar between samples, around 45%, as can be seen in Table 7, exhibiting low breakage before digestion. Both incisors and molars, in situ or isolated, are lightly digested in general, followed at a lower percentage with moderate degrees of digestion, while heavy

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TABLE 3. Coprolites from Bois Roche containing osseous material: LM, large-mammal fossils; SM, small-mammal fossils. A total of 135 individual coprolites were analyzed, 39% of which had no fossil bone in the interior. Large mammal fossil fragments were present in 83 coprolites; almost 60% of these coprolites (57%) contained rodent remains, and almost half had no traces of digestion.

Year	Square	*n*	Level	Coprolites with bone	Coprolites with small mammals	Coprolites + digested small mammal	Remarks on digestion and coprolite contents
1995 (98 coprolites)	A1	20	2	14	9	6	LM, heavily digested; SM, from undigested to heavily digested and frequent digested broken edges; 1 containing charcoal fragments; 2 containing vegetation
			1	1	1		LM, heavily digested; SM, non-digested
	A3	2	1c	No content			
	A50	2	2	1			LM, heavily digested;
	B1	70	2	41	21	13	LM, heavy to extreme digestion; SM, from non-digested to heavily digested, and in 6 coprolites postcranial broken edges are digested; 3 coprolites containing digested and rounded charcoal fragments; 2 containing vegetation fibers
	B5	2	2	1			LM, heavily digested
	B50	1	2	1			LM, heavily digested
	C3	1	1a	No content			
1998 (12 coprolites)	A4	2	1c	No content			
	B1	4	2	3	3	1	LM, heavily digested; SM, light to moderate digestion; vegetation fibers
	B50	4	2	3	3	1	LM, heavily digested; vegetation fibers
	Z2	1	1a/1b	No content			
	Z3	1	1c/1a	1	1		LM, digested
1999 (18 coprolites)	A1	1	2	1			LM, heavily digested
	B5	11	2	9	6	3	LM, heavily digested; SM, from undigested to light to moderate digestion, and in 2 coprolites post-cranial broken edges are heavily digested; vegetation fibers
			1d	1			LM, heavily digested
	B50	1	2	No content			
	B6	1	2	1	1		LM, heavily digested; rounded charcoal fragments and vegetation fibers
	Z3	4	1b	1			LM, heavily digested
			1c	No content			
2000 (7 coprolites)	B4	1	2	No content			
	B5	4	2	3	1		LM, heavily digested
	Z3	2	1c	1	1		LM, heavily digested
Totals		135		83 (61%)	47 (57%)	24(51%)	

and extreme degrees are rare, although present in most samples.

Postcranial digestion affects about 25% of proximal femurs and 30% of distal humeri (Table 8). The higher figures reaching 40% in unit 1 and Grande Salle are likely to be a product of small sample size. Digestion ranges from a mild pitting of the epiphyses to total digestion of these areas and loss of bone. Digestion is also observed on the proximal ulna, in some cases resulting in significant loss of bone.

Coprolites.—Coprolites were treated separately, as they have a reduced fossil

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TABLE 4. Survival rates of anatomical elements represented in the samples of Bois Roche. The "Total" column is the sum of data from either unit 1 and unit 2 or the Vestibule and the Grande Salle areas. Note that the "Molar" row includes the M1 teeth from the sieved samples recovered from the sediment (i.e., all samples except coprolites), which were removed for taxonomic analysis before this taphonomic study started).

Anatomical representation	Vestibule		Grande Salle		Unit 2		Unit 1		Total		Coprolites	
Maxilla	1221	54%	201	59%	1124	56%	298	48%	1422	54%	4	33%
Mandible	1371	60%	201	59%	1146	58%	426	69%	1572	60%	4	33%
Incisor	4545	100%	677	100%	3983	100%	1239	100%	5222	100%	21	88%
Molar	8525	63%	1264	62%	7682	64%	2107	57%	9789	62%	24	33%
Scapula	512	23%	46	14%	457	23%	101	16%	558	21%	5	42%
Humerus	1789	79%	220	65%	1675	84%	334	54%	2009	77%	11	92%
Radius	266	12%	29	9%	268	13%	54	9%	322	12%	3	25%
Ulna	796	35%	110	32%	774	39%	132	21%	906	35%	5	42%
Pelvis	1001	44%	82	24%	934	47%	149	24%	1083	41%	5	42%
Femur	2036	90%	176	52%	1895	95%	317	51%	2212	85%	8	67%
Tibia	1062	47%	94	28%	963	48%	193	31%	1156	44%	5	42%
Vertebra	2419	6%	267	4%	2129	6%	557	5%	2686	6%	40	19%
Calcaneus	98	4%	14	4%	72	4%	40	6%	112	4%	4	33%
Astragalus	13	1%	4	1%	11	1%	6	1%	17	1%	2	17%
Rib	74	0%	7	0%	60	0%	21	0%	81	0%	31	22%
Metapodial	599	3%	24	1%	504	3%	119	2%	623	2%	34	28%
Phalange	28	0%	7	0%	26	0%	9	0%	35	0%	38	11%
MNE	26,381		3424		23,703		6102		29,805		244	
MNI	1136		170		996		310		1306		6	

TABLE 5. Postcranial/cranial indices, isolated teeth (including the M1 removed for taxonomic studies) and incisor and molar loss from the mandible and maxilla.

Indices (Andrews 1990)	Vestibule	Grande Salle	Unit 2	Unit 1	Total	Coprolites
Postcranial/cranial	86%	61%	90%	58%	83%	160%
Femur + humerus/mandible + maxilla	148%	99%	157%	90%	141%	238%
Tibia + radius/femur + humerus	35%	31%	34%	38%	35%	42%
Isolated incisors (destruction of jaws)	246%	212%	245%	229%	241%	350%
Isolated molars (destruction of jaws)	114%	107%	117%	99%	113%	120%
Jaw incisor loss	71%	80%	72%	75%	72%	75%
Jaw molar loss	96%	98%	96%	98%	96%	79%

content and because they are a reference for the traits of predation that should be diagnostic of hyena predation. In total, 135 coprolites were studied, 83 of which contained bones. Charcoal and plant remains are also present in a number of coprolites. About 57% of the 83 coprolites contain small mammal bones, also with evidence of digestion (Table 3).

Breakage is high, although femurs and humeri include complete elements (Table 6), as observed in samples recovered from the sediment.

Digestion of teeth is frequently light (Table 7), but moderate and heavy digestion is also recorded. Twenty-three coprolites contain small mammal bones showing no signs of digestion. The low number of microfaunal skeletal elements recovered from the coprolites ($n = 244$; Tables 4–7) does affect the resulting percentages of breakage, postcranial versus cranial indices, relative abundance of skeletal elements, and especially the digestion of distal humeri (Table 8). Nonetheless, digestion of femurs and teeth from coprolites seems to show similar digestion traits and percentages compared with samples obtained from the sediment.

Statistical Treatment.—The *p*-values obtained for each of the variables analyzed are shown in Table 9. Anatomical elements and breakage show differences between Grande Salle and Vestibule and for units 1 and 2. Nonetheless, for digestion of molars and incisors, a comparison of both stratigraphic units shows a *p*-value higher than 0.05, which indicates that there are no differences with respect to the total percentage of digested remains. In addition, if

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TABLE 6. Breakage in cranial and postcranial elements. Note totals of femur, tibia, and humerus are here the number of identified specimens (NISP), while Table 4 provides the minimum number of elements (MNE) of these anatomical elements.

Breakage	Vestibule		Grande Salle		Unit 2		Unit 1		Total		Coprolites	
Total skulls	1221		201		1124		298		1422		4	
Complete	1	0%	0	0%	1	0%	0	0%	1	0%	0	0%
Maxilla with zygomatic process intact	20	2%	11	5%	21	2%	10	3%	31	2%	0	0%
Maxilla missing zygomatic process	896	73%	168	84%	932	83%	132	44%	1064	75%	2	50%
Palates	68	6%	0	0%	33	3%	35	12%	68	5%	2	50%
Molar alveoli empty	3444	94%	580	96%	3172	94%	852	95%	4024	94%	8	67%
Incisor alveoli empty	1106	91%	189	94%	1010	90%	285	96%	1295	91%	2	50%
Total mandible	1371		201		1146		426		1572		4	
Complete	2	0%	0	0%	2	0%	0	0%	2	0%	0	0%
Ascending ramus broken	277	20%	34	17%	181	16%	130	31%	311	20%	4	100%
Inferior process broken	829	60%	122	61%	840	73%	111	26%	951	60%	4	100%
Molar alveoli empty	4041	98%	601	100%	3368	98%	1274	100%	4642	98%	12	100%
Incisor alveoli empty	742	54%	131	65%	618	54%	255	60%	873	56%	4	100%
Total (NISP) femur	2934		205		2733		406		3139		13	
Complete	650	22%	41	20%	578	21%	113	28%	691	22%	2	15%
Proximal	1386	47%	134	65%	1317	48%	203	50%	1520	48%	6	46%
Distal	463	16%	19	9%	421	15%	61	15%	482	15%	4	31%
Shaft	435	15%	11	5%	417	15%	29	7%	446	14%	1	8%
Total (NISP) tibia	1933		154		1771		316		2087		12	
Complete	188	10%	30	19%	167	9%	51	16%	218	10%	0	0%
Proximal	847	44%	47	31%	779	44%	115	36%	894	43%	4	33%
Distal	599	31%	50	32%	546	31%	103	33%	649	31%	5	42%
Shaft	299	15%	27	18%	279	16%	47	15%	326	16%	3	25%
Total (NISP) humerus	2726		282		2567		441		3008		13	
Complete	855	31%	90	32%	767	30%	178	40%	945	31%	1	8%
Proximal	548	20%	49	17%	523	20%	74	17%	597	20%	10	77%
Distal	1155	42%	123	44%	1108	43%	170	39%	1278	42%	2	15%
Shaft	168	6%	20	7%	169	7%	19	4%	188	6%	0	0%
Total ulna	796		100		764		132		896		5	
Complete	182	23%	27	27%	165	22%	44	33%	209	23%	0	0%
Proximal	614	77%	73	73%	599	78%	88	67%	687	77%	5	100%
Total radius	266		29		241		54		295		3	
Complete	116	44%	16	55%	105	43%	27	50%	132	45%	0	0%
Proximal	150	56%	13	45%	136	57%	27	50%	163	55%	3	100%

we compare the distribution of the degrees of digestion in both units, no differences are observed either in molars ($p = 0.09455$) or in incisors ($p = 0.4053$).

Statistical results obtained when comparing taphonomic variables of fossil assemblages present in the coprolites and those from the total sample (the sum of the two stratigraphic units: unit 1 and unit 2) show values above $p = 0.05$. The p-values obtained for each variable show that there are no significant differences between total and coprolites for the percentage of digested dental remains (Table 10).

Postdepositional Modifications.—In addition to predepositional bone modification related to predator action, a number of postdepositional impacts on the bones can be recognized. These include puncture marks, which are most frequent on flakes of large mammal bones, and breakage (most likely as a result of trampling). One further peculiar phenomenon seen in these samples is the presence on some molars of tubular formations, composed mainly of calcite. These may be root casts, although there is no evidence of root marking on bones or teeth. No manganese or any other postdepositional mineral staining is observed.

Discussion

The small mammal assemblage from Bois Roche is characterized by an extremely high abundance of individuals that were relatively poor in species richness. Most small mammals were identified to the genera *Microtus* and *Arvicola* (Sesé and Villa 2008; Villa et al. 2010). The lack of prey diversity is one

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TABLE 7. Digestion in cranial elements. Note that these figures do not include the M1 teeth removed for taxonomic analysis, except in the "Coprolites" column.

Digestion	Vestibule		Grande Salle		Unit 2		Unit 1		Total		Coprolites	
In situ mandibular incisors	629		70		528		171		699		0	
Light	426	68%	33	47%	340	64%	119	70%	459	66%		
Moderate	47	7%	2	3%	38	7%	11	6%	49	7%		
Heavy	1	0%	0	0%	1	0%	0	0%	1	0%		
Extreme	0	0%	0	0%	0	0%	0	0%	0	0%		
Broken and digested	43	7%	0	0%	21	4%	22	13%	43	6%		
Digested mandibular incisors	474	75%	35	50%	379	72%	130	76%	509	73%		
In situ maxillary incisors	115		12		114		13		127		2	
Light	86	75%	5	42%	85	75%	6	46%	91	72%	2	100%
Moderate	3	3%	0	0%	3	3%	0	0%	3	2%	0	0%
Heavy	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%
Extreme	1	1%	0	0%	1	1%	0	0%	1	1%	0	0%
Broken and digested	19	17%	0	0%	17	15%	2	15%	19	15%	0	0%
Digested maxillary incisors	90	78%	5	42%	89	78%	6	46%	95	75%	2	100%
Isolated incisors	4545		677		3983		1239		5222		21	
Light	2589	57%	312	46%	2228	56%	673	54%	2901	56%	10	48%
Moderate	611	13%	58	9%	492	12%	177	14%	669	13%	7	33%
Heavy	220	5%	19	3%	176	4%	63	5%	239	5%	1	5%
Extreme	99	2%	19	3%	97	2%	21	2%	118	2%	0	0%
Broken and digested	138	3%	6	1%	90	2%	54	4%	144	3%	8	38%
Digested isolated incisors	3519	77%	408	60%	2993	75%	934	75%	3927	75%	18	86%
In situ mandibular molars	72		3		70		5		75		0	
Light	36	50%	2	67%	35	50%	3	60%	38	51%		
Moderate	2	3%	0	0%	1	1%	1	20%	2	3%		
Heavy	0	0%	0	0%	0	0%	0	0%	0	0%		
Extreme	0	0%	0	0%	0	0%	0	0%	0	0%		
Broken and digested	3	4%	0	0%	2	3%	1	20%	3	4%		
Digested mandibular molars	38	53%	2	67%	36	51%	4	80%	40	53%		
In situ maxillary molars	219		23		200		42		242		5	
Light	91	42%	13	57%	79	40%	25	60%	104	43%	1	20%
Moderate	6	3%	0	0%	5	3%	1	2%	6	2%	1	20%
Heavy	1	0%	0	0%	0	0%	1	2%	1	0%	0	0%
Extreme	0	0%	0	0%	0	0%	0	0%	0	0%	0	0%
Broken and digested	14	6%	0	0%	6	3%	8	19%	14	6%	0	0%
Digested maxillary molars	98	45%	13	57%	84	42%	27	64%	111	46%	2	40%
Isolated molars	5616		1264		5266		1614		6880		24	
Light	2139	38%	321	25%	1899	36%	561	35%	2460	36%	7	29%
Moderate	304	5%	40	3%	257	5%	87	5%	344	5%	2	8%
Heavy	98	2%	20	2%	91	2%	27	2%	118	2%	1	4%
Extreme	68	1%	5	0%	69	1%	4	0%	73	1%	0	0%
Broken and digested	100	2%	9	1%	63	1%	46	3%	109	2%	1	4%
Digested isolated molars	2609	46%	386	31%	2316	44%	679	42%	2995	44%	10	42%

TABLE 8. Summary of digestion rates. Note that these figures do not include the M1 teeth removed for taxonomic analysis, except in the "Coprolites" column. The number of distal elements of the humerus and proximal end of femurs are given in Table 6 by the complete and distal/proximal end of the humerus/femur (NISP).

	Vestibule		Grande Salle		Unit 2		Unit 1		Total		Coprolites	
% Incisors digested in situ	564	76%	40	49%	468	73%	136	74%	604	73%	2	100%
% Isolated incisors digested	3519	77%	408	60%	2993	75%	934	75%	3927	75%	18	86%
% Total incisors digested	4083	77%	448	59%	3461	75%	1070	75%	4531	75%	20	87%
% Molars digested in situ	136	47%	15	58%	120	44%	31	66%	151	48%	2	40%
% Isolated molars digested	2609	46%	386	31%	2316	44%	679	42%	2995	44%	10	42%
%Total molars digested	2745	46%	401	31%	2436	44%	710	43%	3146	44%	12	41%
% Femur head digested	461	24%	62	35%	445	23%	78	40%	523	25%	2	25%
% Humerus distal end digested	551	29%	76	36%	542	29%	85	37%	627	30%	2	67%

indication that an assemblage has been accumulated by a specialist predator that has adapted a prey acquisition strategy specific to a particular prey species (discussed in Andrews 1990). The large mammal fauna and the presence of numerous coprolites indicate

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TABLE 9. The *p*-values obtained for each of the variables analyzed in relation to the cave areas and the stratigraphic units studied. Numbers shown in bold are those *p*-values that are not significant and therefore indicate similarities. df = 1.

Variable	Comparison	*G*-value	*p*-value
Anatomical representation	Grande Salle vs. Vestibule	247.84	<2.2e-16
	Unit 2 vs. unit 1	170.39	<2.2e-16
Breakage	Grande Salle vs. Vestibule	52.303	4.757e-13
	Unit 2 vs. unit 1	44.871	2.105e-11
Molar digestion	Grande Salle vs. Vestibule	104.64	<2.2e-16
	Unit 2 vs. unit 1	0.8222	**0.3645**
Incisor digestion	Grande Salle vs. Vestibule	106.59	<2.2e-16
	Unit 2 vs. unit 1	0.075522	**0.7835**

TABLE 10. The *p*-values obtained for each of the variables analyzed in relation to coprolites and total. Numbers shown in bold are the *p*-values that do not indicate differences between the samples. df = 1.

Variable	*G*-value	*p*-value
Anatomical representation	119.49	<2.2e-16
Breakage	9.7364	0.001807
Molar digestion	0.26702	**0.6053**
Incisor digestion	2.0309	**0.1541**

that the cave was a hyena maternity den, as shown in previous taphonomic studies of the large mammal remains by Villa and d'Errico (d'Errico and Villa 1997; Villa and d'Errico 2001). Other Pleistocene sites may have a predominance of a single rodent species or genus, but these usually fall within the range of 45% to 70% of the assemblage. The hyperabundance of a single species seen in Bois Roche (*Microtus gregalis* 80–94%) is unusual. Given that hyena predation of large mammals is usually characterized as being opportunistic , it seems somewhat contradictory that hyenas should become specialized predators of rodents. The overrepresentation of *Microtus*, most especially, *Microtus gregalis*, was therefore most likely caused by periodic population outbreaks among this prey species.

There are no taphonomically analyzed modern hyena scat samples containing rodents currently available for comparison with the Bois Roche fauna. Many of the 135 hyena coprolites from Bois Roche contained bone remains (64%), and almost 60% of the bone content recovered from the coprolites corresponds to rodents. As 52% of the small mammal remains display evidence of having been digested, it is clear that hyenas consumed rodents. The 86 coprolites containing bone always yielded heavily digested large mammal bone flakes, but the small mammal teeth and bones in these same coprolites exhibited a variable degree of digestion, from none to heavily digested specimens (see Fig. 3). The apparent discrepancy between the high levels of digestion seen on bone flakes of large mammals in the coprolites and the lower degree of digestion of small mammal remains in the same coprolite (Fig. 3) may be due to the presence of the soft tissue and fur covering of the small mammals when they were ingested (which helps to protect the bones from the corrosive gastric juices), whereas the larger bone flakes most likely resulted from gnawing and breaking larger (mainly defleshed) bones, which then entered the digestive system without additional protection. It is not surprising, therefore, that the most-exposed skeletal element, the incisor, is also the most frequently digested. The pattern obtained in Bois Roche suggests that rodents were barely chewed (i.e., swallowed whole) and were digested complete. A similar trait has been observed in modern puma scats described by Montalvo et al. (2007); in part, this reflects the large difference in relative size between the prey and its predator (Mondini 2000).

The distribution of digestion of small mammal molars is consistent for both stratigraphic units (unit 1 and unit 2) in the Grande Salle and Vestibule and for all samples (Fig. 4, Tables 7 and 8). All individual samples have a high abundance of non-digested incisors and molars, with most molars showing light digestion. Variation from this pattern only occurs in samples with a low frequency of bones, where small changes can produce large percentage differences. Moderate digestion was seen in

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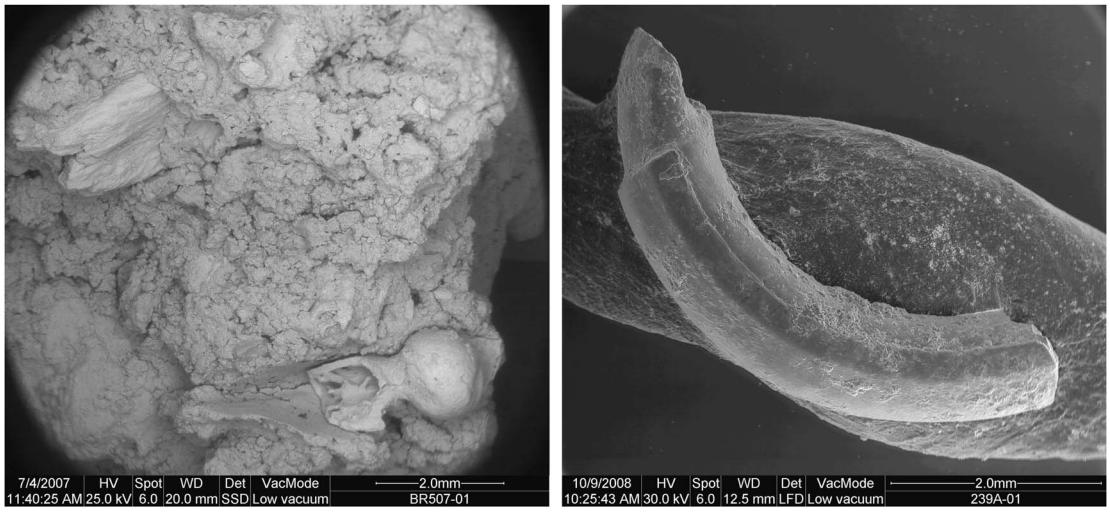

FIGURE 3. Left, Scanning electron microscope of a Bois Roche coprolite, with nondigested proximal end of femur (bottom right) of a small mammal (unfortunately, the shaft was broken during sample preparation) next to a heavily digested large mammal bone flake (top left). Right, small mammal incisor from a coprolite showing digestion concentrated on the tip, frequent in the Bois Roche fossil assemblage.

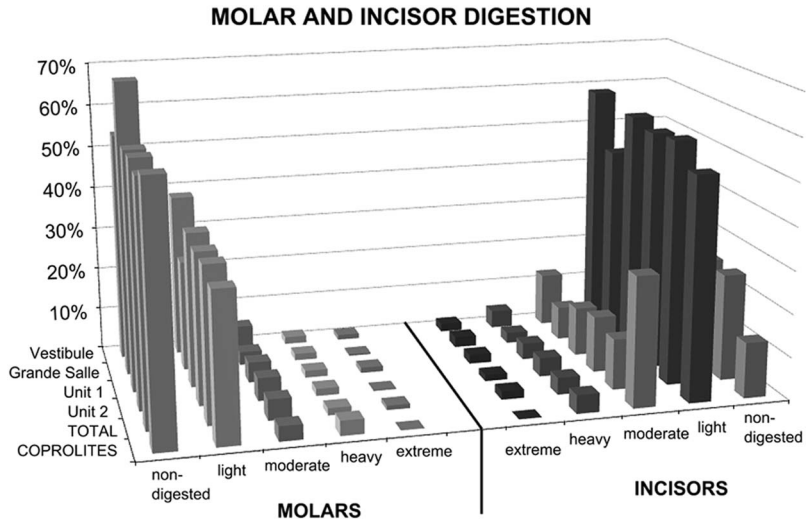

FIGURE 4. Molar and incisor digestion according to the excavation area (Vestibule, Grande Salle) and the stratigraphic level (unit 1, unit 2). "TOTAL" refers to all samples combined, i.e., either stratigraphic units (unit 1 and unit 2) or excavation areas (Vestibule and Grande Salle). Digestion grades from teeth (6048 incisors and 7197 molars) recovered from sediment samples are compared with dental remains (23 incisors and 29 molars) recovered from the interior of 135 individual coprolites. Most digestion is light. See Tables 7 and 8 for digestion levels for individual samples.

about 3% of molars, heavy digestion in 2%, and extreme digestion in 1%, again with large differences seen only in small samples.

Most digested incisors are lightly digested (56–72%). Moderate to heavy digestion is present on incisors, both isolated incisors and those retained in the jaws. There is a high abundance of incisors digested at the tip, indicating they were still in their alveoli when digested. The low rate of broken edges on the teeth affected by digestion also suggests a low rate of breakage during ingestion, further confirming the probability that these animals were ingested complete. Montalvo et al. (2007) described a much lower degree of breakage than referred to by Andrews (1990) for small- to

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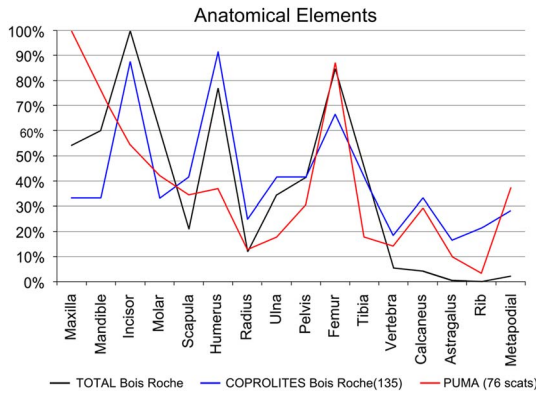

FIGURE 5. Relative abundances of anatomical elements recovered from the sediment (TOTAL Bois Roche). "COPROLITES Bois Roche" refers to small mammal anatomical elements recovered from the 135 individual coprolites compared with the relative abundance obtained from 76 "PUMA" scats (*Puma concolor*, according to Montalvo et al. 2007).

medium-sized carnivores and have proposed that this is a characteristic taphonomic pattern for large-sized mammalian carnivores such as pumas consuming small prey items.

With regard to the anatomical elements recorded (Fig. 5), the Bois Roche assemblage shows a fairly equal representation of post-cranial and cranial elements (pc/c). There is also a good representation of mandibles and maxillae compared with the main long bones (femurs and humeri). Both of these indices add further to the suggestion that prey were swallowed whole. Femurs, humeri, tibiae, radii, and ulnae appear complete (10% to ~30%). However, damage to the skull and lower jaws is evident in the high indices of incisor and molar tooth loss (with the notable exception of mandibular incisors, of which 50% are still preserved in their mandibular alveoli). On that basis, the high frequency of isolated teeth and thus relative absence of jaws cannot be entirely explained by destruction by chewing during ingestion and digestion of the prey, as this occurred when the prey was still largely intact.

In general terms, the digestion pattern observed in the coprolites, that is, abundance of light digestion grades both in molars and incisors and a high number of non-digested molars (Fig. 4), is similar to that observed for the small mammal assemblages obtained from the sediment in both units (in the coprolite sample, molar digestion is 41% and incisor digestion is 87%; in the total sample, molar digestion is 44% and incisor digestion is 75%) The coprolite sample size is small compared with the rest of the samples recovered from the sediment, and this size difference may yield percentages different from those observed in sediment samples. Statistical analysis of tooth digestion indicates similarities between unit 1 and unit 2 (Table 9) and between coprolite and total (Table 10). The Vestibule and unit 2 are very similar, because almost all samples of this area are from unit 2. The Grande Salle sample, however, contains both unit 1 and unit 2 (Table 2) and has the lowest fossil content among samples recovered from the sediment (Table 4). This may be the cause of the significant differences observed between the Grande Salle and the rest of the samples (Fig. 6). With respect to fragmentation and anatomical representation, the differences may depend not only on predation, but also on different processes linked to postdepositional factors. Nonetheless, the fact that units 1 and 2 are statistically similar, as are the coprolite and the total samples (Tables 9, 10), does suggest that a single predator was involved in the predation and accumulation of rodents in Bois Roche during the time period covered by units 1 and 2. We have not been able to identify any other predator that might have contributed prey remains to the microfauna accumulations at Bois Roche through our taphonomic analysis of the bones and teeth and statistical treatment of the results.

Given that the cave was repeatedly used as a hyena maternity den, the most parsimonious hypothesis is that hyenas were the only predator that produced this almost monospecific small mammal assemblage. As hyenas, in common with most mammalian predators, are opportunistic hunters, we can conclude that *Microtus gregalis* was periodically abundant due to population outbreaks or behaved in a manner that made it particularly susceptible to hyena predation.

Hyena movement into, out of, and around the cave caused the coprolites to disintegrate, although some coprolites were deposited in parts of the cave where they were protected

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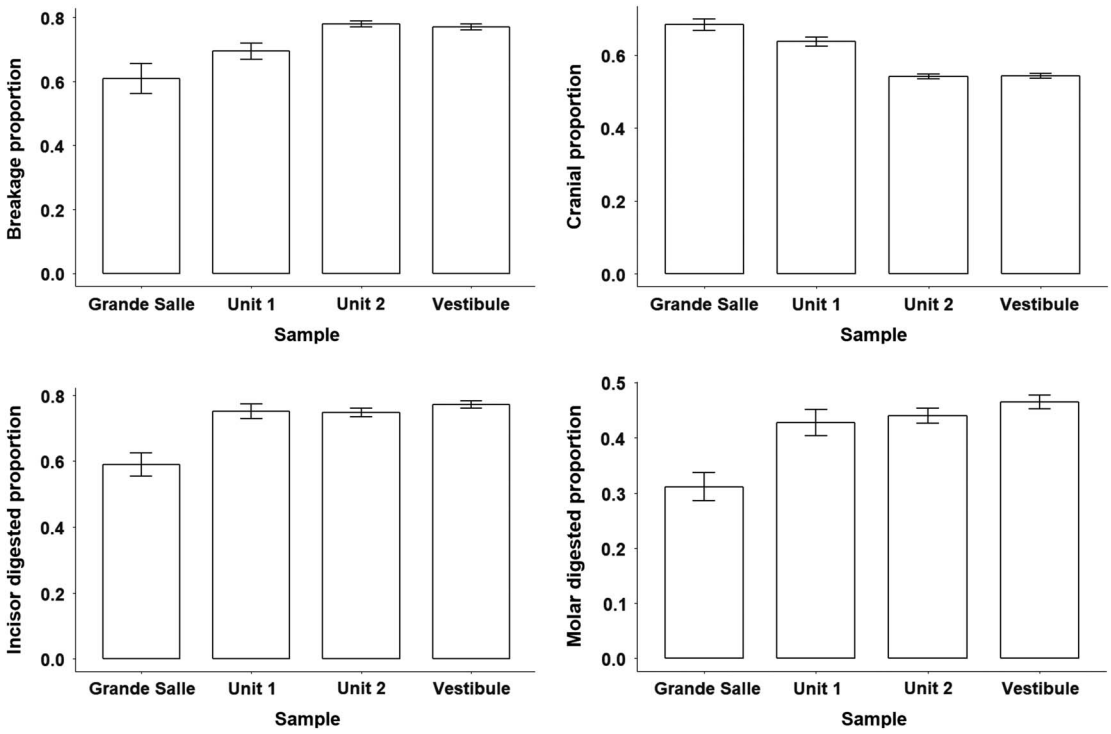

FIGURE 6. Bar charts and error bars of breakage, cranial remains, and incisor and molar digestion obtained from Grande Salle, Vestibule, unit 1, and unit 2.

from trampling, hardening over time and surviving whole. The low frequency survival of some skeletal elements (e.g., vertebrae, ribs, metapodials, phalanges) is probably due to loss during sieving (2 mm mesh) and subsequent human bias in selection of bone material for analysis.

Conclusions

An exceptional abundance of microfauna was found at Bois Roche in association with large mammal faunas bearing clear indication of hyena breakage, chewing, and digestion. This type of damage on large mammals suggests that these bones were deposited at Bois Roche within a maternity hyena den. In this context, our working hypothesis is that the rodents also had entered the assemblage through hyena predation.

Although many coprolites disaggregated during recovery, some were complete and compact and had avoided obvious damage by trampling. It is also interesting to note the overall low number of small mammal bones in each coprolite analyzed, suggesting that survival of complete coprolites was a fairly rare occurrence, since a substantial number would have had to disaggregate to produce the quantities of small mammals recorded.

The absence of taphonomic studies of modern hyenas feeding on small mammals makes the taphonomic pattern of small mammals from Bois Roche a useful source of reference for other researchers studying hyena predation of fossil micromammals. The general pattern of postcranial versus cranial elements and the relatively high percentage of complete long bones indicates that small mammals were ingested complete. This pattern of swallowing prey whole without chewing has also been observed in modern large predators feeding upon rodents, such as pumas. The fact that the bones and teeth survived within the aggressive digestive tract of hyenas is probably due to protection provided by indigestible elements such as hair, skin, hoofs, and other bone fragments of large and small mammals already within the stomach. Nevertheless, the frequency

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of digestion of teeth is high (75% incisors, 44% molars), but with light degrees of digestion and long-bone epiphyses also affected by digestion.

The presence of small mammal bones within hyena coprolites indicates beyond doubt that the hyenas were feeding on small mammals. A consistent pattern emerges in which some micromammal bones show no signs of digestion or were lightly digested while others were very heavily digested. Statistical similarities between unit 1 and unit 2 and between the coprolite and the total samples analyzed suggest that only one predator was involved in the fossil assemblage of Bois Roche, and this predator was hyena. The presence of a second predator bringing rodent remains to Bois Roche has been discarded.

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Literature Cited

Andrews, P. 1983. Small mammal diversity at Olduvai Gorge. Pp. 77–85 *in* J. C. Brook and C. Grigson, eds. Animals and archaeology, Vol. 1. Hunters and their prey. British Archaeological Reports, International Series, Oxford.

——. 1990. Owls, caves and fossils. Chicago University Press, Chicago.

Avery, D. M. 1992. The environment of early modern humans at Border Cave, South Africa: micromammalian evidence. Palaeogeography, Palaeoclimatology, Palaeoecology 91:71–87.

Bartram, L., and P. Villa. 1998. The archaeological excavation of prehistoric hyena dens: why bother? Pp. 15–29 *in* J. P. Brugal, L. Meignen, and M. Patou-Mathis, eds. Economie préhistorique: les comportements de subsistance au Paléolithique. Actes des XVIII Rencontres Internationales d'Archéologie et d'Histoire d'Antibes. Editions APDCA, Sophia-Antipolis, France.

Bennett, E. A., O. Gorgé, T. Grange, Y. Fernández-Jalvo, and E.-M. Geigl. 2016. Coprolites, paleogenomics and bone content analysis. Pp. 271–286 *in* Y. Fernández-Jalvo, T. King, L. Yepiskoposyan, and P. Andrews, eds. Azokh Cave and the Transcaucasian Corridor. Springer, Dordrecht, Netherlands.

Binford, L. R. 1981. Bones: ancient men and modern myths. Academic, New York.

Blain, H. A., and P. Villa. 2006. Amphibians and squamate reptiles from the early Upper Pleistocene of Bois Roche Cave (Charente, southwestern France). Acta Zoologica Cracoviensia 49A:1–32.

Blumenschine, R. J., J. A. Cavallo, and S. D. Capaldo. 1994. Competition for carcasses and early hominid behavioral ecology: a case study and conceptual framework. Journal of Human Evolution 27:197–213.

Bon, C., V. Berthonaud, F. Maksud, K. Labadie, J. Poulain, F. Artiguenave, P. Wincker, J. M. Aury, and J. M. Elalouf. 2012. Coprolites as a source of information on the genome and diet of the cave hyena. Proceedings of the Royal Society of London B 279:2825–2830.

Bramwell, D., D. W. Yalden, and P. E. Yalden. 1990. Ossum's Eyrie Cave: an archaeological contribution to the recent history of vertebrates in Britain. Zoological Journal of the Linnean Society 98:1–25.

Brain, C. K. 1969. The contribution of Namib desert Hottentots to an understanding of australopithecine bone accumulations. Scientific Papers of the Namib Desert Research Station 39: 13–22.

——. 1981. The hunters or the hunted? An introduction to African cave taphonomy. University of Chicago Press, Chicago.

Brantingham, P. J. 1998. Hominid–carnivore coevolution and invasion of the predatory guild. Journal of Anthropological Archaeology 17:237–353.

Buckland, P. C. 1976. The environmental evidence from the Church Street Roman sewer system. The archaeology of York 14/1. Council for British Archaeology, London.

Bunn, H. T., J. W. K. Harris, G. Isaac, Z. Kaufulu, E. Kroll, K. Schick, N. Toth, and A. K. Behrensmeyer. 1980. FxJj50: an early Pleistocene site in northern Kenya. World Archaeology 12:109–136.

Demirel, A., P. Andrews, I. Yalçinkaya, and A. Ersoy. 2011. The taphonomy and palaeoenvironmental implications of the small mammals from Karain Cave, Turkey. Journal of Archaeological Science 38:3048–3059.

Denys, C. 1986. Le gisement Pliocene de Laetoli (Tanzanie, Afrique de l'Est): analyse taphonomique des assemblages de microvertebres. Paleontographica 194:69–98.

d'Errico, F., and P. Villa. 1997. Holes and grooves. The contribution of microscopy and taphonomy to the problem of art origins. Journal of Human Evolution 33:1–31.

Diamond, J. 2002. Evolution, consequences and future of plant and animal domestication. Nature 418:700–707.

Dobney, K., D. Jaques, J. Carrott, A. Hail, M. Issitt, and F. Large. 1996. Biological remains from excavations at Carr Naze, Filey, N. Yorkshire: Technical Report. Reports from the Environmental Archaeology Unit, York 96/26. York Archaeological Trust, York, U.K.

https://doi.org/10.1017/pab.2018.13 Published online by Cambridge University Press

Dodson, P., and D. Wexlar. 1979. Taphonomic investigations of owl pellets. Paleobiology 5:275–284.

Fernández-Jalvo, Y. 1995. Small mammal taphonomy at La Trinchera de Atapuerca (Burgos, Spain). A remarkable example of taphonomic criteria used for stratigraphic correlations and palaeoenvironmental interpretations. Palaeogeography, Palaeoclimatology, Palaeoecology 114:167–195.

Fernández-Jalvo, Y., and P. Andrews. 1992. Small mammal taphonomy of Gran Dolina, Atapuerca (Burgos), Spain. Journal of Archaeological Science 19:407–428.

——. 2016. Atlas of taphonomy. Springer, New York.

Fernández-Jalvo, Y., C. Denys, P. Andrews, T. Williams, Y. Dauphin, and L. Humphrey. 1998. Taphonomy and palaeoecology of Olduvai Bed-1 (Pleistocene, Tanzania). Journal of Human
Evolution 34:137–172.

Fernández-Jalvo, Y., P. Andrews, P. Sevilla, and V. Requejo. 2014. Digestion versus abrasion features in rodent bones. Lethaia 47:323–336.

Fernández-Jalvo, Y., P. Andrews, C. Denys, C. Sesé, E. Stoetzel, D. Marin-Monfort, and M. D. Pesquero. 2016. Taphonomy for taxonomists: implications of predation in small mammal studies. Quaternary Science Reviews 139:138–157.

Gómez, G. N. 2003. Análisis Tafonómico y Paleoecológico de micro y mesomamíferos del sitio arqueológico de Arroyo Seco (Partido de Tres Arroyos, Buenos Aires, Argentina). Ph.D. thesis. University Complutense, Madrid.

Goldberg, P. 2001. Some micromorphological aspects of prehistoric cave deposits. Cahiers d'Archèologie du CELAT, Quebec 10: 161–175.

Harrison, T. 2011. Coprolites: taphonomic and paleoecological implications. Pp. 279–292 *in* T. Harrison, ed. Paleontology and geology of Laetoli: human evolution in context, Vol. 1. Geology, geochronology, paleoecology and paleoenvironment. Springer, Dordrecht, Netherlands.

Haynes, G. 1983. A guide for differentiating mammalian carnivore taxa responsible for gnaw damage in herbivore limb bones. Paleobiology 9:164–172.

Hill, A. 1984. Hyaenas and hominids: taphonomy and hypothesis testing. Pp. 111–128 *in* R. Foley, ed. Hominid evolution and community ecology. Academic, London.

Hofer, H. 1998. Spotted hyaena *Crocuta crocuta* (Erxleben, 1777). Pp. 29–38 *in* M. G. L. Mills, and H. Hofer, eds. Hyaenas: status survey and conservation action plan. IUCN, Gland, Switzerland.

Holekamp, K. E. 2007. Questioning the social intelligence hypothesis. Trends in Cognitive Sciences 11:65–69.

Holekamp, K. E., and L. Smale. 1990. Provisioning and food sharing by lactating spotted hyenas, *Crocuta crocuta* (Mammalia, Hyaenidae). Ethology 86:191–202.

Horwitz, L. K., and P. Goldberg. 1989. A study of Pleistocene and Holocene hyaena coprolites. Journal of Archaeological Science 16:71–94.

Jenks, S. M., and L. Werdelin. 1998. Taxonomy and systematics of living hyaenas (Family Hayenidae). Pp. 8–17 *in* M. G. L. Mills, and H. Hofer, eds. Hyaenas: status survey and conservation action plan. IUCN, Gland, Switzerland.

Korb, J. 2000. Methods to study elusive spotted hyenas in the Comoé National Park, Côte d'Ivoire. Hyaena Specialist Group Newsletter IUCN 7:3–12.

Korth, W. W. 1979. Taphonomy of microvertebrate fossil assemblages. Annals of Carnegie Museum 48:235–285.

Kruuk, H. 1972. The spotted hyaena. A study of predation and social behavior. University of Chicago Press, Chicago.

Kuhn, B. 2011. Hyaenids: taphonomy and implications for the palaeoenvironment. Cambridge Scholars Publishing, Newcastle upon Tyne, U.K.

Kurten, B. 1968. Pleistocene mammals of Europe. Weidenfeld and Nicholson, London.

Larkin, N. R., J. Alexander, and M. D. Lewis. 2000. Using experimental studies of recent faecal material to examine hyaena coprolites from the West Runton Freshwater Bed, Norfolk, U.K. Journal of Archaeological Science 27:19–31.

Lewis, M. 2011. Pleistocene hyaena coprolite palynology in Britain: implications for the environments of early humans. Pp. 263–278 *in* N. M. Ashton, S. G. Lewis, and C. B. Stringer, eds. The ancient human occupation of Britain. Elsevier, Amsterdam.

López, J. M., M. I. Rossi, S. Tabeni, B. Bender, and H. Chiavazza. 2017. Taphonomic analysis of small mammal bone remains preyed upon by wildcats (Carnivora: Felidae) from the central Monte Desert (Mendoza, Argentina). Boreas 47:282–293.

Lupo, K. D., and D. N. Schmitt. 2005. Small prey hunting technology and zooarchaeological measures of taxonomic diversity and abundance: ethnoarchaeological evidence from Central African forest foragers. Journal of Anthropological Archaeology 24:335–353.

Maas, M. C. 1985. Taphonomy of a Late Eocene microvertebrate locality, Wind River Basin, Wyoming (U.S.A.). Palaeogeography, Palaeoclimatology, Palaeoecology 52:123–142.

Marra, C., P. Villa, C. Beuval, L. Bonfiglio, and P. Goldberg. 2004. Same predator, variable prey: taphonomy of two Upper Pleistocene hyena dens in Sicily and SW France. *In* J. P. Brugal, and P. Fosse, eds. Humans and carnivores. Revue de Paléobiologie, Special Issue 23: 787–801.

Mayhew, D. F. 1977. Avian predators as accumulators of fossil mammal material. Boreas 6:25–31.

Medina, M. E., P. Teta, and D. Rivero. 2012. Burning damage and small mammal human consumption in Quebrada del Real 1 (Cordoba, Argentina): an experimental approach. Journal of Archaeological Science 39:737–743.

Mills, G., and H. Hofer. 1998. Hyaenas: status survey and conservation action plan. World Conservation Union, Devon, U.K.

Mills, M. G. L. 1990. Kalahari hyaenas: comparative behavioral ecology of two species. Unwin Hyman, London.

Mondini, M. 2000. Tafonomía de abrigos rocosos de la Puna. Formación de conjuntos escatológicos por zorros y sus implicancias arqueológicas. Archaeofauna 9:151–164.

Montalvo, C. I., M. E. M. Pessino, and V. H. González. 2007. Taphonomic analysis of remains of mammals eaten by pumas (*Puma concolor* Carnivora, Felidae) in central Argentina. Journal of Archaeological Science 34:2151–2160.

Montalvo, C. I., S. Bisceglia, M. S. Kin, and R. A. Sosa. 2012. Taphonomic analysis of rodent bone accumulations produced by Geoffrey's cat (*Leopardus geoffroyi*, Carnivora, Felidae) in Central Argentina. Jouirnal of Archaeological Science 39:1933–1941.

Murphey, P. C., L. L. Torick, E. S. Bray, R. Chandler, and E. Evanoff. 2001. Taphonomy, fauna and depositional environment of the *Omomys* Quarry, an unusual accumulation from the Bridger Formation (Middle Eocene) of Southwestern Wyoming (USA). Pp. 361–402 *in* G. F. Gunnell, ed. Eocene biodiversity: unusual occurrences and rarely sampled habitats. Kluwer Academic/ Plenum, New York.

Pesquero, M. D., M. J. Salesa, E. Espílez, L. Mampel, G. Siliceo, and L. Alcalá. 2011. An exceptionally rich hyaena coprolites concentration in the Late Miocene mammal fossil site of La Roma 2 (Teruel, Spain): taphonomical and palaeoenvironmental inferences. Palaeogeography, Palaeoclimatology, Palaeoecology 311:30–37.

Pokines, J. T., and J. C. Kerbis Peterhans. 2007. Spotted hyena (*Crocuta crocuta*) den use and taphonomy in the Masai Mara National Reserve, Kenya. Journal of Archaeological Science 34:1914–1931.

https://doi.org/10.1017/pab.2018.13 Published online by Cambridge University Press

Potts, R. 1989. Olorgesailie: new excavations and findings in Early and Middle Pleistocene contexts, southern Kenya rift valley. Journal of Human Evolution 18:477–484.

Prendergast, M. E., and M. Dominguez-Rodrigo. 2008. Taphonomic analyses of a hyena den and a natural-death assemblage near Lake Eyasi (Tanzania). Journal of Taphonomy 6:301–335.

R Core Team 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org.

Rodríguez-Hidalgo, A. J., P. Saladié, and A. Canals. 2011. Following the white rabbit: a case of small game procurement site in the Upper Palaeolithic (Sala de las Chimeneas, Maltravieso Cave, Spain). International Journal of Osteoarchaeology 23: 34–54.

Rohland, N., J. L. Pollack, D. Nagel, C. Beauval, J. Airvaux, S. Pääbo, and M. Hofreiter. 2005. The population history of extant and extinct hyenas. Molecular Biology and Evolution 22:2435–2443.

Sealy, J. 2006. Diet, mobility and settlement patterns among Holocene hunter-gatherers in southernmost Africa. Current Anthropology 47:569–595.

Sesé, C., and P. Villa. 2008. Micromammals (rodents and insectivores) from the early Upper Pleistocene cave site of Bois Roche (Charente, France): systematics and paleoclimatology. Geobios 41:399–414.

Shipman, P., and A. Walker. 1989. The costs of becoming a predator. Journal of Human Evolution 18:373–392.

Skinner, J. D., M. A. Haupt, M. Hoffmann, and H. M. Dott. 1998. Bone collection by brown hyaenas *Hyaena brunnea* in the Namib Desert: rate of accumulation. Journal of Archeological Science 25:69–71.

Stiner, M. C. 1991. Food procurement and transport by human and non-human predators. Journal of Archaeological Science 18:455–482.

——. 1994. Honor among thieves. A zooarchaeological study of Neandertal ecology. Princeton University Press, Princeton, N.J.

——. 2004. Comparative ecology and taphonomy of spotted hyenas, humans and wolves in Pleistocene Italy. Revue de Paléobiologie 23:771–785.

Stiner, M. C., N. D. Munro, and T. A. Surovell. 2000. The tortoise and the hare: small game use, the broad spectrum revolution, and Paleolithic demography. Current Anthropology 41:39–79.

Sutcliffe, A. J. 1970. Spotted hyena: crusher, gnawer, digestor and collector of bones. Nature 227:1110–1113.

Turner, A. 1990. The evolution of the guild of larger terrestrial carnivores during the Plio-Pleistocene in Africa. Geobios 23:349–368.

Turner, A., and M. Anton. 1996. The giant hyaena, *Pachycrocuta brevirostris* (Mammalia, Carnivora, Hyaenidae). Geobios 29: 455–468.

Villa, P., and L. Bartram. 1996. Flaked bone from a hyena den. Paléo 8:1–22.

Villa, P., and F. d'Errico. 2001. Bone and ivory points in the Lower and Middle Paleolithic of Europe. Journal of Human Evolution 41:69–112.

Villa, P., and M. Soressi. 2000. Stone tools in carnivore sites: the case of Bois Roche. Journal of Anthropological Research 56:187–215.

Villa, P., J. C. Castel, V. Bourdillat, C. Beauval, and P. Goldberg. 2004. Human and carnivore sites in the European Middle and Upper Paleolithic: similarities and differences in bone modification and fragmentation. *In* J. P. Brugal, and P. Fosse, eds. Humans and carnivores. Revue de Palébiologie, Special Issue 23: 705–730.

Villa, P., M.F. Sánchez-Goñi, G. Cuenca Bescós, R. Grün, A. Ajas, J.C. García Pimienta, and W. Lees. 2010. The archaeology and paleoenvironment of an Upper Pleistocene hyena den: an integrated approach. Journal of Archaeological Science 37:919–935.

Werdelin, L., and N. Solounias. 1991. The Hyaenidae: taxonomy, systematics and evolution. Fossils and Strata 30:1–104.

Wesselman, H. B. 1984. The Omo micromammals. Contributions to vertebrate evolution 7. Karger, London.

Wiesel, I. 2006. Predatory and foraging behaviour of brown hyenas (*Parahyaena brunnea* (Thunberg, 1820) at Cape fur seal (*Arctocephalus pusillus pusillus* Schreber, 1776) colonies. University of Hamburg, Hamburg, Germany.

Williams, J. 2003. Bones of comprehension: the analysis of small mammal predator–prey relationships. Pp. 341–358 *in* P. Kelley, ed. Predator–prey interactions in the fossil record. Kluwer, New York.

Williams, J. P. 1997. What is the contribution of small mammals to our understanding of palaeoecology, how is it relevant to archaeology, and how can taphonomic studies aid in that interpretation. Undergraduate dissertation. Department of Archaeology and Prehistory, University of Sheffield, Sheffield, U.K.

https://doi.org/10.1017/pab.2018.13 Published online by Cambridge University Press