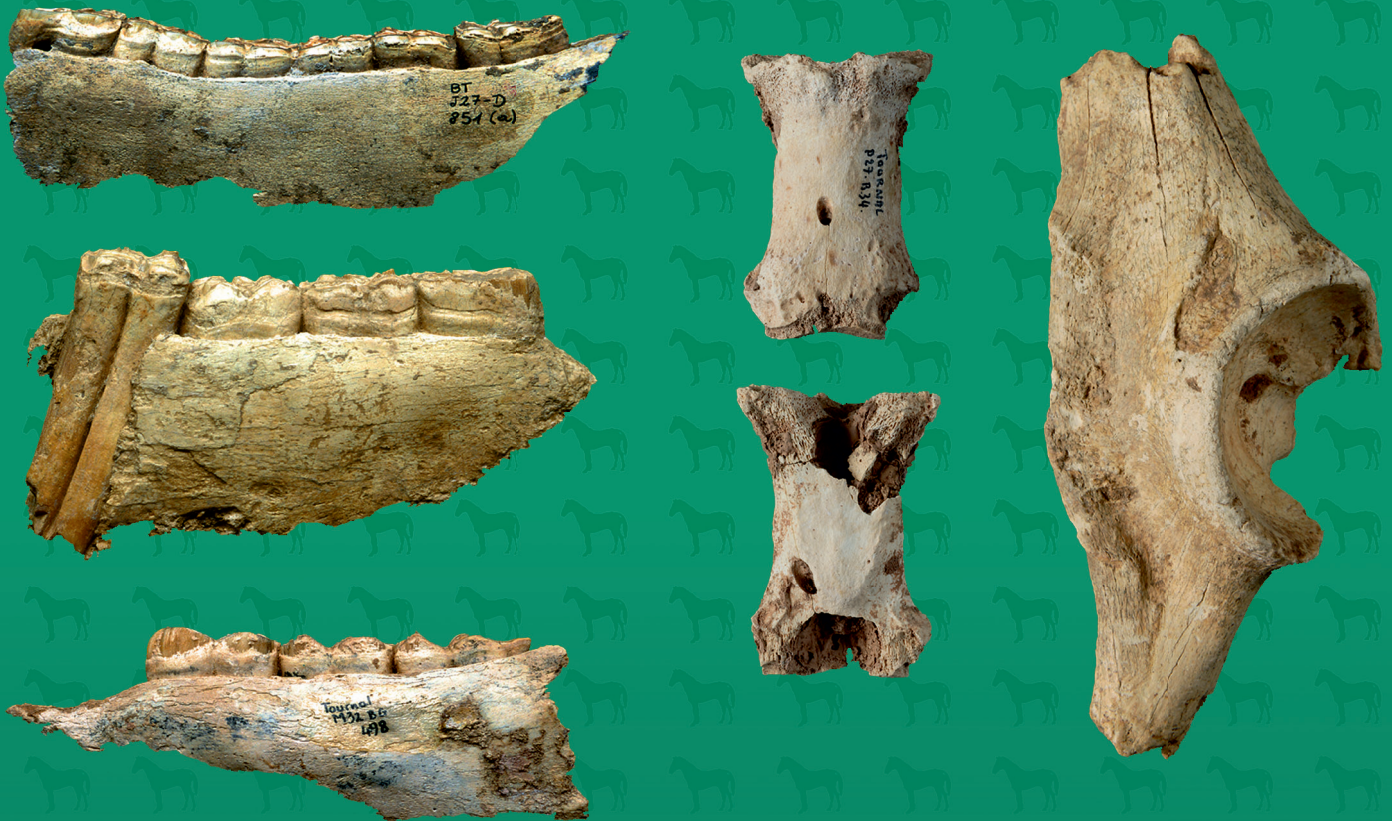


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CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)

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diff.pub@mnhn.fr / <http://sciencepress.mnhn.fr>

Académie des sciences, Institut de France, 23 quai de Conti, 75006 Paris.

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ISSN (imprimé / *print*) : 1631-0683/ ISSN (électronique / *electronic*) : 1777-571X

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Submitted on 30 September 2019 | Accepted on 3 December 2019 | Published on 14 December 2020

Marín J., Rodríguez-Hidalgo A., Saladié P., Boulbes N., Magniez P., Testu A. & Moigne A.-M. 2020. — Taphonomic analysis of horse remains from Mousterian and Aurignacian Units from Bize-Tournal Cave (Aude, France). *Comptes Rendus Palevol* 19 (11): 187-213. <https://doi.org/10.5852/cr-palevol2020v19a11>

ABSTRACT

The study of ungulate assemblages is essential to understand hominins and carnivore behavior and interactions. For this reason, many studies involve the taphonomic analysis of faunal remains, focusing on the identification of the various biotic actors. This study looks at the horse assemblages from Mousterian and Aurignacian Units I, II and III from Bize-Tournal cave with the aim to characterizing the nature of this accumulation. Here we show that the horse remains in these units are mainly the consequence of carnivorous activity. Unit II also clearly evidences the fact that the assemblage is the result of hyena activity. Our analysis indicates a predominance of cranial remains and lower long limb bones (metapodials). The mortality profiles of the three units are different, although two are classic of a cursorial predator. Taphonomical and statistical analysis indicated that carnivores were the main modifying agent at the three units. Our results demonstrate that hominins played a minor role in horse accumulation. Additionally, it seems that there was little difference in the exploitation in this specie by Mousterian and Aurignacian groups, and this probably took place during short, sporadic hominin occupations.

KEY WORDS

Mousterian,
Aurignacian,
carnivores,
Taphotype,
hyena,
horse.

RÉSUMÉ

Analyse taphonomique des restes de chevaux des unités moustériennes et aurignaciennes de la grotte de Bize-Tournal (Aude, France).

L'étude des assemblages d'ongulés est essentielle pour comprendre le comportement et les interactions entre hominidés et carnivores. Pour cette raison, de nombreuses études impliquent l'analyse taphonomique des restes de faune, en se concentrant sur l'identification des différents acteurs biotiques. Cette étude examine les assemblages de chevaux des Unités I, II et III (moustériennes et aurignaciennes) de la grotte de Bize-Tournal dans le but de caractériser la nature de cette accumulation. Nous montrons ici que les restes de cheval dans ces unités sont principalement la conséquence de l'activité de mammifères carnivores. L'Unité II met également en évidence le fait que l'assemblage est le résultat de l'activité de la hyène. Notre analyse indique une prédominance des restes crâniens et des os de membres inférieurs longs (métapodes). Les profils de mortalité des trois unités sont différents, bien que deux soient classiques d'un prédateur coureur. Des analyses taphonomiques et statistiques ont montré que les carnivores étaient le principal agent modificateur dans les trois unités. Nos résultats démontrent que les hominins ont joué un rôle mineur dans l'accumulation des restes de chevaux. De plus, il semble qu'il y ait eu peu de différences dans l'exploitation de cette espèce par les groupes moustériens et aurignaciens, et cela s'est probablement passé pendant des occupations courtes et sporadiques d'hominines.

MOTS CLÉS

Moustérien,
Aurignacien,
carnivore,
Taphotype,
hyène,
cheval.

INTRODUCTION

In the Palaearctic area, caves were the focus for occupation by hominins and carnivores. In fact, these taxa shared several characteristics that included diet (importance/dependence on ungulates), social organisation, the types of food resource catchment zones, and the use of shelters (Brugal & Fosse 2004). These common features must have led them to interact fairly frequently (Binford 1981; Brain 1981; Capaldo 1997; Daujeard & Moncel 2010; Egeland *et al.* 2004; Patou-Mathis 2012; Selvaggio 1998). Carnivores were actively involved in the accumulation and modification of bone assemblages at the large majority of Pleistocene sites (e.g. Binford 1981; Brain 1981; Brugal & Fosse 2004; Egeland *et al.* 2004; Faith & Behrensmeyer 2006; Saladié *et al.* 2017; Stiner 2010). For this reason, understanding the role of carnivores as tapho-

nomic agents has been crucial in zooarchaeological studies focused on reconstructing site formation (Faith & Behrensmeyer 2006; Lacruz & Maude 2005; Mills & Mills 1977). With the aim a large number of ethological and actualistic studies have been developed (Andrés *et al.* 2012; Arriaza *et al.* 2016; Binford 1981; Brugal & Fosse 2004; Cruz-Urbe 1991; Domínguez-Rodrigo & Piqueras 2003; Domínguez-Rodrigo *et al.* 2012; Fourvel *et al.* 2012; Gidna *et al.* 2015; Kruuk 1972; Pokines & Peterhans 2007; Selvaggio 1994).

All carnivorous mammals modify the bones of their prey to some degree. Large canids (tribe *Canini* or wolf-like canids; genera *Canis*, *Lycan*, and *Cuon*) have been studied as significant bone modifiers (Binford 1981; Sala *et al.* 2012); some authors have characterised them as bone accumulators (Binford 1981; Fourvel *et al.* 2012; Mallye *et al.* 2012; Stiner 2002), while others classify them as agents of carcass dispersal

(Yravedra *et al.* 2011, 2012). Several studies converge on the limited capability of the large and medium felids (genera *Panthera*, *Puma*, and *Acinonyx*) to modify bones. As recently proved, medium-sized felids, like the leopard (Sauqué & Sanchis 2017; Sauqué *et al.* 2014, 2018), are true bone accumulators, although lions can be bone accumulators under determined conditions (Arriaza *et al.* 2016; Brain 1981; Stiner *et al.* 2012). However, their position in the food web and their gregarious behaviour indicate that this species is not a typical bone collector (Schaller 1972). Other carnivores commonly present in Pleistocene assemblages were the various species of bear (Pinto & Andrews 2004; Pinto *et al.* 2005; Sala *et al.* 2014; Stiner 2010; Stiner *et al.* 1996, 1998). Their remains are particularly abundant as the result of death during hibernation, meaning bear skeletons are common at sites used as hibernation dens (Stiner 2010). Actualistic studies of brown and black bears indicate that these carnivores were bone modifiers but not bone accumulators (McNamee 1990; Rogers 1981). The taphonomic signal generated by these taxa has been described in both actualistic (Arilla *et al.* 2014; Sala & Arsuaga 2013; Saladié *et al.* 2013) and archaeological contexts (Fernández-Jalvo & Andrews 2011; Pinto & Andrews 2004; Stiner 2010). The three species of extant hyena, brown hyena (*Parahyaena brunnea* Thunberg, 1820) (Lacruz & Maude 2005; Mills & Mills 1977; Skinner & Aarde 1991), striped hyena (*Hyaena hyaena* Linnaeus, 1758) (Becker & Reed 1993; Kempe *et al.* 2006), and spotted hyena (*Crocuta crocuta* Erxleben, 1777) (Egeland *et al.* 2008; Faith 2007; Fourvel *et al.* 2015; Mills & Mills 1977; Skinner *et al.* 1986) are the most studied species because they are among the highest-volume bone accumulators (Cruz-Urbe 1991; Kuhn *et al.* 2010; Lam 1992; Pickering 2002; Skinner *et al.* 1986; Stiner 1991a).

The transition between Mousterian and Aurignacian have been widely studied (Boyle 2000; Chase 1989; Clark 1997; Gaudzinski-Windheuser & Niven 2009; Grayson & Delpech 2008, 2003, 2002; Hoffecker 2009; Marean 2005; Marín-Arroyo *et al.* 2018; Mellars 1973, 2004; Straus 2013; Tagliacozzo *et al.* 2013). For the point of view of faunal studied some works proposed a progressively specialization in hunting strategies (Mellars 1973, 2004). Although, another tendency of studies defend that didn't existed great differences between Mousterian and Aurignacian hunting at the first moments Middle-Upper Palaeolithic transition (e.g. Grayson & Delpech 2002; Otte 1990; Straus 2013).

This paper focuses on a complete zooarchaeological and taphonomic analysis of the horse remains from the Mousterian and Aurignacian levels of Bize-Tournal Cave. Our goal is to clarify the origin of the horse accumulations and their taphonomic history, a point of special interest is identifying the role played by humans and carnivores in the accumulation of this species. The horse assemblage of Bize-Tournal constitutes a good sample in which to investigate the carnivore/hominin procurement of this species, considering the large number of remains recovered from this cave. In addition, we try to identify possible differences in horse management between Mousterian and Aurignacian hominin groups.

TABLE 1. — Archaeological levels included on this study of Bize-Tournal Cave. Units from: **a**, Tavoso (1987a); **b**, Patou-Mathis (1994). Dating from Yokoyama *et al.* (1987). Ages in ka B.P., radiocarbon dates uncalibrated.

Period	Unit	Level	Dates
Aurignacian	III	E3a	F3F4b
		E2a	F1F2b
		E1a	>29 a B.P. (Ly1895) (14C) >35.8 a B.P. (Ly1898) (14C)
Mousterian	II	D1/D2a	33.6 ± 1.2 B.P. (Ly1676) (14C)
		B/Ca	38 ± 8 a (ESR) 56.2 ± 1.7 a (U-series)
	I	Aa	

BIZE-TOURNAL

Bize-Tournal Cave is situated in southern France (43°20'N, 2°52'E), approximately 20 km north of Narbonne and 2.5 km north from Bize-Minervois. Located in the foothills of the limestone massif “La Montagne Noire”, which flanks the Mediterranean Sea, the cave is on the left banks of the Cesse River. The cave was discovered and excavated by P. Tournal in 1827, and the site became a reference for the first prehistoric and taphonomic studies (Tournal 1829, 1828, 1827). The last excavations of the Pleistocene horizons were conducted between 1970 and 1987 by A. Tavoso in a preserved area of approximately 75 m². He found a well-stratified sequence from the Mousterian to the Magdalenian period, which provides record to the regional transition from the Middle to Upper Palaeolithic (Tavoso 1987a, 1987b).

At least 11 levels have been identified in four units. Unit I (level A) is characterised by highly weathered coarse gravel, alternating with greenish plastic clays and clayey silts. The bone assemblage was strongly biased due to post-depositional water- and karst-related modification. Unit II (level B/C and D1/D2) is a 0.5 to 2 m-thick complex, formed of brown clay alternating with silts and clayey silty sands. It contains archaeological layers with very rich assemblages of large mammals and lithic series. The stratigraphy of Unit III is clearer: the lower part comprises clayey gravelly silts and brecciated gravels with limited archaeological material (level E1, after Tavoso 1987a; F1-F2, after Patou-Mathis 1994); the middle part is formed of a pink breccia and yellow clayey silt and is archaeologically sub-sterile (level E2, sub-sterile); the upper layer is a breccia with a relatively richer archaeological series (level E3, after Tavoso 1987a; F3-F4, after Patou-Mathis 1994). The lowest layers comprise fine gravel with a silty matrix whereas the upper ones are hard breccia. Archaeological levels G and H (Unit IV) are characterised by abundant lithic and faunal remains. Unit IV contains the most significant archaeological records and bellow to Magdalenian cultural period.

The dating of the archaeological sequence is based on series of charcoal samples (non-calibrated dates), horse bones and teeth (uranium dating), and cervid and bovid bones (non-destructive gamma-ray spectrometry and electron spin resonance [ESR]) (Bischoff *et al.* 1988; Yokoyama *et al.* 1987). The most consistent results indicate that the Mousterian horizon from Unit II is between 56 200 ± 1700 B.P. cal. (Bischoff *et al.* 1988) and 38 000 ± 8000 B.P. cal. (Yokoyama *et al.* 1987).

TABLE 2. — Number of identified specimens (NISP), minimum number of individuals (MNI) and frequencies (%) of large mammals in Bize-Tournal Cave. Data from Magniez (2009).

Taxa	Unit I				Unit II				Unit III			
	NISP	%NISP	MNI	%MNI	NISP	%NISP	MNI	%MNI	NISP	%NISP	MNI	%MNI
<i>Bos primigenius</i> / <i>Bison priscus</i> Linnaeus, 1758	2	2.2	1	3.3	190	10.3	20	11.1	27	5.0	7	11.5
<i>Capra praepyreanaica</i> / <i>Capra pyrenaica</i> Schinz, 1838	1	1.1	1	3.3	143	7.7	23	12.7	8	1.5	4	6.6
<i>Megaloceros giganteus</i> Blumenbach, 1799	—	—	—	—	50	2.7	8	4.4	—	—	—	—
<i>Cervus elaphus</i> Linnaeus, 1758	1	1.1	1	3.3	41	2.2	7	3.8	—	—	—	—
<i>Rangifer tarandus</i> Linnaeus, 1758	24	25.8	5	16.8	194	10.5	17	9.4	170	31.3	16	26.2
<i>Sus scrofa</i> Linnaeus, 1758	—	—	—	—	14	0.8	6	3.3	—	—	—	—
<i>Equus ferus germanicus</i> Nehring, 1804	51	54.8	14	46.7	767	41.4	25	13.8	—	—	—	—
<i>Equus ferus gallicus</i> Prat, 1968	—	—	—	—	—	—	—	—	266	48.9	7	11.5
<i>Caelodonta antiquitatis</i> Blumenbach, 1807	—	—	—	—	10	0.5	3	1.7	1	0.2	1	1.6
<i>Ursus spelaeus</i> Rosenmuller, 1794	11	11.8	6	20	299	16.1	32	17.7	32	5.9	8	13.1
<i>Ursus arctos</i> Linnaeus, 1758	1	1.1	1	3.3	8	0.4	4	2.2	1	0.2	1	1.6
<i>Crocota crocuta spelaea</i> Goldfuss, 1823	—	—	—	—	91	4.9	19	10.5	23	4.2	9	14.7
<i>Canis lupus</i> Linnaeus, 1758	—	—	—	—	20	1.1	6	3.3	7	1.3	4	6.6
<i>Vulpes vulpes</i> Linnaeus, 1758	—	—	—	—	18	1.0	5	2.8	9	1.7	4	6.6
<i>Panthera leo spelaea</i> Goldfuss, 1810	—	—	—	—	4	0.2	3	1.7	—	—	—	—
<i>Panthera pardus</i> Linnaeus, 1758	2	2.2	1	3.3	1	0.1	1	0.5	—	—	—	—
<i>Lynx lynx</i> Linnaeus, 1758	—	—	—	—	2	0.1	2	1.1	—	—	—	—
Total	93	100	30	100	1852	100	181	100	544	100	61	100

The Aurignacian horizon from Unit III is dated as 29 000 B.P. and 35 800 B.P. (Yokoyama *et al.* 1987) (Table 1).

The lithic tools from Units I and II correspond to denticulate Mousterian with non-laminar Levallois flakes, with practically no technological and typological variations (Chacón 2009; Lumley 1971; Lumley & Isetti 1965; Tavoso 1987b). From Unit III, an early Aurignacian technology with Dufour bladelets has been recovered, and there is a typical Aurignacian layer dominated by end scrapers (Sacchi 1986; Tavoso 1987b).

A total of seven ungulate species and seven carnivore taxa (Magniez 2009) (Table 2) have been identified from the Mousterian levels. The most numerous ungulates in Units I, II and III is *Equus ferus* Boddaert, 1785, followed by *Rangifer tarandus* Linnaeus, 1758 and *Bos/Bison* sp. Linnaeus, 1758 (Table 2). *Ursus spelaeus* was the most abundant carnivore taxon in all the units, followed by *Panthera pardus* Linnaeus, 1758 (Unit I), and *Crocota crocuta spelaea* Goldfuss, 1823 (Units II and III) (Table 2). The Mousterian phase involved short-term, recurrent hominin occupations, essentially focused on the exploitation of horse, reindeer, and large bovids, through collective hunting, while giant deer, red deer, ibex, and wild boar remains were accumulated by carnivores, especially the cave hyena (Magniez 2009, 2010; Magniez & Boulbes 2014).

The horse from Tournal corresponds to a medium-sized horse with “heavy” proportions and broad muzzle. The skeleton shows a clear decrease in body size through the stratigraphy (Magniez & Boulbes 2014). The remains from Units I and II correspond to the chrono-subspecies *Equus ferus germanicus* Nehring, 1804, those from Unit III (and Unit IV) can be attributed to *E. f. gallicus* Prat, 1968. Body mass estimations vary between 400 and 480 kg in the Unit II and 380–450 kg in the Unit III. Another particular feature of Tournal horse is the strong diaphysis robustness of the metapodials. This pattern corresponds to an ecomorphological trait correlated to the high level of humidity (Boulbes & van Asperen 2019).

MATERIAL AND METHODS

The *Equus ferus* remains analysed come from the Tavoso excavation, focused on the three first units: the Mousterian Unit I (Number of identified specimens (NISP) = 51) and Unit II (NISP = 767); and the Aurignacian Unit III (NISP = 266) (Table 2). In this study were included coordinate bone splinters identified as horse remains after a survey of the unidentified remains of the faunal assemblages, which allows to have a more complete corpus to discuss the impact the different taphonomic agents.

The features described for each specimen are element, taxa, size, face (anterior, posterior, lateral or medial), portion, lateralisation (right/left), and age-at-death group. We have used four quantitative units: number of identified specimens (NISP); minimum number of elements (MNE); the standardised expression of the minimum number of animal units (%MAU); and the minimum number of individuals (MNI) (Binford 1984; Grayson 1984). Following Domínguez-Rodrigo (1997), to represent skeletal parts, the carcasses were divided into anatomical segments: head (cranium, mandible, hyoid, and teeth); axial (vertebrae, ribs); and appendicular (limb bones). Long bones were divided into upper limb bones (humerus and femur), intermediate limb bones (radius/ulna and tibia), and lower limb bones (metapodials).

We used the Spearman's rank-order to test the correlation between %MAU of each portion of the elements and bone mineral density (Lam *et al.* 1999), to identify any possible differential destruction of less dense portions of bones.

Age of death and seasonality was determined through a study of the teeth, considering the time of eruption, replacement of teeth, and the degree of occlusal surface wear and root development (Fernandez & Legendre 2003; Forsten & Moigne 1998). Isolated teeth were analysed together with the dental series. Anatomical refitting was performed based on lateralisa-

TABLE 3. — Estimated number of identified specimens (NISP), minimum number of elements (MNE) and frequencies (%) of horse elements by archaeological unit at Bize-Tournal.

	Unit I				Unit II				Unit III			
	NISP	%NISP	MNE	%MNE	NISP	%NISP	MNE	%MNE	NISP	%NISP	MNE	%MNE
Cranium	—	—	7	30.4	19	2.5	25	7.8	1	0.4	10	11.5
Mandible	4	7.8	7	30.4	30	3.9	37	11.6	12	4.5	23	26.4
Isolated teeth	35	68.6	—	—	341	44.5	—	0.0	171	64.3	—	—
Vertebra	—	—	—	—	6	0.8	4	1.3	1	0.4	1	1.1
Rib	—	—	—	—	11	1.4	7	2.2	3	1.1	1	1.1
Scapula	2	4	2	8.6	8	1.0	4	1.3	—	—	—	—
Coxal bone	—	—	—	—	31	4.0	19	6.0	5	1.9	4	4.6
Humerus	3	5.8	2	8.6	20	2.6	9	2.8	5	1.9	2	2.3
Radius/ulna	—	—	—	—	29	3.8	20	6.3	7	2.6	3	3.4
Carpal	—	—	—	—	3	0.4	3	0.9	3	1.1	3	3.4
Metacarpal	—	—	—	—	55	7.2	35	11.0	13	4.9	5	5.7
Metacarpal vestigial	—	—	—	—	7	0.9	7	2.2	3	1.1	3	3.4
Femur	1	2	1	4.4	30	3.9	16	5.0	8	3.0	3	3.4
Patella	1	2	1	4.4	4	0.5	4	1.3	—	—	—	—
Tibia	—	—	—	—	52	6.8	23	7.2	9	3.4	5	5.7
Astragalus	1	2	1	4.4	18	2.3	16	5.0	6	2.3	6	6.9
Calcaneum	—	—	—	—	12	1.6	11	3.4	1	0.4	1	1.1
Tarsal	—	—	—	—	7	0.9	7	2.2	3	1.1	3	3.4
Metatarsal	3	5.8	1	4.4	49	6.4	40	12.5	4	1.5	4	4.6
Metatarsal vestigial	—	—	—	—	3	0.4	3	0.9	—	—	—	—
Sesamoid	—	—	—	—	3	0.4	3	0.9	1	0.4	1	1.1
Phalanx I	—	—	—	—	9	1.2	8	2.5	4	1.5	3	3.4
Phalanx II	—	—	—	—	8	1.0	8	2.5	3	1.1	3	3.4
Phalanx III	1	2	1	4.4	12	1.6	10	3.1	3	1.1	3	3.4
Total	51		23		767		319		266		87	

tion, wear, and size, and this permitted an accurate MNE and MNI to be obtained for the mandibles and maxillae. The horse birthing period, between spring and early summer, has been taken as standard (Burke 2002; Levine 1983). Horse mortality curves were created by identifying age of death (Fernandez *et al.* 2006). Following Fernandez & Legendre (2003) and Fernandez *et al.* (2006), we calculated the parameters of life tables. The individuals were grouped into the groups juvenile, prime adult, and old and plotted in a ternary plots according with Stiner (1990) and Discamps & Costamagno (2015).

Following Bunn (1983) and Villa & Mahieu (1991), shaft circumference, shaft length, and the fracture outline, angle and edge were listed to explore the nature of the fragmentation observed in the assemblage. We considered the ratio of limb bone shaft fragments (NISP) to epiphyseal specimens (Blumenschine & Marean 1993; Marean & Spencer 1991), and the percentage of change in the epiphysis of the long bones [(MNE before ravaging-MNE after ravaging)/(MNE before ravaging)*100] (Blumenschine & Marean 1993) using the total MNE according to Domínguez-Rodrigo *et al.* (2002), assuming that each element was represented by two epiphyses.

The carnivore modifications identified were pits and scores (Binford 1981; Johnson 1985; Maguire *et al.* 1980), furrowing (Brain 1981; Haynes 1983), pitting (Binford 1981) and digested remains (Sutcliffe 1970). The dimensions of the pits and scores were determined using the criteria of Domínguez-Rodrigo & Piqueras (2003) and Andrés *et al.* (2012) and these were compared with the experimental data of Selvaggio (1994), Delaney-Rivera *et al.* (2009), Andrés *et al.* (2012), and Saladié

et al. (2013). The type, delineation, location, and positions of the cut marks on the bones allowed the identification of butchering activities (Binford 1981; Domínguez-Rodrigo *et al.* 2009; Galán & Domínguez-Rodrigo 2013; Nilssen 2000; Shipman & Rose 1983). The post-depositional modifications identified were rounding, polishing, fissures, concretions, and manganese oxides stains, and these were recorded as being present or absent for each specimen.

We followed the method of Domínguez-Rodrigo *et al.* (2015), who classified upper and intermediate long bones into different taphotypes according to the carnivore modifications (presence/absence; location of furrowing and tooth marks). This method is used to evaluate only long limb bones (humerus, femur, radius-ulna, tibia) that preserve their complete diaphyseal circumference (Domínguez-Rodrigo *et al.* 2015).

RESULTS

ANATOMICAL PROFILES AND BONE PRESERVATION

Unit II contained the largest number of horse remains according the NISP and MNE, followed by Unit III, and finally Unit I (Table 3). According to the NISP, the most numerous remains in all layers were isolated teeth, followed by long limb bones (humerus in Unit I and metapodials in Units II and III) (Table 3). The anatomical distribution of %MAU used to estimate the anatomical profiles indicated a predominance of skulls (cranium and mandible) in Unit I, followed in importance by coxa and humerus remains, with values of

TABLE 4. — The total sample number of identified specimens (NISP) and minimum number of individuals (MNI), the frequency of right and left teeth and the differential preservation rate.

Cultural Attribution	Unit	Tooth/Dental NISP(MNI)	Left teeth	Right teeth	Total expected	Differential preservation (%)
Aurignacian	Unit III	97 (14)	36	61	122	79.5
Mousterian	Unit II	342 (25)	164	178	356	96.06
	Unit I	34 (7)	17	16	34	97.05

TABLE 5. — Minimum number of individuals (MNI) by age categories, frequencies (%), seasonality, and interpreted mortality.

Cultural Attribution	Unit	MNI (MNI%)				Seasonality	Mortality
		Juvenile	Prime adult	Old	Total		
Aurignacian	Unit III	4 (28.57)	8 (57.14)	2 (14.29)	14	Annual	Catastrophic
Mousterian	Unit II	11 (44)	9 (36)	5 (20)	25	Annual	Attritional
	Unit I	1 (14.29)	5 (71.43)	1 (14.29)	7	Seasonal (Summer-Fall)	Prime-dominated

TABLE 6. — Life tables of horses from Units I, II, and III.

Age group	Frequency (fx)			Mortality (qx)			Survival (lx)			Killing factor (kx)		
	Unit I	Unit II	Unit III	Unit I	Unit II	Unit III	Unit I	Unit II	Unit III	Unit I	Unit II	Unit III
0-3	6.89	20.43	23.18	6.89	20.43	23.18	100	100	100	0.39	0.11	0.9
3-6	17.24	15.69	2.89	18.51	19.72	3.77	93.10	79.56	76.81	0.38	0.019	0.81
6-9	41.37	16.42	18.84	54.54	25.71	25.49	75.86	63.86	73.91	0.12	0.05	0.18
9-12	31.03	14.59	28.98	90	30.76	52.63	34.48	47.45	55.07	0.95	0.22	0.3
12-15	3.44	8.75	14.49	100	26.67	55.56	3.44	32.84	26.08	0	0.06	0.39
15-18	0	10.21	5.79	0	42.42	50	0	24.08	11.59	0	0.27	0.6
18-21	0	5.47	1.44	0	39.47	25	0	13.86	5.79	0	0.18	0.47
21-25	0	8.39	4.34	0	100	100	0	8.39	4.34	0	0	0.9

less than 20%. Unit II presented the greatest values of %MAU for mandibles, followed by cranium remains, metatarsal and metacarpal. After these elements, the next most important were: tibia, radius/ulna, and femur. The post-cranial axial skeleton presented an irregular distribution, with a value of around 40% for coxa and values of less than 10% for scapula, ribs and vertebrae. From the carpals and tarsals were better represented astragalus and calcaneus bones (Fig. 1). Unit III was dominated by skull elements, followed astragalus, tibia, metacarpal and coxal bones (Fig. 1).

In Units II and III we identified a significant and positive statistical correlation between the bone mineral density of anatomical portions and their %MAU (Unit II: $r_s = 0.394$, $p = 0.0001$ /Unit III: $r_s = 0.3$, $p = 0.003$) (Fig. 4). In Unit I there was no significant correlation between %MAU and bone density ($r_s = 0.160$, $p = 0.128$). These results indicate bone-mediated attrition of less dense parts in Units II and III.

MORTALITY PROFILES AND MORTALITY CURVES

The percentages of dental preservation between the right and left teeth clearly indicate good preservation of the original deposits (Table 4).

For MNI, the unit with most individuals was Unit II (MNI = 25), followed by Unit III (MNI = 14), and then Unit I (MNI = 7) (Table 5). Units I and III were dominated by prime-adult individuals. In Unit II, juveniles were the most numerous, although there was also a significant number of prime adults.

The juvenile individuals identified in Unit I must have died during the summer/autumn. In Unit II, the wear and eruption of the juvenile teeth indicates that they were killed in all seasons; some individuals with deciduous dentition were recovered with no wear, and in some cases the dentition was not completely formed, indicating that these animals died in their first weeks of life, in addition to individuals with deciduous dentition with all degrees of wear. Unit III presented a similar seasonal pattern to that found in Unit II, with multi-seasonal death, including the birth period (Table 5).

The mortality profiles differ significantly between the units. In terms of frequency (f_x), the proportion of juvenile individuals was similar in Units II and III, but these are less well represented in Unit I; in contrast, the proportion of adults was more important in Units I and III than Unit II. Old individuals were better represented in Units II and III, with none present at all in Unit I (Fig. 2). Indeed, Unit I contained no remains of adults older than 15 years (Table 6). The mortality based on life tables indicated for Unit I shows an increase in animals between 9 and 15 years old, with no older individuals. Unit II presents a moderate L-shaped mortality curve (Fig. 2). In Unit III, individuals aged between 0-3 and 6-12 years were the best represented, with a bias towards individuals aged 3-6 years. An exponential increase in mortality rates (q_x) was identified for adult individuals in Units I and III, and a regular increase in mortality in Unit II for all age groups (Fig. 2). The survivorship (l_x) obtained for all the samples corresponds to a regular

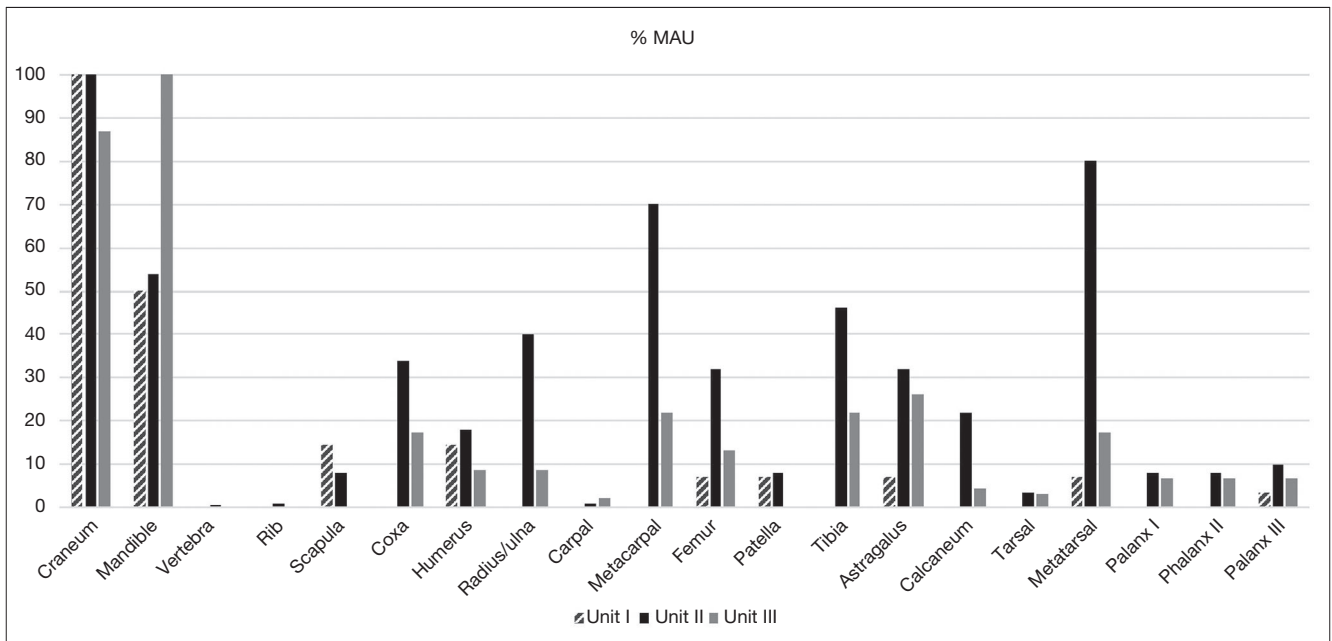


FIG. 1. — Standardized expression of the minimum number of animal units (%MAU) distribution by elements of horse remains from Units I, II, and III from Bize-Tournal.

decrease in the successive groups, most highlighted in Unit I from the age of 6 and accentuated in Unit III from 9 years old. In contrast, the curve for Unit II shows a slowly linear decrease (Fig. 2). Predation considered in the Killing Factor (Kx) indicated higher values of K in Units I ($K = 1.8$) and III ($K = 3.6$) and lower values in Unit II ($K = 0.9$), revealing a more stable predation structure.

The mortality profiles indicate a prime-adult dominated profile in Unit I, an attritional profile in Unit II, and a catastrophic profile in Unit III (Fig. 3). All the mortality profiles fall into the juvenile/prime/old areas, designed by Discamps and Costamagno (Discamps & Costamagno 2015).

BONE ASSEMBLAGE INTEGRITY

With regard to fragmentation, a high percentage of complete remains was found in all the units (Unit I = 68.6%; Unit II = 51%; Unit III = 50.6%). Of these, the majority were dental remains (Unit I = 88.5%; Unit II = 72.4%; Unit III = 84.4%), followed by articular bones (Unit I = 2.8%; Unit II = 7.6%; Unit III = 10.6%), and phalanges (Unit I = 8.5%; Unit II = 4.8%; Unit III = 4.6%). An elevated percentage of long limb bones were complete in Units II and III. From Unit II, a total of 54 complete metapodials (metacarpal = 28 (50.9%); metatarsal = 26 (52%)) two radius (8%) and one tibia 52 (1.9%) were recovered. In Unit III, three complete metapodials (metacarpal = 2 (15.3%); metatarsal = 1 (25%)) were found. No complete long bones were recorded from Unit I.

The percentage of long limb bone diaphyses with less than one-quarter of their original length preserved were 37.5% in Unit I, 34.8% in Unit II, and 55.8% in Unit III; those with less than one third of their original circumference were 37.5% in Unit I, 39.4% in Unit II, and 51.1% in Unit III. This indicates a moderate degree of fragmentation and is related to the high number of complete bones and those remains

TABLE 7. — Total number and percentage of remains by carnivore and human surface modifications. Number of identified specimens (NISP), number of remains (NR) and frequencies (%).

Surface Modification	Unit I		Unit II		Unit III	
	NISP	%NR	NR	%NR	NR	%NR
Pits and scores	4	7.8	234	30.5	10	3.8
Digested	0	0	17	2.2	0	0.0
Carnivore bone breakage	1	2	74	9.6	15	5.6
Cylinders	0	0	68	8.9	4	1.5
Cut-marked	0	0	6	0.8	5	1.9

that preserve the complete length and circumference of the shaft, formally mid-shaft cylinders (Unit I = 37.5%; Unit II = 47.1%; Unit III = 34.8%).

Analysis of long limb bone breakage indicated that the most common combination of fracture edge features in all levels were transversal delineations, mixed angles, and smooth surfaces (Unit I = 28.5%; Unit II = 25.8%; Unit III = 35.8%), indicating that the fractures predominantly occurred when the bones were dry. The second most frequent combination of fractures were: curve delineations, oblique angles, and jagged surfaces in Unit I (21.4%); longitudinal, oblique, and smooth surfaces in Unit II (15.1%); and longitudinal, right, and smooth in Unit III (16.4%). The combination of curve delineation and oblique angles were recorded in 7.1% of the long limb bones from Unit I, 12.1% from Unit II, and 8.9% from Unit III; these could be related to green bone breakage.

During the analysis of MNE it was possible to appreciate an imbalance in the representation of certain parts of limb bones (Fig. 5). In Unit I, fragments of epiphyses and near epiphyses were better represented than humerus, femur, and metatarsal mid-shaft portions. In Unit II, only humerus and femur bones presented a large proportion of mid-shaft fragments with near

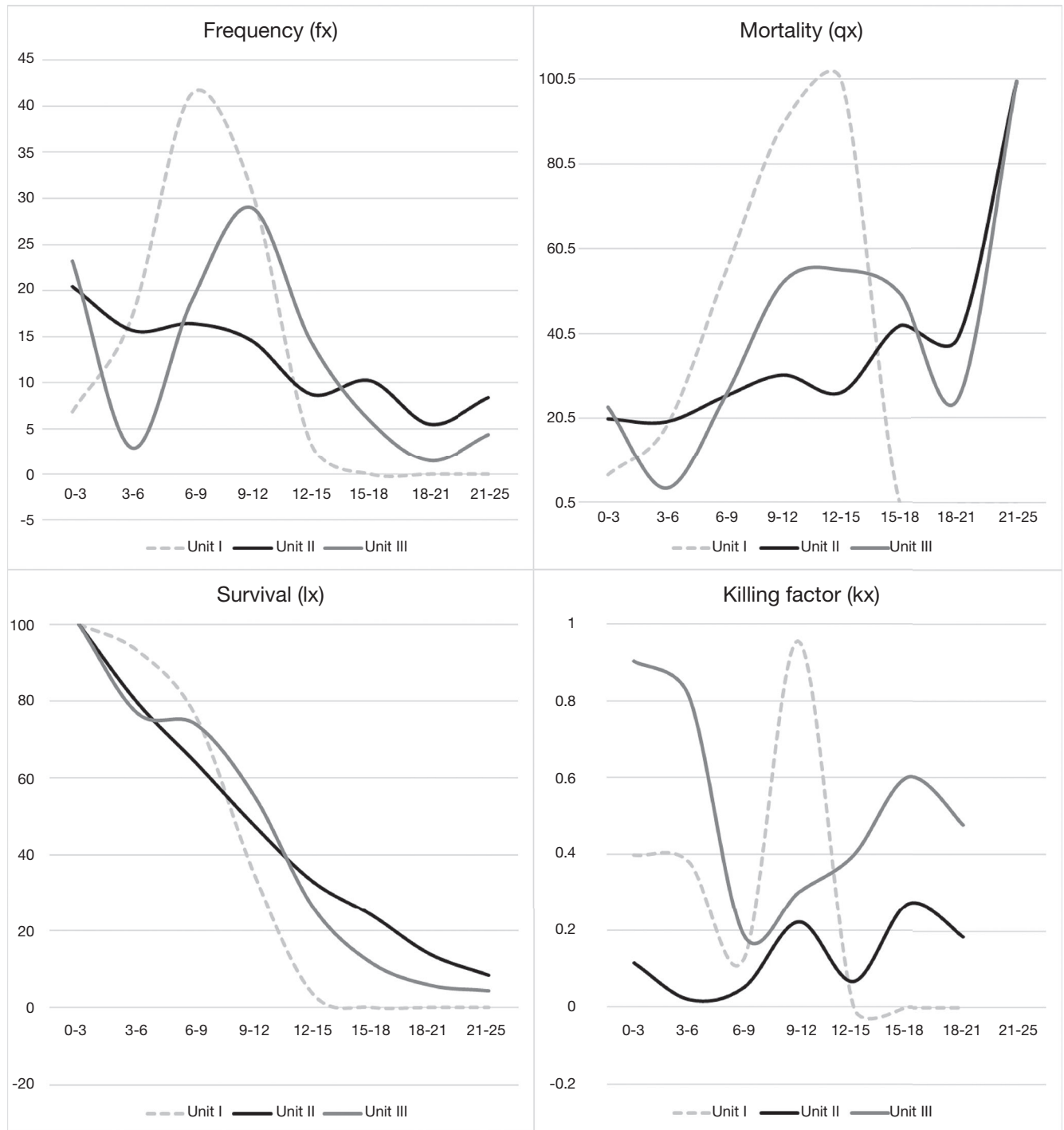


FIG. 2. — Mortality and survivorship curves. The abscissa axis indicates frequency values and the ordinate axis indicates age groups. Abbreviations: J, juvenile; P, prime-adult; O, old; JOP, juvenile/old/prime; JPO, juvenile/prime/old.

epiphyses and proximal and distal ends. Fewer distal epiphyses were found for tibia remains. Radius and metapodial bones were represented in equal proportions in all bone portions. The sample from Unit III was more diverse: the portions of humerus, femur and metapodial remains were similarly represented; no tibia distal epiphysis fragments were found, and no fragments of the proximal ends and shafts of radius bones were found (Fig. 5). The disappearance of epiphyses may also be related to the low proportion of axial skeleton remains.

The percentage of change and the epiphysis-shaft ratio indicate a significant underrepresentation of epiphyses in Unit II (%change = 70.6; epiphysis/shaft = 0.3). These factors also reveal that about half the epiphyses were missing in both Unit I (%change = 66.7; epiphysis/shaft: 0.5) and Unit III (%change = 58.3; epiphysis/shaft = 0.5). The results of the linear regression between shaft/epiphysis ratio and percentage of Bize-Tournal Cave units with values of the Peninj sites and Syokimau indicate intense carnivore

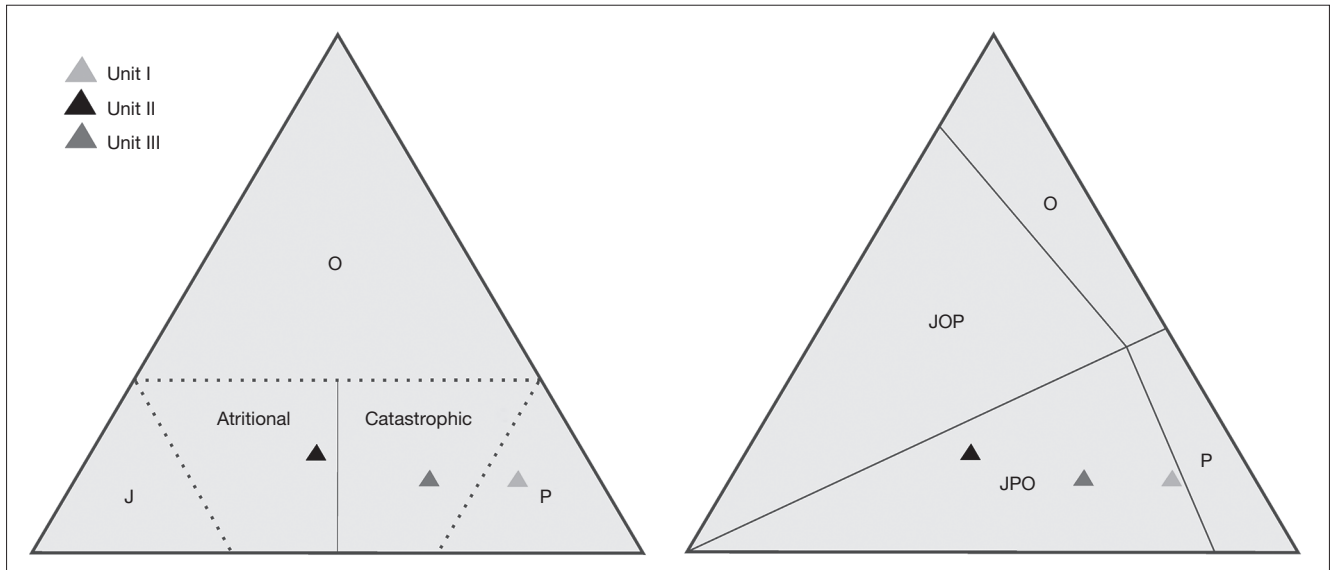


FIG. 3.— Mortality profiles for horse samples. Ternary classification from Stiner (1990) and Discamps & Costamagno (2015). Abbreviations: J, juvenile; P, prime-adult; O, old; JOP, juvenile/old/prime; JPO, juvenile/prime/old.

TABLE 8.— Number of remains and frequency of remains with carnivore modifications by type of bones and anatomical part.

Unit I	Long bones			Flat bones		Articular bones
	Prox. Ep.	Shaft	Dist. Ep.	Cortical	Cancellous	Compact bone
Pits	0/0	0/0	0/0	0/0	0/0	0/0
Scores	0/0	1/16.7	0/0	0/0	0/0	0/0
Punctures	0/0	0/0	0/0	0/0	0/0	0/0
Pitting	0/0	3/50	0/0	0/0	0/0	0/0

Unit II	Long bones			Flat bones		Articular bones
	Prox. Ep.	Shaft	Dist. Ep.	Cortical	Cancellous	Compact bone
Pits	2/0.9	17/7.6	0/0	2/3.4	1/1.7	0/0
Scores	5/2.2	35/15.6	5/2.2	11/19	0/0	4/10
Punctures	1/0.4	2/0.9	0/0	0/0	1/1.7	1/2.5
Pitting	2/0.9	46/20.4	6/2.7	43/74.1	0/0	11/27.5

Unit III	Long bones			Flat bones		Articular bones
	Prox. Ep.	Shaft	Dist. Ep.	Cortical	Cancellous	Compact bone
Pits	0/0	1/14.3	0/0	0/0	0/0	0/0
Scores	0/0	0/0	0/0	0/0	0/0	0/0
Punctures	0/0	0/0	0/0	0/0	0/0	0/0
Pitting	0/0	4/57.1	0/0	2/100	0/0	0/0

ravaging, especially in Unit II, with more moderate activity in Unit III (Fig. 6).

CARNIVORE MODIFICATIONS

In Units I, II, and III, carnivore-induced modification was the most commonly seen on horse bones. Tooth marks and carnivore bone breakage were the most numerous modifications (Table 7). If we exclude isolated teeth when generating the percentages, the rates of carnivore-modified bone increases to 25% in Unit I, 52.8% in Unit II, and 11.8% in Unit III. Anthropogenic modifications were identified exclusively in Units II and III, through the presence of cut marks. In addition, within Unit II, some remains presenting cut marks show a modification coincidence with carnivore tooth marks.

The distribution of tooth marks on the anatomical portions indicated that in Unit I, 33.3% of appendicular elements (NISP: 4/12) had carnivore modifications, while the axial and cranial elements did not. In Unit II, 60.34% of the axial remains (NISP: 35/58), 54.31% of appendicular elements (NISP: 170/313), and 41.67% of cranial elements (NISP: 20/48) bore carnivore modifications. In Unit III, 25% of the axial remains (NISP: 2/8), and 17.02% of appendicular elements (NISP: 8/47) displayed carnivore alterations, while none of the cranial specimens did. With regard to the distribution of tooth marks on long bone portions, the remains from Unit I presented carnivore modifications on 33.3% of the near epiphyses (NISP: 1/3), 25% on the shaft fragments (NISP: 1/4), and there were none on the epiphyses.

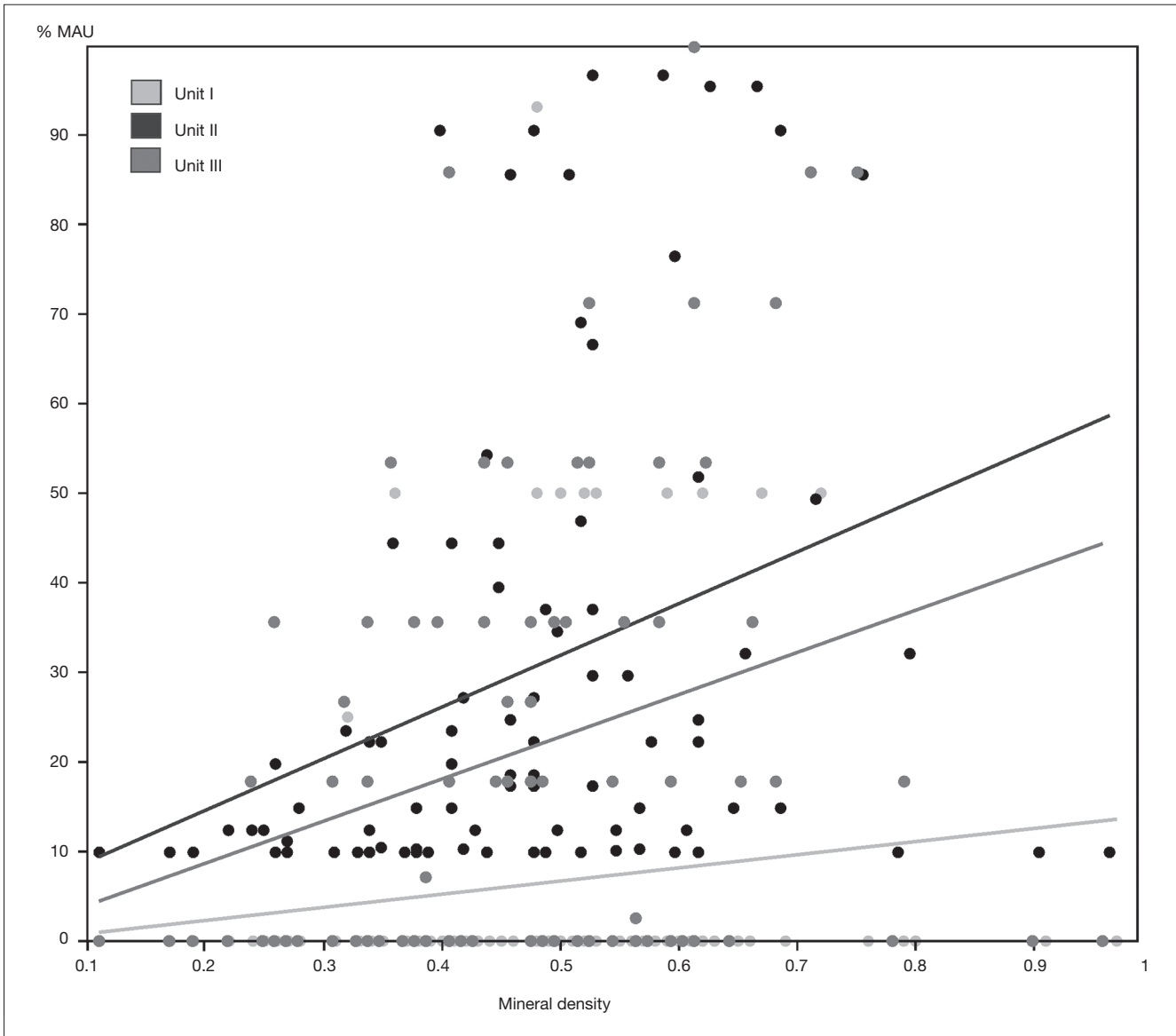


FIG. 4. — Statistical correlation between the standardized expression of the minimum number of animal units (%MAU) and bone mineral density.

TABLE 9. — Number of remains with furrowing on long bones by section. Numerators are for the number of elements with damage. Denominators are for the total number of elements (sections). Frequency are in brackets.

	Humerus prox	Humerus dist	Radius prox	Radius dist	Ulna prox	Femur prox	Femur dist	Tibia prox	Tibia dist	Metapodial prox	Metapodial dist
Unit II	5/9 (55.6)	4/8 (50)	4/11 (36.4)	3/11 (27.3)	1/2 (50)	9/12 (75)	7/19 (36.8)	11/17 (64.7)	3/24 (12.5)	28/74 (37.8)	(36/76 (47.4)
Unit III	1/2 (50)	0/2 (0)	0/2 (0)	0/0 (0)	0/2 (0)	1/6 (16.7)	1/3 (33.3)	0/2 (0)	0/5 (0)	0/6 (0)	1/9 (11.1)

In Unit II, 66.3% of shaft fragments presented modifications (NISP: 59/89), as did 46.03% of the near epiphyses (NISP: 29/63), and 7.7% of the epiphyses (NISP: 1/13). Additionally, 59.7% of the complete long bones evidenced carnivore modifications (NISP: 34/57). Finally, in Unit III, 25% of near epiphyses (NISP: 3/12) presented some type of tooth marks, as did 14.29% of the epiphyses (NISP: 1/7), and 13.1% of the shafts (NISP: 3/23). Cylinders were especially numerous in Unit II (NISP = 68). Tooth marks were abundant on

compact bones, especially phalanx remains (NISP: Unit I = 2; Unit II = 23; Unit III = 1). These modifications could explain the lower presence of these types of bones in the assemblage, as they were probably consumed by carnivores (Cruz-Urbe 1991; Marean 1991). Digested bones were identified exclusively in Unit II, with a total of 17 specimens, comprising 11 complete remains and six bone fragments. The complete remains were: 6 isolated teeth corresponding to the superior and inferior dentition of juvenile and adult individuals; two

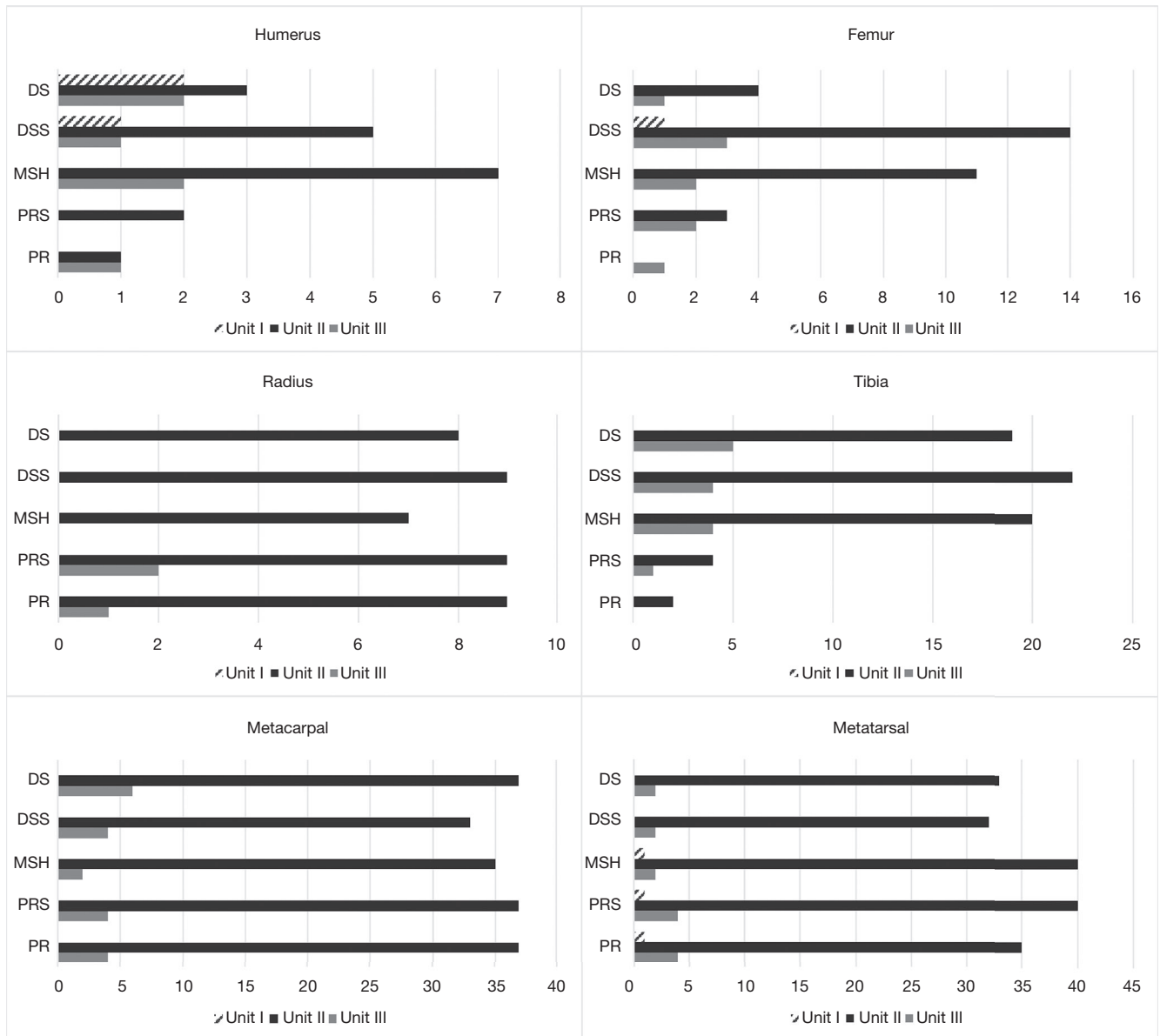


FIG. 5. — Portions of the minimum number of elements (MNE) for limb bones by body size class. Abbreviations: **DS**, distal end; **DSS**, distal shaft; **MSH**, medium shaft; **PRS**, proximal shaft; **PR**, proximal end.

TABLE 10. — Dimensions (length and breadth) of tooth pits in the Unit II. Data include mean values, 95% confidence interval, standard deviation and minimum and maximum values documented at the sample.

		N°	Mean	95% confidence interval lower	95% confidence interval upper	SD	Min	Max
Pits cortical	Width	11	2.58	1.79	3.31	0.84	1.75	4.07
	Length	11	3.83	2.66	4.91	1.45	1.33	6.53
Pits cancellous	Width	8	4.49	2.51	6.41	1.88	2.07	6.82
	Length	8	7.14	4.26	8.8	2.78	4.11	11.98
Scores cortical	Width	104	2.01	1.21	2.38	1.22	0.53	8.13

proximal and two medial phalanges; and one petrosal bone. The fragmented specimens with evidence of digestion were: one tibia fragment; one metapodial; the head of a rib; one calcaneus fragment; and two long bone fragments.

With regard to the type of carnivore modification in Unit I, scores and pits were identified on long bone shafts

(Table 8). In Unit II, tooth marks were identified on all the elements and portions of the horse carcasses. It was possible to verify the presence of pits, scores, punctures, and pitting (Table 8) (Fig. 7). On long bones, the modifications were more abundant on shaft fragments. On flat bones, such as the coxa, pitting modifications were the most abundant

TABLE 11. — Description of CSI and CSII taphotypes (Domínguez-Rodrigo *et al.* 2015) for Bize-Tournal Units and number of epiphyses identified. In brackets number of remains with the same modification.

CSI		
Element		Unit II
Humerus		h4 (2), h15 (7)
Femur		f4 (2), f6, f15 (8)
Radius		r0 (2), r4 (2), r6 (2), r11 (2), r12 (3), r15
Ulna		u9, u12
Tibia		t0, t2 (2), t3 (3), t4 (7), t6 (2), t15 (3)
CSII		
Element	Portion	Unit II
Humerus	Proximal	hp1_3, hp6, hp7, hp5_6_7, hp5_6_8, hp5_6_7_8
	Distal	hd2, hd5_6_7_8
Femur	Proximal	fp0, fp2, fp4, fp1_2, fp2_4, fp1_2_3_4, fp5_6_7_8
	Distal	fd0, fd1_2, fd2_4, fd1_2_3, 4, fd3_4_5_6_7_8, fd5_6_7_8
Radius	Proximal	rp0, rp3, rp5, rp7, rp5_6_7_8
	Distal	rd0, rd1, rd3, rd5, rd5_6_7_8
Ulna	Proximal	up0, up2_7_8
	Distal	ud0
Tibia	Proximal	tp0, tp1, tp3, tp5, tp1_2, tp1_2_3, Tp2_4, tp5_6_7_8, tp6_8
	Distal	td0, td2, td4, td8, td1_2_4, td2_4, td5_6_7_8
Nº epiphyses		30

TABLE 12. — Chi-square analyses of taphotypes samples.

Element	X2	df	p
Femur	136.54	84	0.0002559
Humerus	162.26	78	7.285e-08
Radius	69.223	28	2.388e-5
Tibia	213.14	111	1.968e-8

(Fig. 8). Compact bones showed high degrees of modification, particularly phalanx remains, where 82.1% of the total presented tooth marks. In Unit III pits and pitting were identified on the shafts of long bones (Table 8). Furrowing was well represented, especially on long bone epiphyses (Table 9). Furrowing was the most abundant modification in Unit II, particularly on femur distal epiphyses and tibia proximal epiphyses (Table 9). In Unit III, furrowing was present on proximal humerus, and proximal and distal femur remains (Table 9).

The pit measurements were treated statistically for Unit II, because this unit presented the majority of measurable modifications (Table 10). Unit III had one pit that could be measured, but Unit I had no measurable pits or score marks. With regard to the average dimensions of the pit and puncture marks, and considering their 95% confidence interval, the small size of the sample did not give a statistically significant result (Andrés *et al.* 2012) (Table 10; Fig. 9). However, the size of the modifications suggests the action of at least one large carnivore (Andrés *et al.* 2012; Selvaggio & Wilder 2001) (Fig. 9).

TAPHOTYPE

The results of the taphotype analysis for Unit I are included in Table 11. Differences in bone damage between the assemblage from Unit II and the equid samples modified by lions and hyenas were statistically significant (Table 12). The bootstrapped femur CA showed that the taphotypes indicated equal damage in dimensions 1 and 2 (inertia = 49.2%; inertia = 45.1%) (Appendix 1). The modifications identified in Unit II show similarities with hyena modifications, especially on the proximal femur (Fig. 10A). The bootstrapped humerus CA revealed that taphotypes with greater proximal modifications have more influence in dimension 1 (inertia = 44.6%), whereas humerus taphotypes with distal modifications in dimension 2 (inertia = 30.1%) refer to different types of tooth marking (Appendix 2). This distribution separates the modifications seen in Unit II from lion modifications, although it shows a similar tendency between Unit II and hyenas, with high degrees of modifications (Fig. 10B). The bootstrapped radius CA showed a two-dimensional solution, accounting for 100% of the inertia. Dimension 1 (inertia = 80.9%) showed the high degrees of bone destruction in Unit II in contrast to low levels of modification by lions (Fig. 11A) (Appendix 3). The bootstrapped tibia CA showed that taphotypes with greater modification have more influence on dimension 1 (inertia = 43.9%), corresponding to captive hyenas and lions, whereas tibia taphotypes with lower modifications influence dimension 2 (inertia = 30.1%), corresponding to Tarangure lions and the Unit II assemblage (Fig. 11B; Appendix 4). These results indicate that the modifications of long bones in Unit II are similar to the modifications generated by hyenas. Even in cases where similarities with hyena modifications were not observed, the modifications in Unit II were still different to modifications caused by lions.

ANTHROPOGENIC MODIFICATIONS

Anthropogenic modifications were scarce in Units II and III, and non-existent in Unit I. Cut marks were identified on six specimens in Unit II and five in Unit III (Table 13). Anthropogenic bone breakage was not identified. In Unit II, the cut marks were on long, flat bones, and in Unit III only at long bones. The cuts were exclusively slice marks (Fig. 13).

In Unit II, cut marks were located on two femurs, two tibias, one mandible, and one coxa (Table 13). In Unit II defleshing activities were identified (Fig. 12): one femur showed a slice mark on the cranial side of the midshaft and on the inferior part of the supracondylar fossa, the first probably related to the extraction of the vastus intermedius muscle, and the second with the extraction of gastrocnemius muscle; the tibia had an incision on the popliteus line and lateral edge, both related to the extraction of popliteus muscle; the coxa had cut marks on the inferior edge related to the extraction of the iliac muscle; finally, on the mandible, the cut marks were documented on the labial face, below M2, related to the extraction of the masseter muscle. In Unit III, cut marks were found on two humeri, two

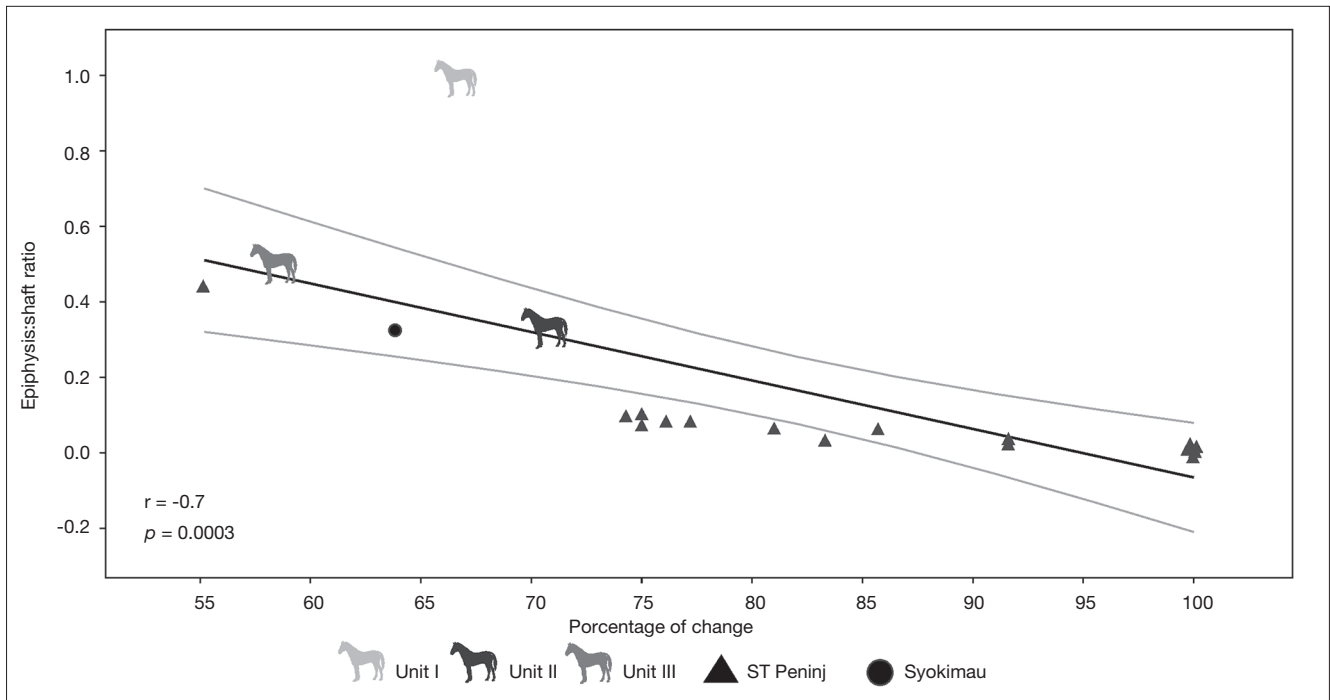


FIG. 6. — Distribution of epiphysis/shaft ratio and percentage of change from Bize-Tournal data, Peninj (Domínguez-Rodrigo *et al.* 2002) and hyena den of Syokimau (Egeland *et al.* 2008).

TABLE 13. — Number of remains with cut marks by type of element, location, morphology of marks and butchering activities.

	Element	Number of remains with cut marks	Location	Cut marks morphology	Activity
Unit II	Mandible	1	Labial face	Slicing marks	defleshing
	Coxa	1	lower edge of the neck of the ilium	Slicing marks	defleshing
	Femur	2	Supracondylar fossa/lateral edge	Slicing marks	defleshing
	Tibia	2	Popliteus line/lateral edge	Slicing marks	defleshing
Unit III	Humerus	2	Epicondylar crest	Slicing marks	defleshing
	Femur	1	Trochanter minor	Slicing marks	defleshing
	Tibia	2	Popliteus line	Slicing marks	defleshing

tibias, and one femur (Table 13). The distribution of cut marks on the Unit III remains indicated defleshing as the only butchering activity: the tibia remains presented slice marks on the popliteus line and on the medial side of the midshaft, related to the extraction of the popliteus muscle or medial flexor muscle; the humeri presented an incision on the epicondylar ridge, related to extraction of the anconeus muscle, and posterior midshaft for the extraction of the coracobrachialis muscle; the femur had cut marks on the posterior side of the midshaft, related to the extraction of the vastus intermedius muscle.

In both units, the long limb bones with cut marks also presented green bone breakage features. This combination of cut marks and green breakage has been related to early access to animal carcasses by humans (Capaldo 1997; Domínguez-Rodrigo & Barba 2006; Domínguez-Rodrigo & Pickering 2003; Selvaggio 1994, 1998).

In Unit II, two remains with cut marks also presented carnivore tooth marks: one femur with scooping-out, and one coxal bone with pitting. In Unit III, none of the specimens with cut marks presented carnivore modifications.

TABLE 14. — Percentage of remains with post-depositional modifications of the three units.

	Unit I	Unit II	Unit III
Concretions	31.4	32.8	25.7
Manganese oxides	25.5	20.2	9.3
Fissures	17.6	32.8	17.1
Rounding	23.5	32.8	16.7
Polishing	19.6	28.6	16
Trampling		2.2	0.4

POST-DEPOSITIONAL MODIFICATIONS

The most common post-depositional modifications in Unit I were sediments cemented onto bones, followed by manganese oxides stains and rounding. In addition, polishing and fissures were identified (Table 14). In Unit II, rounding, fissures and concretions presented the greatest proportions, followed by polishing and manganese oxide. Trampling was also identified. Finally, in Unit III concretions were the most common post-depositional modification, followed by fissures, rounding and polishing. Manganese oxide stains and trampling were identified.



FIG. 7. — Horse remains from Unit II modified by carnivore activity: **A**, humerus with pitting and carnivore breakage; **B**, radius with scores, pits and heavy furrowing; **C**, femur with scores, heavy furrowing and pits over fracture edge; **D**, tibiae with heavy pitting. Photos: Denis Dainat, EPCC CERP Tautavel. Scale bar: 1 cm.

DISCUSSION

The analysis of horse remains from Units I, II, and III from Bize-Tournal Cave has provided information of the origin and processes that affected the formation of the faunal assemblages. The results indicate that hominins played a minor role in the taphonomic history of the horse specimens. The main accumulator and modifier seem to have been carnivores, particularly in the formation of the Unit II assemblage. Finally, the major post-depositional modifications were concretions and rounding, due to the action of water flow, of diverse intensities, that affected part of the assemblages.

Previous research point to hominins as the principal accumulators of horses, and in Unit II shared with a primary and secondary of carnivores (Magniez 2009, 2010; Magniez & Boulbes 2014). According to these proposals, the equid carcasses were brought back in large portions after primary treatment at the kill site to discard the axial skeleton. Horse family groups were hunted from summer to autumn, generating mortality profiles dominated by prime adults. Carnivore modifications are common on bones from Mousterian and

Aurignacian units, but the majority have been explained as a product of secondary access to carcasses by carnivores after the hominids abandoned the site. Those assemblages were only slightly affected by natural post-depositional processes (Magniez 2009, 2010; Magniez & Boulbes 2014).

Alternating carnivore and hominin occupations would indicate short human occupations (Aura *et al.* 2002; Daujeard & Moncel 2010; Stiner 1991a; Valensi 2000). According to Costamagno *et al.* (2006), the presence of carnivore tooth marks in the bone assemblages indicates short occupations; this should be considered an additional argument that corroborates other evidence of short-term occupation. Long-term residential camps, such as the French sites of Baume des Peyrards, show a specialised hunting spectrum while short-duration sites, such as Payre-F, Baume Flandin, and Le Figuier (France), show a varied faunal spectrum (Daujeard & Moncel 2010). According to these criteria and the results from this work, we agree that the hominin occupations were short, even expedite, in the three units. However, we cannot underestimate the role of carnivores, particularly hyenas, in the accumulations and/or modification of Units I, II, and III at Bize-Tournal Cave.

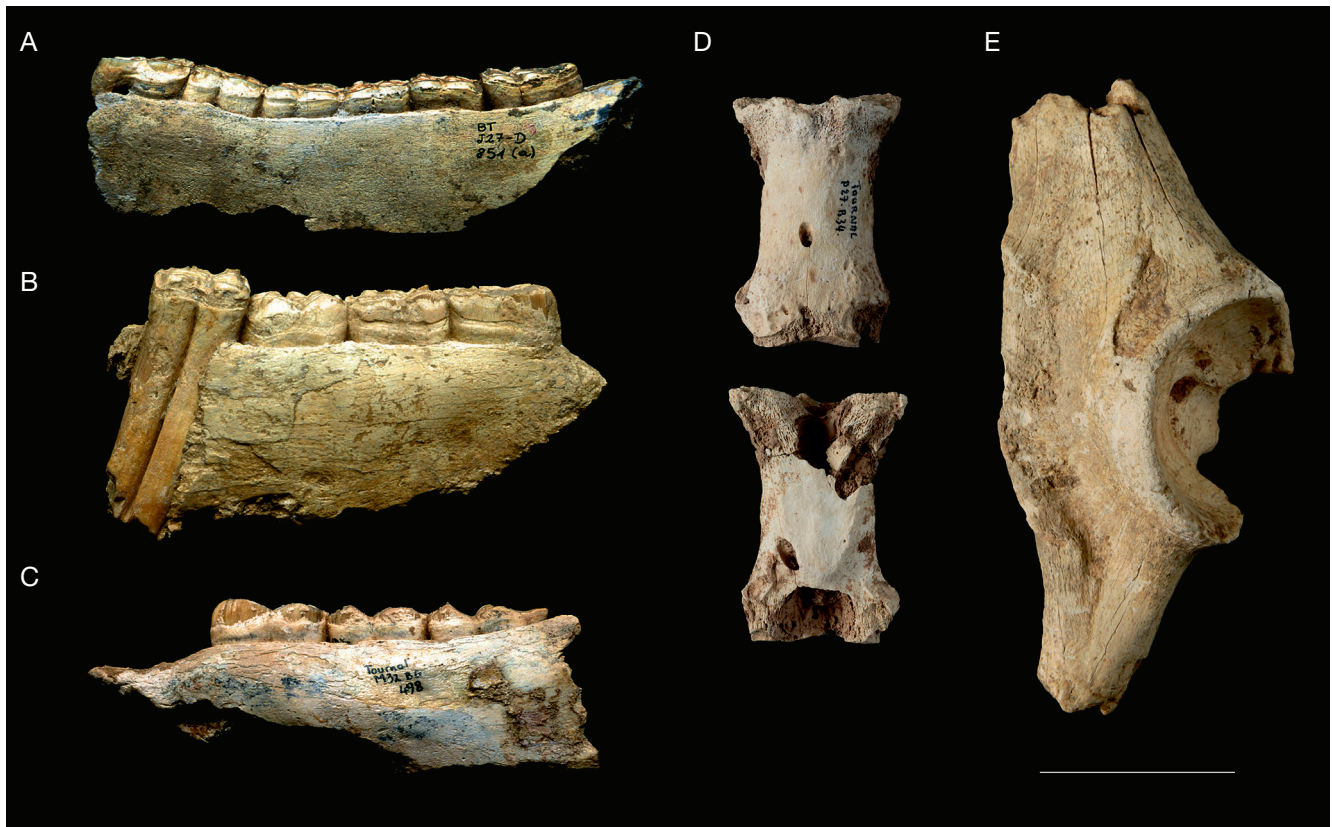


FIG. 8. — Horse remains from Unit II modified by carnivore action: **A**, mandible of old individual; **B**, mandible of prime adult with pitting; **C**, mandible of juvenile individual with two pits on fracture edge; **D**, first phalanx with marks of high digestions; **E**, coxal with pitting on the ilion and ischium extremes and scores at the acetabulum fossa. Photos: Denis Dainat, EPCC CERP Tautavel. Scale bar: 1 cm.

Multiple specialists have proposed a predominance of juvenile and subadult hyena as a factor characterising hyena dens (Cruz-Urbe 1991; Klein *et al.* 1991; Stiner 1991a). However, the research of Pickering (2002) and Kuhn *et al.* (Kuhn *et al.* 2010) highlighted the fact that an abundance of juvenile individuals together with an abundance of coprolites were the most convincing features for classifying a hyena accumulation. According to the proportions of hyena remains from juvenile, adult, and old individuals it is possible to distinguish between cub-raising dens, with a dominance of juvenile remains (more than 50%); communal dens with equal proportions of the ages or even a tendency towards more adult and old remains; and prey depot dens, dominated by adult remains (Diedrich 2011a, 2012). A predominance of juvenile individuals has been observed in archaeological hyena dens from Grotta di Guattari (Italy) (Stiner 1991b), the sites of Equus Cave and Swartklip (South Africa) (Cruz-Urbe 1991; Klein *et al.* 1991), Manot Cave area D (Israel) (Orbach & Yeshurun 2019), Nad Kakakem Cave and Bad Wildungen hyena dens (Germany) (Diedrich 2013), at the French sites of Fouvent (Fourvel *et al.* 2014), La Chauverie and Camiac (Discamps *et al.* 2012) and on the Iberian Peninsula at Furninha Cave (Portugal) (Brugal *et al.* 2012), Cova del Gegant (Spain) (Samper Carro & Martínez-Moreno 2014), and El Buho Cave (Sala *et al.* 2012), among others. These characteristics

were recorded in previous works on Bize-Tournal Cave. In Units I, II, and III, carnivore remains (Unit I: NISP = 14; Unit II: NISP = 443; Unit III: NISP = 72) represent 33% of MNI in Unit I, 34% in Unit II, and 28% in Unit III (Magniez 2009). The hyena mortality profiles indicate that the three age groups were present in the same proportions (Magniez 2009). Additionally, a great number of coprolites were found in Unit I (n = 125), Unit II (n = 389), and Unit III (n = 67). They seem to be mainly attributable to the cave hyena. The quantity and the great accumulation, indicated long occupation of hyenas or their used as a recurrent communal den (Magniez 2009).

The horse remains found in the Bize-Tournal units are dominated by skulls and long limb bones, especially metapodials, with low percentages of axial skeleton (except for coxa in Unit II) and compact bones. The scarcity of axial elements and compact bones is consistent with work on actualistic studies and fossil assemblages that have been modified by carnivores (Capaldo 1998; Marean *et al.* 1992; Pickering *et al.* 2003). These anatomical profiles are similar at other sites inhabited by hyenas in a similar manner (Brugal *et al.* 1997; Diedrich 2011b; Fosse 1996, 1995; Fourvel & Fosse 2017; Fourvel *et al.* 2014; Stiner 1991b). Modern spotted hyenas also transport zebra carcasses, resulting in a similar overrepresentation of distal long limb bones, as well as large quantities of teeth from crushed skulls (Kruuk 1972).

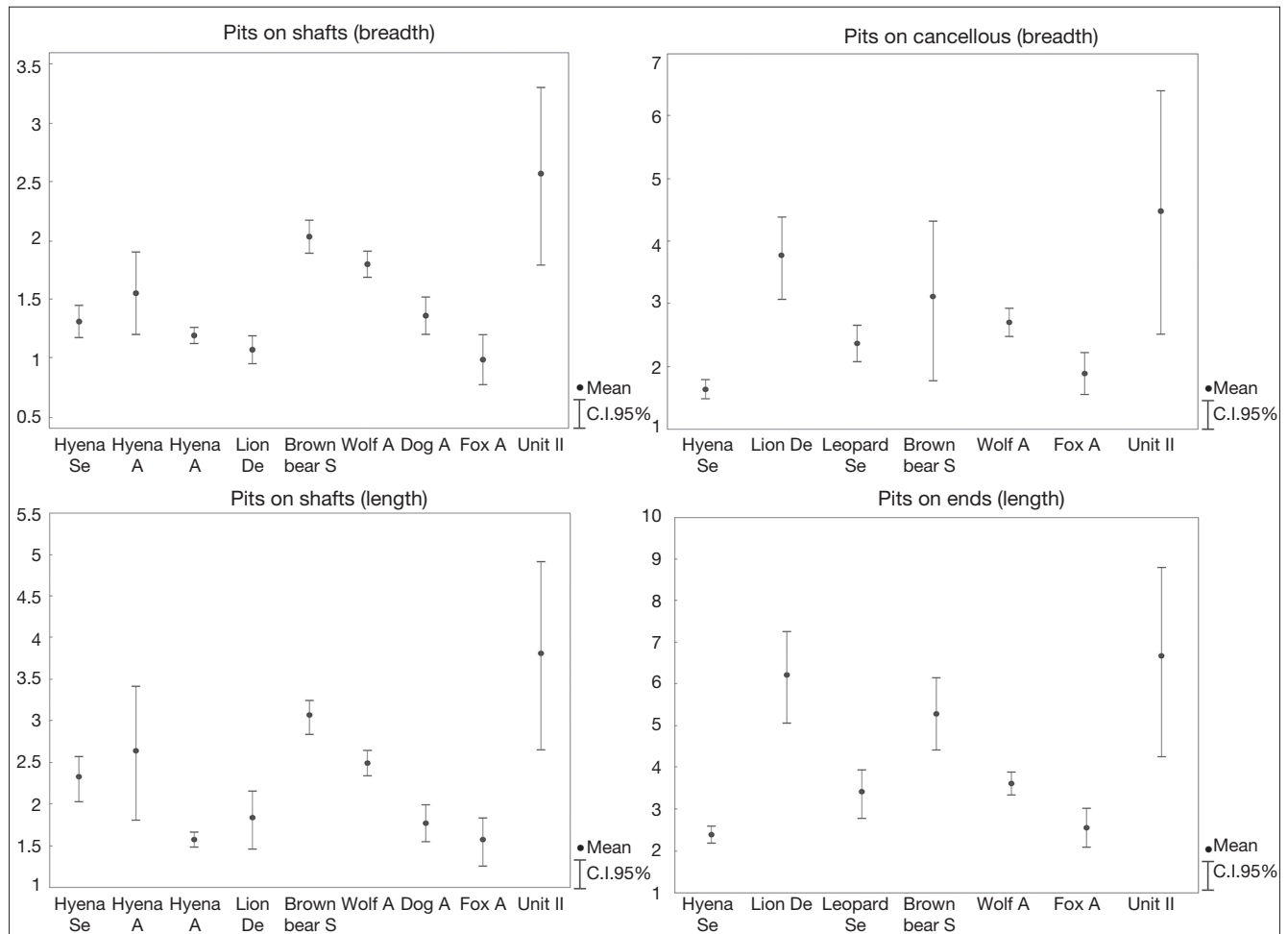


FIG. 9. — Mean percentages and one S.D. of tooth pit sizes stratified by bone type (dense cortical, cancellous), and by length and width. Data for sampled/specimens marked by **A** from Andrés *et al.* (2012), with **D** from Domínguez-Rodrigo & Piqueras (2003) and with **S** from Saladié *et al.* (2013).

In addition, it has been proven that this species has the capacity to transport large animal elements (Egeland *et al.* 2008; Kruuk 1970, 1972; Lam 1992; Pokines & Peterhans 2007). Present-day spotted hyenas can move a complete carcass over long distances to protect the prey from other carnivores (Kruuk 1972). This supports the fact that these animals would have been able to transport the horse segments to Bize-Tournal Cave.

The mortality profiles identified for horses in the three units are: prime-adult dominated (Unit I); catastrophic (Unit III); and attritional (Unit II), no different to those generated by present-day carnivores (Stiner 1990) (Fig. 13). A prime adult dominated profile is not always an indicator of selective hunting, this can be dependent on the hunted groups. In Unit I, the prime-adult dominated profile may be related to hunting episodes when adult male horses aggregated, at the beginning of autumn (Denzau & Denzau 1999; Klimov 1988). In addition, it is not always possible to confidently distinguish L-shaped and U-shaped profiles on a ternary diagram (Discamps & Costamagno 2015). Therefore, the results from Units II and III, which also demonstrate a similar seasonality, indicate that there were similarities in the choice of prey. The profiles identified in

Unit II and Unit III are similar to those generated by cursorial hunters, like hyenas (Cruz-Urbe 1991). Additionally, the same type of mortality profile has been observed at various archaeological and palaeontological sites with carnivore bone accumulation, like Fouvent (France) (Fourvel *et al.* 2014), Llonin Cave (Spain) (Sanchis *et al.* 2019), and Level TD6.3 of Gran Dolina Cave (Saladié *et al.* 2017). The eruption pattern and wear stages of juvenile dentition indicate that the juvenile horses of Unit I died during the end of summer and beginning of autumn, while those from Units II and III died in various periods of the year. Previously, it was proposed that reindeer hunting involved the capture of isolated individuals (Magniez 2009). The wide seasonal range observed for horses could indicate a similar scenario.

Another aspect of hyena assemblages to consider is the low proportion of long limb bone epiphyses with respect to the abundance of diaphyses (Egeland *et al.* 2008; Pickering 2002), and the relative abundance of shaft cylinders (Kuhn *et al.* 2010; Prendergast & Domínguez-Rodrigo 2008). Positive percentages of change values indicate severe epiphysis loss, and low values for the epiphysis/shaft ratio indicate the intensity of carnivore bone destruction, in addition to

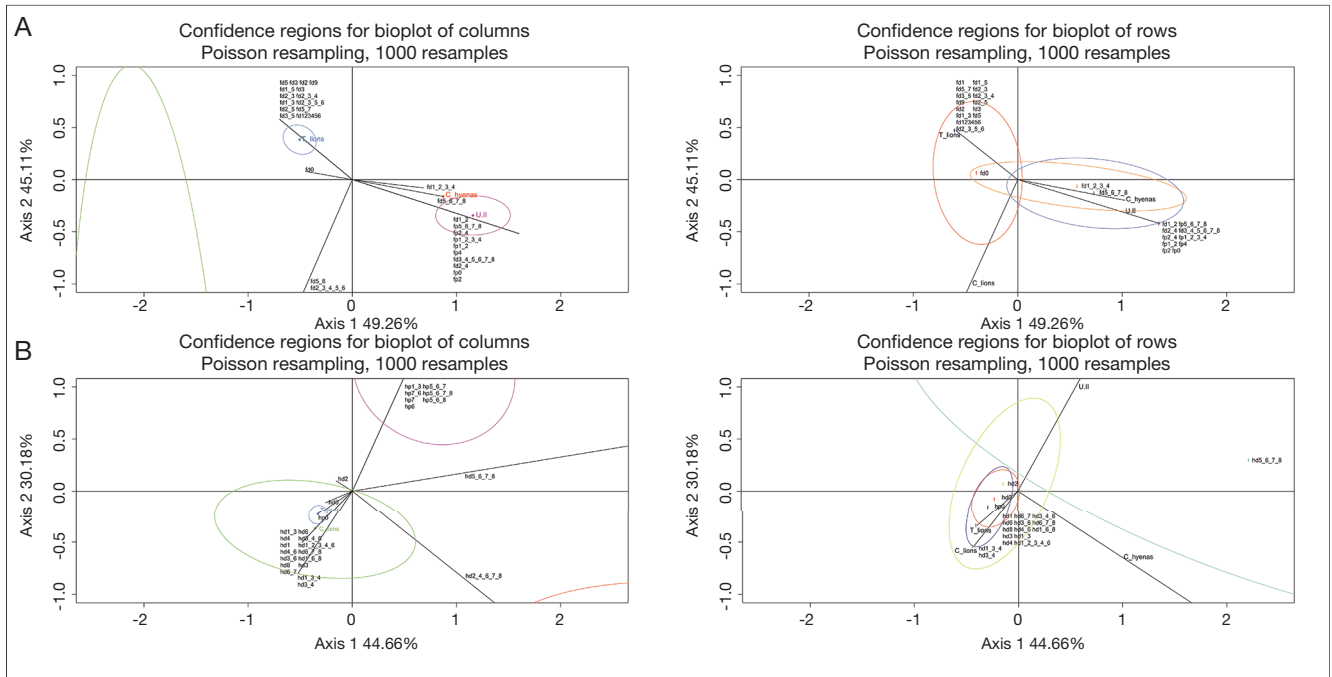


FIG. 10. — Biplots of the bootstrapped CA of each meat-bearing long bone showing the relationship between carnivore and unit II with respect to the taphotypes that determine them: **A**, femur; **B**, humerus. Ellipses with 95% confidence intervals for carnivore (left) and taphotypes (right) are also displayed. Length of the axes shows the importance of the contribution of each variable to the inertia.

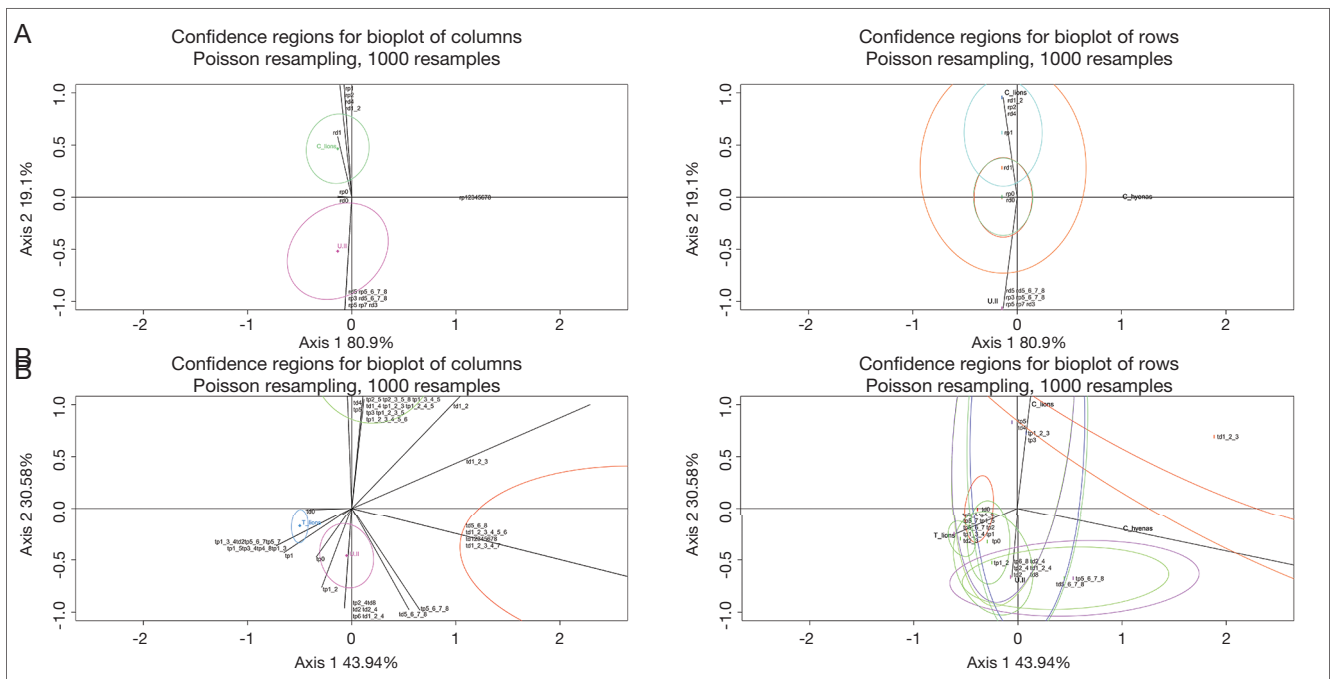


FIG. 11. — Biplots of the bootstrapped CA of each meat-bearing long bone showing the relationship between carnivore and unit II with respect to the taphotypes that determine them: **A**, radius; **B**, tibia. Ellipses with 95% confidence intervals for carnivore (left) and taphotypes (right) are also displayed. Length of the axes shows the importance of the contribution of each variable to the inertia.

a high level of competition between scavengers (Blumenschine & Marean 1993). Egeland *et al.* (2008) indicated that a negative and highly significant relationship for the linear regression between values of percentage of change and the epiphysis/shaft ratio indicated intense ravaging

by carnivores. The results of the linear regression between shaft/epiphysis ratio and percentage of Bize-Tournal Cave units indicate a scenario of moderate competition between carnivores. Cruz-Urbe (Cruz-Urbe 1991) indicated that an elevated presence of limb bones with relatively complete

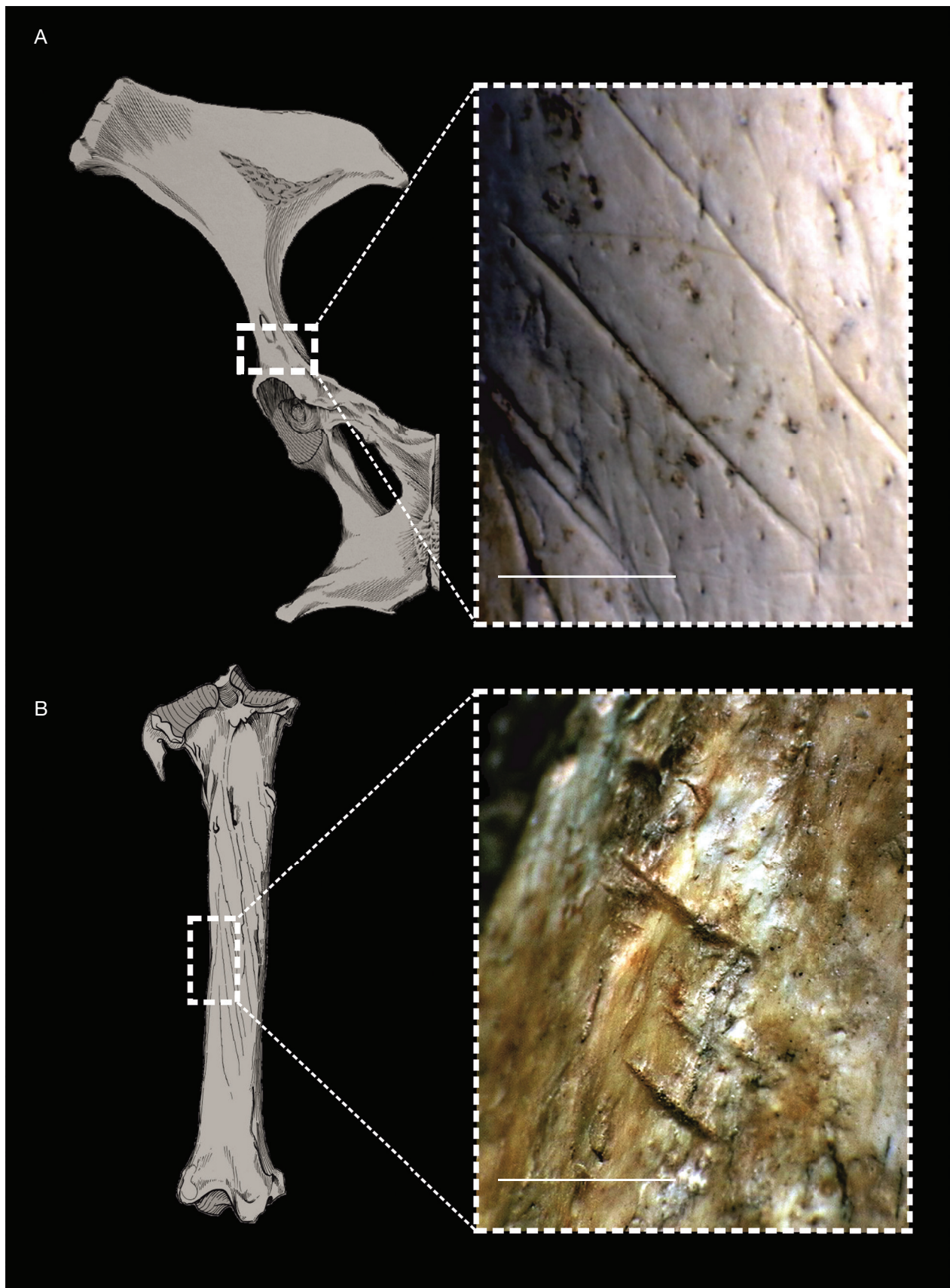


FIG. 12. — Examples of cut marks from Unit II: **A**, slicing marks over lower edge of the neck of the ilium of a coxal; **B**, slicing marks over popliteus line of a tibia. Photos: Juan Marín, IPH. Drawings: modified from Pales & Lambert (1971). Scale bars: 2 mm.

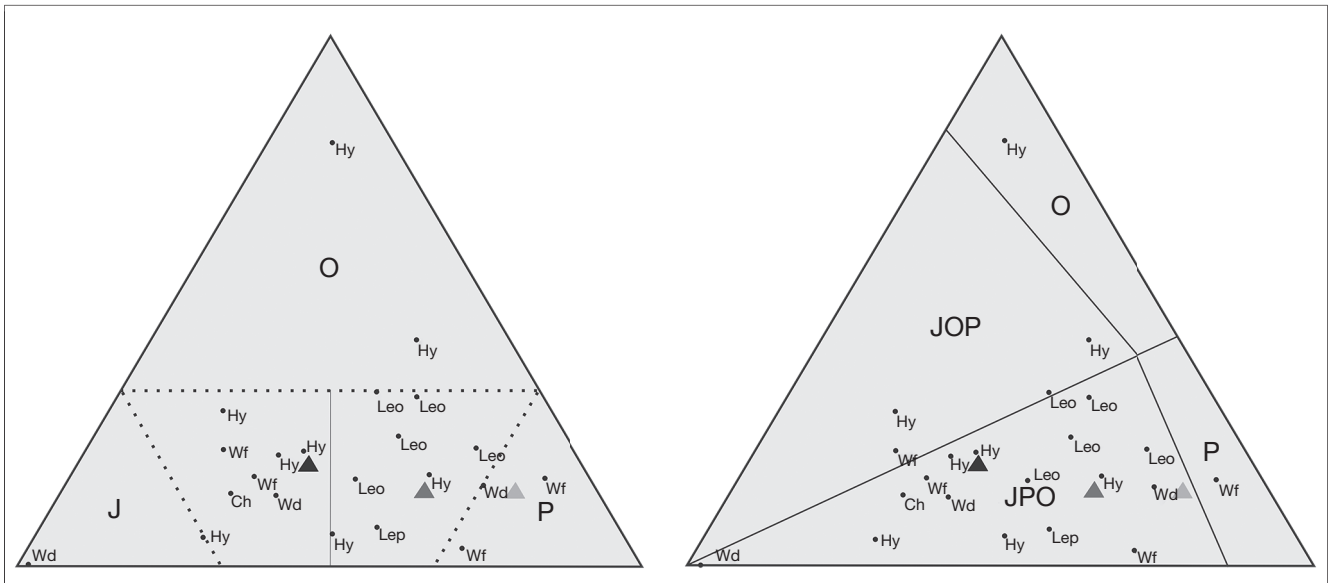


FIG. 13. — Mortality profiles for Bize-Tournal units and current carnivore samples from Stiner (1990). Abbreviations: **Hy**, hyena; **Wf**, wolf; **Tr**, tiger; **Leo**, lion; **Ch**, chita; **Lep**, leopard.

shafts along with a lack of epiphyses is a good indicator of hyena accumulations. In all units the proportion of long bones with complete circumferences was very high. Additionally, cylinders were numerous in Unit II, with a total number of 68 remains. However, according to Kuhn *et al.* (2010) cylinders alone indicate carnivore involvement in the formation of the assemblage, not exclusively hyenas, because lions and leopards could produce similar cylindrical fragments.

Moreover, the bone surface modification analysis of the horse specimens from Units I, II, and III shows that the assemblages were principally modified by carnivores. Magniez (2008, 2009) points to the possibility that carnivores had secondary access to animal carcasses abandoned by hominins in all the units, although their activity was greatest in Unit II. Use of the same space by hominins and carnivores is well attested (Brain 1981; Domínguez-Rodrigo & Lezana 1996; Kruuk 1972; Prendergast & Domínguez-Rodrigo 2008; Saladié *et al.* 2017), so it is common to find elements modified by both agents (Egeland *et al.* 2008). However, only on two specimens from Unit II was there coincidence between anthropogenic and carnivore modifications on the same remain. These were a coxa and a femur: the cut marks were related to defleshing; while the carnivore modification involved pitting on the two fragments, which could indicate posterior scavenging of elements abandoned by hominins. The low percentage of remains with co-occurrence of anthropogenic and carnivore modifications has been interpreted as a signal of great independence between the two groups, linked to a low level of competition (Egeland *et al.* 2008). In addition, the absence of anthropogenic bone breakage compared with the enormous number of remains fractured by carnivores, supports the idea that the majority of the elements were transported and accumulated by carnivores. However, the hyenids could destroy the anthropogenic traces and altered a first human breakage.

The types of modifications, their distribution on the bones, and the tooth mark measurements evidence that a large carnivore was involved during the formation of the assemblage. The taphotype analysis indicates that the consumption of epiphyses, especially femur and humerus, were closer to the action of hyenas, rather than large felids. Furthermore, the presence of numerous digested bones, including a phalanx, and even teeth, indicates the activity of a durophagous carnivore with a metabolism capable of assimilating the nutrients from these bones (Brain 1981; Kruuk 1972; Pickering 2002). Pitting is also characteristic of carnivore den sites or resting places (Binford 1981).

We cannot rule out the possibility that part of the assemblages from Units I, II, and III of Bize-Tournal Cave could have resulted from the ravaging of bones left behind by human groups. Indeed, some remains with both carnivore- and hominin-induced modifications indicate that this scenario was possible. However, the absence of anthropogenic bone breakage and the low percentages of cut marks, along with the large quantity of carnivore modifications, does not support this assertion for the majority of the assemblages. The anatomical distribution, like that seen in other carnivore accumulations, and the mortality profiles, especially in Units II and III, indicate that the main bone accumulation agents were carnivores. In addition, in Unit II, it seems that hyenas were solely responsible for the formation of the horse assemblage, with possible secondary action by other carnivores. An interesting point is that although the volume of horse remains in the Mousterian units differed with respect to the Aurignacian Unit, we found no great differences in the composition of the three samples. The anatomical profiles, dominated by cranial and distal long limb bones, the taphonomic signal, with a high percentage of carnivore damage and little evidence of human activities, indicate that the use of the cave

by Mousterian and Aurignacian groups did not change with respect to the accumulation of horses. This would indicate that the contribution of carnivores, especially hyenas, and their modifications was likely to have been similar, with sporadic hominin occupation.

CONCLUSIONS

Assemblages generated by hyenas are characterised by abundant coprolites and juvenile hyena remains, an abundance of carnivore bone breakage, the presence of cylinders, digested bones, and damage like scoring, pitting, punctures, furrowing, scooping-out, and principally U-shaped prey mortality profiles. Analysing the horse remains from Units I, II, and III from Bize-Tournal Cave has enabled us to identify most of these characteristics, particularly in Unit II. The anatomical distribution is similar to that seen in other carnivore accumulations, and the mortality profiles, especially in Units II and III, indicate that the main agents of bone accumulation were carnivores. The type, distribution, and features of the modifications, together with the taphotype analysis indicate that large durophagous carnivores were involved in the formation of the assemblage, probably hyenas.

Hominins played a minor role in the horse accumulations, although part of the assemblage could have resulted from the ravaging of bones left behind by human groups. No great differences were found in the composition and features of the three units. The systematic analysis of the bone splinters of the studied levels contributed to complete the study of horse remains. The accumulation of horses in Bize-Tournal Cave during the Mousterian and Aurignacian did not change and was characterised by sporadic hominin occupation. This would indicate that the horse remains were introduced and modified in the cave, mainly by carnivores. In this context, it must be considered that carnivores have a more important role than suggested in the previous studies where the impact was clearly identified on the bones of megaceros, deer and ibex.

Acknowledgements

We want to express our deepest gratitude all the researchers and the fieldwork team of the Bize-Tournal and the Centre européen de recherche préhistoriques of Tautavel for the support. We thank the editor and the reviewers for their help and suggestions that improved the original version of the manuscript. This work was supported by the Ministerio de Economía, Industria y Competitividad/Fondo Europeo de Desarrollo Regional [PGC2018-093925-B-C32] and [HAR2016-76760-C3-1-P]; the Agencia de Gestio d'Ajuts Universitaris i de Recerca project number [SGR 2017-1040]; the Univeritat Rovira i Virgili [2014, 2015 and 2016 PFR-URV-B2-17]; the Departament de Cultura de Generalitat de Catalunya [100576, 2014] and is framed in Centres de Recerca de Catalunya Programme/ Generalitat

de Catalunya; The Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA) has received financial support from the Spanish Ministry of Science and Innovation through the “María de Maeztu” program for Units of Excellence (CEX2019-000945-M). Juan Marín is the beneficiary of an Erasmus Mundus Doctorate scholarship for an International Doctorate in Quaternary and Prehistory (IDQP). Antonio Rodríguez-Hidalgo is the beneficiary of a postdoctoral scholarship from the MICINN, Subprograma Juan de la Cierva (IJC-037447-I).

REFERENCES

- ANDRÉS M., GIDNA A. O., YRAVEDRA J. & DOMÍNGUEZ-RODRIGO M. 2012. — A study of dimensional differences of tooth marks (pits and scores) on bones modified by small and large carnivores. *Archaeological and Anthropological Sciences* 4: 209-219. <https://doi.org/10.1007/s12520-012-0093-4>
- ARILLA M., ROSELL J., BLASCO R., DOMÍNGUEZ-RODRIGO M. & PICKERING T. R. 2014. — The “Bear” Essentials: Actualistic Research on *Ursus arctos arctos* in the Spanish Pyrenees and Its Implications for Paleontology and Archaeology. *PLOS ONE* 9: e102457. <https://doi.org/10.1371/journal.pone.0102457>
- ARRIAZA M. C., DOMÍNGUEZ-RODRIGO M., YRAVEDRA J. & BAQUEDANO E. 2016. — Lions as Bone Accumulators? Paleontological and Ecological Implications of a Modern Bone Assemblage from Olduvai Gorge. *PLOS ONE* 11: e0153797. <https://doi.org/10.1371/journal.pone.0153797>
- AURA J. E., BONILLA V. V., RIPOLL M. P., VALLE R. M. & CALATAYUD P. G. 2002. — Big Game and Small Prey: Paleolithic and Epipaleolithic Economy from Valencia (Spain). *Journal of Archaeological Method and Theory* 9, 215-268. <https://doi.org/10.1023/A:1019578013408>
- BECKER B. & REED C. A. 1993. — Studies of the bone detritus of the striped hyena (*Hyaena hyaena*) at a site in Egyptian Nubia, and the interaction of the bone breakage by striped hyenas. *Skeletons in her Cupboard*. Oxbow Monographs 34: 157e182.
- BINFORD L. R. 1981. — *Bones: Ancient men and modern myths*. First edition, Academic Press, New York, 320 p.
- BINFORD L. R. 1984. — *Faunal remains from Klässies River Mouth*. Academic Press, New York, 283 p.
- BISCHOFF J. L., JULIA R. & MORA R. 1988. — Uranium-series dating of the Mousterian occupation at Abric Romani, Spain. *Nature* 332: 68-70. <https://doi.org/10.1038/332068a0>
- BLUMENSCHINE R. & MAREAN C. 1993. — A carnivore's view of archaeological bone assemblages, in *From Bones to Behavior: Ethnoarchaeological and Experimental Contributions to the Interpretation of Faunal Remains*. Southern Illinois University Center for Archaeological Investigations, Carbondale: 273-300.
- BOULBES N. & VAN ASPEREN E. N. 2019. — Biostratigraphy and Palaeoecology of European *Equus*. *Frontiers in Ecology and Evolution* 7: 301. <https://doi.org/10.3389/fevo.2019.00301>
- BOYLE K. V. 2000. — Reconstructing Middle Palaeolithic subsistence strategies in the South of France. *International Journal of Osteoarchaeology* 10: 336-356. [https://doi.org/10.1002/1099-1212\(200009/10\)10:5<336::AID-OA560>3.0.CO;2-5](https://doi.org/10.1002/1099-1212(200009/10)10:5<336::AID-OA560>3.0.CO;2-5)
- BRAIN C. K. 1981. — *The hunters or the hunted?: an introduction to African cave taphonomy*. University of Chicago Press: 384.
- BRUGAL J.-P. & FOSSE P. 2004. — Carnivores et Hommes au Quaternaire en Europe de l'Ouest. *Revue de Paleobiologie* 23: 575-595.
- BRUGAL J.-P., FOSSE P. & GUADELLI J.-L. 1997. — Comparative study of bone assemblages made by recent and Pleistocene Hyenids., in *Proceedings of the 1993 Bone Modification Conference, Hot Springs, South Dakota*. Archeology Laboratory, Augustana College, Sioux Falls, Occasional Publication: 158-187.

- BRUGAL J.-P., ARGANT J., CRISPIM J. A., FIGUEIREDO S., SERRA A. M. & PALMQVIST P. 2012. — The complex carnivore-rich assemblages from Furninha (Peniche, Portugal): a multidisciplinary approach. *Journal of Taphonomy* 10: 417-438.
- BUNN H. T. 1983. — Comparative analysis of modern bone assemblages from a San hunter-gatherer camp in the Kalahari Desert, Botsuana, and from a spotted hyena den near Nairobi, Kenya. *Animals and Archaeology: Hunters and their prey* Ser. 163: 141-148.
- BURKE A. 2002. — Palaeoethology as an archaeological tool: a model for the social and spatial behaviour of *E. hydruntinus*, in *Equids in Time and Space Papers in Honour of Vera Eisenmann*. Presented at the Proceedings of the 9th Conference of the International Council of Archaeozoology, Durham, August 2002, ALBARELLA U., DOBNEY K. & ROWLEY-CONWY P. (eds ser.), Oxbow Books, Park End Place, Oxford: 62-69.
- CAPALDO S. D. 1997. — Experimental determinations of carcass processing by Plio-Pleistocene hominids and carnivores at FLK 22 (Zinjanthropus), Olduvai Gorge, Tanzania. *Journal of Human Evolution* 33: 555-597. <https://doi.org/10.1006/jhev.1997.0150>
- CAPALDO S. D. 1998. — Methods, marks, and models for inferring hominid and carnivore behavior. *Journal of Human Evolution* 35: 317-320. <https://doi.org/10.1006/jhev.1998.0242>
- CHACÓN M. G. 2009. — El Paleolítico medio en el suroeste europeo: Abric Romaní (Capellades, Barcelona, España) Payre (Rompón, Ardèche, Francia) y Tournal (Bize, Aude, Francia). Análisis comparativo de los conjuntos líticos y los comportamientos humanos. Universitat Rovira i Virgili, Tarragona, 607 p.
- CHASE P. G. 1989. — How different was Middle Palaeolithic subsistence? A zooarchaeological perspective on the Middle to Upper Palaeolithic transition, in MELLARS P. & Stringer C. (eds), *The Human Revolution: Behavioural and Biological Perspectives on the Origins of Modern Humans*. Edinburgh University Press, Edinburgh: 321-327.
- CLARK G. A. 1997. — The middle-upper paleolithic transition in Europe: An American perspective. *Norwegian Archaeological Review* 30: 25-53. <https://doi.org/10.1080/00293652.1997.9965608>
- COSTAMAGNO S., MEIGNEN L. M., BEAUVAL C. B., VANDERMEERSCH B. ET MAUREILLE B. 2006. — Les Pradelles (Marillac-le-Franc, France): A Mousterian reindeer hunting camp? *Journal of Anthropological Archaeology* 25: 466-484. <https://doi.org/10.1016/j.jaa.2006.03.008>
- CRUZ-URIBE K. 1991. — Distinguishing Hyena from Hominid Bone Accumulations. *Journal of Field Archaeology* 18: 467-486. <https://doi.org/10.1179/009346991791549068>
- DAUJEARD C. & MONCEL M.-H. 2010. — On Neanderthal subsistence strategies and land use: A regional focus on the Rhone Valley area in southeastern France. *Journal of Anthropological Archaeology* 29: 368-391. <https://doi.org/10.1016/j.jaa.2010.05.002>
- DELANEY-RIVERA C., PLUMMER T. W., HODGSON J. A., FORREST F., HERTEL F. & OLIVER J. S. 2009. — Pits and pitfalls: taxonomic variability and patterning in tooth mark dimensions. *Journal of Archaeological Science* 36: 2597-2608. <https://doi.org/10.1016/j.jas.2009.08.001>
- DENZAU G. & DENZAU H. 1999. — *Wildesel*. Jan Thorbecke Verlag, Stuttgart: 221 p.
- DIEDRICH C. G. 2011a. — One of Europe's last glacial *Crocota crocuta spelaea* (Goldfuss 1823) clans from the Rösenbeck Cave hyena den (Germany) and contribution to cranial shape variability. *Biological Journal of the Linnean Society of London* 103: 189-216.
- DIEDRICH C. G. 2011b. — Periodical use of the Balve Cave (NW Germany) as a late Pleistocene *Crocota crocuta spelaea* (Goldfuss 1823) den: Hyena occupations and bone accumulations vs. human Middle Palaeolithic activity. *Quaternary International* 233: 171-184. <https://doi.org/10.1016/j.quaint.2010.02.027>
- DIEDRICH C. G. 2012. — An Ice Age spotted hyena *Crocota crocuta spelaea* (Goldfuss 1823) population, their excrements and prey from the late Pleistocene hyena den of the Sloup Cave in the Moravian Karst, Czech Republic. *Historical Biology* 24: 161-185. <https://doi.org/10.1080/08912963.2011.591491>
- DIEDRICH C. G. 2013. — Recycling of Badger/Fox Burrows in late Pleistocene Loess by Hyenas at the Den Site Bad Wildungen-Biedensteg (NW, Germany): Woolly Rhinoceros Killers and Scavengers in a Mammoth Steppe Environment of Europe [WWW Document]. *Journal of Geology and Mining Research*: 1-32.
- DISCAMP E., DELAGNES A., LENOIR M. & TOURNÉPICHE J.-F. 2012. — Human and Hyena co-occurrences in Pleistocene sites: Insights from spatial, faunal and lithic analyses at Camiac and La Chauverie (SW France). *Journal of Taphonomy* 10: 291-316.
- DISCAMP E. & COSTAMAGNO S. 2015. — Improving mortality profile analysis in zooarchaeology: a revised zoning for ternary diagrams. *Journal of Archaeological Science* 58: 62-76. <https://doi.org/10.1016/j.jas.2015.03.021>
- DOMÍNGUEZ-RODRIGO M. 1997. — Meat-eating by early hominids at the FLK 22 Zinjanthropus site, Olduvai Gorge (Tanzania): an experimental approach using cut-mark data. *Journal of Human Evolution* 33: 669-690. <https://doi.org/10.1006/jhev.1997.0161>
- DOMÍNGUEZ-RODRIGO M. & LEZANA R. M. 1996. — Estudio etnoarqueológico de un campamento temporal Ndorobo (Maasai) en Kulalu (Kenia). *Trabajos de Prehistoria* 53: 131-144.
- DOMÍNGUEZ-RODRIGO M. & PICKERING T. R. 2003. — Early hominid hunting and scavenging: A zooarchaeological review. *Evolutionary Anthropology*, 12: 275-282. <https://doi.org/10.1002/evan.10119>
- DOMÍNGUEZ-RODRIGO M. & PIQUERAS A. 2003. — The use of tooth pits to identify carnivore taxa in tooth-marked archaeofaunas and their relevance to reconstruct hominid carcass processing behaviours. *Journal of Archaeological Science* 30: 1385-1391. [https://doi.org/10.1016/S0305-4403\(03\)00027-X](https://doi.org/10.1016/S0305-4403(03)00027-X)
- DOMÍNGUEZ-RODRIGO M. & BARBA R. 2006. — New estimates of tooth mark and percussion mark frequencies at the FLK Zinj site: the carnivore-hominid-carnivore hypothesis falsified. *Journal of Human Evolution* 50: 170-194. <https://doi.org/10.1016/j.jhev.2005.09.005>
- DOMÍNGUEZ-RODRIGO M., DE LA TORRE I., DE LUQUE L., ALCALÁ L., MORA R., SERRALLONGA J. & MEDINA V. 2002. — The ST site complex at Peninj, West Lake Natron, Tanzania: implications for early hominid behavioural models. *Journal of Archaeological Science* 29 (6): 639-665.
- DOMÍNGUEZ-RODRIGO M., MABULLA A., BUNN H. T., BARBA R., DIEZ-MARTÍN F., EGELAND C. P., ESPÍLEZ E., EGELAND A., YRAVEDRA J. & SÁNCHEZ P. 2009. — Unraveling hominid behavior at another anthropogenic site from Olduvai Gorge (Tanzania): new archaeological and taphonomic research at BK, Upper Bed II. *Journal of Human Evolution* 57: 260-283. <https://doi.org/10.1016/j.jhev.2009.04.006>
- DOMÍNGUEZ-RODRIGO M., GIDNA A., YRAVEDRA J. & MUSIBA C. 2012. — A comparative neotaphonomic study of felids, hyenids and canids: an analogical framework based on long bone modification patterns. *Journal of Taphonomy* 10: 147-164.
- DOMÍNGUEZ-RODRIGO M., YRAVEDRA J., ORGANISTA E., GIDNA A., FOURVEL J.-B. & BAQUEDANO E. 2015. — A new methodological approach to the taphonomic study of paleontological and archaeological faunal assemblages: a preliminary case study from Olduvai Gorge (Tanzania). *Journal of Archaeological Science* 59: 35-53. <https://doi.org/10.1016/j.jas.2015.04.007>
- EGELAND C. P., PICKERING T. R., DOMÍNGUEZ-RODRIGO M. & BRAIN C. K. 2004. — Disentangling Early Stone Age palimpsests: determining the functional independence of hominid- and carnivore-derived portions of archaeofaunas. *Journal of Human Evolution* 47: 343-357. <https://doi.org/10.1016/j.jhev.2004.08.004>
- EGELAND A. G., EGELAND C. P. & BUNN H. T. 2008. — Taphonomic analysis of a modern spotted hyena (*Crocota crocuta*) den from Nairobi, Kenya. *Journal of Taphonomy* 6: 275-299.
- FAITH J. T. 2007. — Sources of variation in carnivore tooth-mark frequencies in a modern spotted hyena (*Crocota crocuta*) den assemblage, Amboseli Park, Kenya. *Journal of Archaeological Science* 34: 1601-1609. <https://doi.org/10.1016/j.jas.2006.11.014>

- FAITH J. T. & BEHRENSMEYER A. K. 2006. — Changing patterns of carnivore modification in a landscape bone assemblage, Amboseli Park, Kenya. *Journal of Archaeological Science* 33: 1718-1733. <https://doi.org/10.1016/j.jas.2006.03.004>
- FERNANDEZ P. & LEGENDRE S. 2003. — Mortality curves for horses from the Middle Palaeolithic site of Bau de l'Aubiesier (Vaucluse, France): methodological, palaeo-ethnological, and palaeo-ecological approaches. *Journal of Archaeological Science* 30: 1577-1598. [https://doi.org/10.1016/S0305-4403\(03\)00054-2](https://doi.org/10.1016/S0305-4403(03)00054-2)
- FERNANDEZ P., GUADELLI J.-L. & FOSSE P. 2006. — Applying dynamics and comparing life tables for Pleistocene Equidae in anthropic (Bau de l'Aubiesier, Combe-Grenal) and carnivore (Fouvent) contexts with modern feral horse populations (Akagera, Pryor Mountain). *Journal of Archaeological Science* 33: 176-184. <https://doi.org/10.1016/j.jas.2005.07.005>
- FERNÁNDEZ-JALVO Y. & ANDREWS P. 2011. — When humans chew bones. *Journal of Human Evolution* 60: 117-123. <https://doi.org/10.1016/j.jhevol.2010.08.003>
- FORSTEN A. & MOIGNE A. 1998. — The horse from the middle Pleistocene of Orgnac-3 (Ardèche, France) [Les chevaux du site du Pléistocène moyen d'Orgnac 3 (Ardèche, France)]. *Quaternaire* 9: 315-323.
- FOSSE P. 1995. — Le rôle de l'hyène dans la formation des associations osseuses : 150 ans de controverses [L'apport des anciens textes de préhistoire et de paléontologie du Quaternaire aux études taphonomiques actuelles]. *Paléo, Revue d'Archéologie Préhistorique* 7: 49-84. <https://doi.org/10.3406/pal.1995.1208>
- FOSSE P. 1996. — La grotte n° 1 de Lunel-Viel (Hérault, France) : Repaire d'hyènes du Pléistocène moyen. Etude taphonomique du matériel osseux. *Paléo, Revue d'Archéologie Préhistorique* 8: 47-79. <https://doi.org/10.3406/pal.1996.906>
- FOURVEL J.-B. & FOSSE P. 2017. — Conives (Indre, France): a new case of late Pleistocene hyena den. *Quaternaire* 28: 455-469.
- FOURVEL J.-B., FOSSE P., BRUGAL J.-P., TOURNÉPICHE J.-F. & CREGUT-BONNOURE E. 2012. — Consumption of ungulate long bones by Pleistocene Hyenas: a comparative study. *Journal of Taphonomy* 10: 239-263.
- FOURVEL J.-B., FOSSE P., FERNANDEZ P. & ANTOINE P.-O. 2014. — La grotte de Fouvent, dit l'Abri Cuvier (Fouvent-le-Bas, Haute-Saône, France): analyse taphonomique d'un repaire d'hyènes du Pléistocène supérieur (OIS 3). *Paléo, Revue d'Archéologie Préhistorique*: 79-99.
- FOURVEL J.-B., FOSSE P. & AVERY G. 2015. — Spotted, striped or brown? Taphonomic studies at dens of extant hyenas in eastern and southern Africa. *Quaternary International* 369: 38-50. <https://doi.org/10.1016/j.quaint.2014.08.022>
- GALÁN A. B. & DOMÍNGUEZ-RODRIGO M. 2013. — An Experimental Study of the Anatomical Distribution of Cut Marks Created by Filleting and Disarticulation on Long Bone Ends. *Archaeometry* 55: 1132-1149. <https://doi.org/10.1111/j.1475-4754.2012.00730.x>
- GAUDZINSKI-WINDHEUSER S. & NIVEN L. 2009. — Hominin Subsistence Patterns During the Middle and Late Paleolithic in northwestern Europe, in HUBLIN J.-J. & RICHARDS M. P. (eds), *The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence*. Springer Netherlands, Dordrecht: 99-111. https://doi.org/10.1007/978-1-4020-9699-0_7
- GIDNA A., DOMÍNGUEZ-RODRIGO M. & PICKERING T. R. 2015. — Patterns of bovid long limb bone modification created by wild and captive leopards and their relevance to the elaboration of referential frameworks for paleoanthropology. *Journal of Archaeological Science: Reports* 2: 302-309. <https://doi.org/10.1016/j.jasrep.2015.03.003>
- GRAYSON D. K. 1984. — Quantitative zooarchaeology: topics in the quantification of archaeofaunas. Academic Press, Orlando, 202 p.
- GRAYSON D. K. & DELPECH F. 2002. — Specialized Early Upper Palaeolithic Hunters in southwestern France? *Journal of Archaeological Science* 29: 1439-1449. <https://doi.org/10.1006/jasc.2002.0806>
- GRAYSON D. K. & DELPECH F. 2003. — Ungulates and the Middle-to-Upper Paleolithic transition at Grotte XVI (Dordogne, France). *Journal of Archaeological Science* 30: 1633-1648. [https://doi.org/10.1016/S0305-4403\(03\)00064-5](https://doi.org/10.1016/S0305-4403(03)00064-5)
- GRAYSON D. K. & DELPECH F. 2008. — The large mammals of Roc de Combe (Lot, France): The Châtelperronian and Aurignacian assemblages. *Journal of Anthropological Archaeology* 27: 338-362. <https://doi.org/10.1016/j.jaa.2008.04.002>
- HAYNES G. 1983. — A guide for differentiating mammalian carnivore taxa responsible for gnaw damage to herbivore limb bones. *Paleobiology* 9, 164-172. <https://doi.org/10.1017/S0094837300007545>
- HOFFECCKER J. F. 2009. — Neanderthal and Modern Human Diet in Eastern Europe, in HUBLIN J.-J. & RICHARDS M. P. (eds), *The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence*. Springer Netherlands, Dordrecht: 87-98. https://doi.org/10.1007/978-1-4020-9699-0_6
- JOHNSON E. 1985. — Current Developments in Bone Technology, in SCHIFFER M. B. (ed.), *Advances in Archaeological Method and Theory*. Academic Press, San Diego: 157-235. <https://doi.org/10.1016/B978-0-12-003108-5.50010-5>
- KEMPE S., AL-MALABEH A., DOPPEL D., FREHAT M., HENSCHEL H.-V. & ROSENDAHL W. 2006. — Hyena caves in Jordan. *Επιστημονική Επετηρίδα Του Τμήματος Γεωλογίας ΑΠΘ* 98: 201-212.
- KLEIN R. G., CRUZ-URIBE K. & BEAUMONT P. B. 1991. — Environmental, ecological, and paleoanthropological implications of the late Pleistocene mammalian fauna from Equus Cave, northern Cape Province, South Africa. *Quaternary Research* 36: 94-119. [https://doi.org/10.1016/0033-5894\(91\)90019-2](https://doi.org/10.1016/0033-5894(91)90019-2)
- KLIMOV V. V. 1988. — Spatial-ethological organization of the herd of Przewalski horses (*Equus przewalskii*) in Askania-Nova. *Applied Animal Behaviour Science* 21: 99-115. [https://doi.org/10.1016/0168-1591\(88\)90103-7](https://doi.org/10.1016/0168-1591(88)90103-7)
- KRUUK H. 1970. — Interactions between populations of spotted hyenas (*Crocuta crocuta* Erxleben) and their prey species, in WATSON A. (ed.), *Animal Populations in Relation to their Food Resources*. Blackwell, Oxford: 359-374.
- KRUUK H. 1972. — *The spotted hyena: a study of predation and social behavior*. University of Chicago Press, Chicago: 335.
- KUHN B. F., BERGER L. R. & SKINNER J. D. 2010. — Examining criteria for identifying and differentiating fossil faunal assemblages accumulated by hyenas and hominins using extant hyenid accumulations. *International Journal of Osteoarchaeology* 20: 15-35. <https://doi.org/10.1002/oa.996>
- LACRUZ R. & MAUDE G. 2005. — Bone accumulations at brown hyena (*Parahyaena brunnea*) den sites in the Makgadikgadi Pans, northern Botswana: taphonomic, behavioral, and palaeoecological implications. *Journal of Taphonomy* 3: 43-54.
- LAM Y. M. 1992. — Variability in the behaviour of spotted hyenas as taphonomic agents. *Journal of Archaeological Science* 19: 389-406. [https://doi.org/10.1016/0305-4403\(92\)90057-A](https://doi.org/10.1016/0305-4403(92)90057-A)
- LAM Y. M., CHEN X. & PEARSON O. M. 1999. — Intertaxonomic Variability in Patterns of Bone Density and the Differential Representation of Bovid, Cervid, and Equid Elements in the Archaeological Record. *American Antiquity* 64: 343-362. <https://doi.org/10.2307/2694283>
- LEVINE M. A. 1983. — *Mortality models and the interpretation of horse population structure*, in Geoff Bailey (ed.), *Hunter-Gatherer economy in Prehistory: A European perspective*. Cambridge University Press, Cambridge: 23-46.
- LUMLEY H. DE 1971. — *Le Paléolithique inférieur et moyen du Midi méditerranéen dans son cadre géologique: V^e supplément à Gallia-Préhistoire*. Gallia préhistoire. Supplément 5-2. Tome II. Éditions du Centre National de la Recherche Scientifique, Bas-Languedoc, Roussillon, Catalogne, 411 p.
- LUMLEY H. DE & ISETTI G. 1965. — Le Moustérien à denticulés tardif de la station de San Francesco (San Remo) et de la Grotte Tournal (Aude). *Cahiers ligures de préhistoire et d'Archéologie* 14: 5-30.

- MAGNIEZ P. 2008. — *Stratégies d'acquisition des grands mammifères au Moustérien et au Magdalénien à la grotte Tournal (Bize-Minervois, Aude, France)*. in BAILLIS H. (ed), Groupe de réflexion sur l'arrivée de l'Homme moderne dans l'Arc Latin: le Gravettien et ses descendances. Perpignan: 51-65.
- MAGNIEZ P. 2009. — Taphonomic study of the Middle and Upper Palaeolithic large mammal assemblage from Tournal cave (Bize-Minervois, France). *Journal of Taphonomy* 7: 203-233.
- MAGNIEZ P. 2010. — *Étude paléontologique des artiodactyles de la grotte Tournal (Bize-Minervois, Aude, France) : étude taphonomique, archéozoologique et paléocéologique des grands Mammifères dans leur cadre biostratigraphique et paléoenvironnemental*. Université de Perpignan Via Domitia, Tautavel, 410 p.
- MAGNIEZ P. & BOULBES N. 2014. — Environment during the Middle to Late Palaeolithic transition in southern France: The archaeological sequence of Tournal Cave (Bize-Minervois, France). *Quaternary International* 337: 43-63. <https://doi.org/10.1016/j.quaint.2013.08.021>
- MAGUIRE J. M., PEMBERTON D. & COLLETT M. H. 1980. — The Makapansgat Limeworks grey breccia: hominids, hyaenas, hystri-cids or hillwash? *Palaeontologica Africana* 23: 75-98.
- MALLYE J., COSTAMAGNO S., BOUDADI-MALIGNE M., PRUCCA A., LAUROULANDIE V., THIÉBAUT C. & MOURRE V. 2012. — Dhole (*Cuon alpinus*) as a bone accumulator and new taphonomic agent? The case of Noisetier Cave (French Pyrenees). *Journal of Taphonomy* 10 (3-4): 317-347.
- MAREAN C. W. 1991. — Measuring the post-depositional destruction of bone in archaeological assemblages. *Journal of Archaeological Science* 18: 677-694. [https://doi.org/10.1016/0305-4403\(91\)90029-O](https://doi.org/10.1016/0305-4403(91)90029-O)
- MAREAN C. W. 2005. — From the tropics to the colder climates: contrasting faunal exploitation adaptations of modern humans and Neanderthals, in ERRICO F. & BACKWELL L. R. (eds), *From tools to symbols. From hominids to modern humans*. Witwatersrand University Press, Johannesburg: 333-371.
- MAREAN C. W. & SPENCER L. M. 1991. — Impact of Carnivore Ravaging on Zooarchaeological Measures of Element Abundance. *American Antiquity* 56: 645-658. <https://doi.org/10.2307/281542>
- MAREAN C. W., SPENCER L. M., BLUMENSCHINE R. J. & CAPALDO S. D. 1992. — Captive hyaena bone choice and destruction, the Schlep effect and olduvai archaeofaunas. *Journal of Archaeological Science* 19: 101-121. [https://doi.org/10.1016/0305-4403\(92\)90009-R](https://doi.org/10.1016/0305-4403(92)90009-R)
- MARÍN-ARROYO A. B., GEILING J.-M., JONES J. R., GONZÁLEZ MORALES M. R., STRAUS L. G. & RICHARDS M. P. 2018. — The Middle to Upper Palaeolithic transition at El Mirón Cave (Cantabria, Spain). *Quaternary International*: 23-31. <https://doi.org/10.1016/j.quaint.2018.06.036>
- MCNAMEE T. 1990. — *The grizzly bear*, KNOPF, A. A. (ed.). Penguin Group, New York, 308 p.
- MELLARS P. 1973. — The character of the Middle-Upper Paleolithic transition in South-West France, in *The Explanation of Culture Change: Models in Prehistory*. Duckworth, London: 255-276.
- MELLARS P. A. 2004. — Reindeer specialization in the early Upper Palaeolithic: the evidence from South-West France. *Journal of Archaeological Science* 31: 613-617. <https://doi.org/10.1016/j.jas.2003.10.010>
- MILLS M. G. L. & MILLS M. E. J. 1977. — An analysis of bones collected at hyaena breeding dens in the Gemsbok National Parks (Mammalia: Carnivora). *Annals of the Transvaal Museum* 30: 145-155.
- NILSSEN P. J. 2000. — *An actualistic butchery study in South Africa and its implications for reconstructing hominid strategies of carcass acquisition and butchery in the upper Pleistocene and Plio-Pleistocene*. University of Cape Town South Africa, 684 p.
- ORBACH M. & YESHURUN R. 2019. — The hunters or the hunters: Human and hyena prey choice divergence in the late Pleistocene Levant. *Journal of Human Evolution*: 102572. <https://doi.org/10.1016/j.jhevol.2019.01.005>
- OTTE M. 1990. — Les processus de transition du Paléolithique moyen au supérieur, in FARIZY C. (ed.), *Paléolithique moyen récent et Paléolithique supérieur ancien en Europe*. Mémoires de Musée de Préhistoire d'Ile-de-France 3: 145-149.
- PALES L. & LAMBERT C. 1971. — *Atlas ostéologique: pour servir à l'identification des mammifères du Quaternaire. Les membres Herbivores*. Centre National de la Recherche Scientifique, Paris: 88.
- PATOU-MATHIS M. 1994. — Archéozoologie des niveaux moustériens et aurignaciens de la grotte Tournal à Bize (Aude). *Gallia préhistoire*, tome 36: 1-64.
- PATOU-MATHIS M. 2012. — Interactions between Neanderthals and carnivores in eastern Europe. *Journal of Taphonomy* 10: 277-290.
- PICKERING T. R. 2002. — Reconsideration of criteria for differentiating faunal assemblages accumulated by hyenas and hominids. *International Journal of Osteoarchaeology* 12: 127-141. <https://doi.org/10.1002/oa.594>
- PICKERING T. R., MAREAN C. W. & DOMÍNGUEZ-RODRIGO M. 2003. — Importance of limb bone shaft fragments in zooarchaeology: a response to "On in situ attrition and vertebrate body part profiles" (2002), by M.C. Stiner. *Journal of Archaeological Science* 30: 1469-1482. [https://doi.org/10.1016/S0305-4403\(03\)00042-6](https://doi.org/10.1016/S0305-4403(03)00042-6)
- PINTO A. C. & ANDREWS P. J. 2004. — Scavenging behaviour patterns in cave bears *Ursus spelaeus*. *Rev. Paléobiol.* 23, 84.
- PINTO A. C., ANDREWS P. J. & GABILONDO F. E. 2005. — *Tafonomía y paleoecología de úrsidos cuaternarios cantábricos: Taphonomy and palaeoecology of bears from the quaternary of cantabrian Spain*. Fundación oso de Asturias, Oviedo, 688 p.
- POKINES J. T. & PETERHANS J. C. K. 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/10.1016/j.jas.2007.01.012>
- PRENDERGAST M. E. & DOMÍNGUEZ-RODRIGO M. 2008. — Taphonomic analyses of a hyena den and a natural-death assemblage near Lake Eyasi (Tanzania). *Journal of Taphonomy* 6: 301-336.
- ROGERS L. L. 1981. — A bear in its lair. *Nat. Hist.* 90, 64-70.
- SACCHI D. 1986. — Le Paléolithique supérieur du Languedoc occidental et du Roussillon. *Supplément à Gallia Préhistoire* 21: 1-284.
- SALA N. & ARSUAGA J. L. 2013. — Taphonomic studies with wild brown bears (*Ursus arctos*) in the mountains of northern Spain. *Journal of Archaeological Science* 40: 1389-1396. <https://doi.org/10.1016/j.jas.2012.10.018>
- SALA N., ALGABA M., ARSUAGA J. L., ARANBURU A. & PANTOJA A. 2012. — A taphonomic study of the Búho and Zarzamora caves. Hyenas and humans in the Iberian Plateau (Segovia, Spain) during the late Pleistocene. *Journal of Taphonomy* 10: 477-497.
- SALA N., ARSUAGA J. L., MARTÍNEZ I. & GRACIA-TÉLLEZ A. 2014. — Carnivore activity in the Sima de los Huesos (Atapuerca, Spain) hominin sample. *Quaternary Science Reviews* 97: 71-83. <https://doi.org/10.1016/j.quascirev.2014.05.004>
- SALADIÉ P., HUGUET R., DÍEZ C., RODRÍGUEZ-HIDALGO A. & CARBONELL E. 2013. — Taphonomic modifications produced by modern brown bears (*Ursus arctos*). *International Journal of Osteoarchaeology* 23: 13-33. <https://doi.org/10.1002/oa.1237>
- SALADIÉ P., FERNÁNDEZ P., RODRÍGUEZ-HIDALGO A., HUGUET R., PINEDA A., CÁCERES I., MARÍN J., VALLVERDÚ J., & CARBONELL E. 2017. — The TD6.3 faunal assemblage of the Gran Dolina site (Atapuerca, Spain): a late early Pleistocene hyena den. *Historical Biology* 0: 1-19. <https://doi.org/10.1080/08912963.2017.1384476>
- SAMPER CARRO S. C. & MARTÍNEZ-MORENO J. 2014. — Who let the hyenas out? Taphonomic analysis of the faunal assemblage from GL-1 of Cova del Gegant (Sitges, Spain). *Quaternary International*, Taphonomy and Archaeozoological Research: Recent Approaches 2nd ICAZ Taphonomy Working Group Meeting 330: 19-35. <https://doi.org/10.1016/j.quaint.2013.10.052>
- SANCHIS A., REAL C., SAUQUÉ V., NÚÑEZ-LAHUERTA C., ÉGÜEZ N., TORMO C., RIPOLL M. P., MARCO Y. C., DUARTE E. & RASILLA M. DE LA 2019. — Neanderthal and carnivore activities at Llonin Cave, Asturias, northern Iberian Peninsula: Faunal study of Mousterian levels (MIS 3). *Comptes Rendus Palevol* 18: 113-141. <https://doi.org/10.1016/j.crpv.2018.06.001>

- SAUQUÉ V. & SANCHIS A. 2017. — Leopards as taphonomic agents in the Iberian Pleistocene, the case of Racó del Duc (Valencia, Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology* 472: 67-82. <https://doi.org/10.1016/j.palaeo.2017.01.016>
- SAUQUÉ V., RABAL-GARCÉS R., SOLA-ALMAGRO C. & CUENCA-BESCÓS G. 2014. — Bone Accumulation by Leopards in the late Pleistocene in the Moncayo Massif (Zaragoza, NE Spain). *PLOS ONE* 9: e92144. <https://doi.org/10.1371/journal.pone.0092144>
- SAUQUÉ V., SANCHIS A. & MADURELL-MALAPEIRA J. 2018. — Late Pleistocene leopards as a bone accumulator: taphonomic results from S'Espasa cave and other Iberian key sites. *Historical Biology* 30: 821-834. <https://doi.org/10.1080/08912963.2017.1343313>
- SCHALLER G. B. 1972. — *Serengeti Lion: A Study of Predator-Prey Relations*. University of Chicago Press, Chicago, 504 p.
- SELVAGGIO M. M. 1994. — Carnivore tooth marks and stone tool butchery marks on scavenged bones: archaeological implications. *Journal of Human Evolution* 27: 215-228. <https://doi.org/10.1006/jhev.1994.1043>
- SELVAGGIO M. M. 1998. — Evidence for a Three-Stage Sequence of Hominid and Carnivore Involvement with Long Bones at FLKZinjantropus, Olduvai Gorge, Tanzania. *Journal of Archaeological Science* 25: 191-202. <https://doi.org/10.1006/jasc.1997.0281>
- SELVAGGIO M. M. & WILDER J. 2001. — Identifying the Involvement of Multiple Carnivore Taxa with Archaeological Bone Assemblages. *Journal of Archaeological Science* 28: 465-470. <https://doi.org/10.1006/jasc.2000.0557>
- SHIPMAN P. & ROSE J. 1983. — Early hominid hunting, butchering, and carcass-processing behaviors: Approaches to the fossil record. *Journal of Anthropological Archaeology* 2: 57-98. [https://doi.org/10.1016/0278-4165\(83\)90008-9](https://doi.org/10.1016/0278-4165(83)90008-9)
- SKINNER J. D. & AARDE R. J. VAN 1991. — Bone collecting by brown hyaenas *Hyaena brunnea* in the central Namib Desert, Namibia. *Journal of Archaeological Science* 18: 513-523. [https://doi.org/10.1016/0305-4403\(91\)90051-P](https://doi.org/10.1016/0305-4403(91)90051-P)
- SKINNER J. D., HENSCHER J. R. & JAARSVELD A. S. VAN 1986. — Bone-collecting habits of spotted hyaenas *Crocuta crocuta* in the Kruger National Park. *South African Journal of Zoology* 21: 303-308-308. <https://doi.org/10.1080/02541858.1986.11448003>
- STINER M. C. 1990. — The use of mortality patterns in archaeological studies of hominid predatory adaptations. *Journal of Anthropological Archaeology* 9: 305-351. [https://doi.org/10.1016/0278-4165\(90\)90010-B](https://doi.org/10.1016/0278-4165(90)90010-B)
- STINER M. C. 1991a. Food procurement and transport by human and non-human predators. *Journal of Archaeological Science* 18: 455-482. [https://doi.org/10.1016/0305-4403\(91\)90038-Q](https://doi.org/10.1016/0305-4403(91)90038-Q)
- STINER M. C. 1991b. The Faunal Remains From Grotta Guattari: A Taphonomic Perspective. *Current Anthropology* 32: 103-117. <https://doi.org/10.1086/203930>
- STINER M. C. 2002. — On in situ Attrition and Vertebrate Body Part Profiles. *Journal of Archaeological Science* 29: 979-991. <https://doi.org/10.1006/jasc.2001.0798>
- STINER M. C. 2010. — A taphonomic study of bone assemblage formation and artifact-bear associations in Yarımburgaz Cave, in HOWELL F. C., ARSEBÜK G., KUHN S. L., ÖZBAŞARAN M. & STINER M. C. (eds), *Culture and Biology at a Crossroads: The Middle Pleistocene Record of Yarımburgaz Cave (Thrace, Turkey)*. Zero BooksEge Publisher, Istanbul: 131-166.
- STINER M. C., ARSEBÜK G. & HOWELL F. C. 1996. — Cave bears and Paleolithic artifacts in Yarımburgaz Cave, Turkey: Dissecting a palimpsest. *Geoarchaeology* 11: 279-327. [https://doi.org/10.1002/\(SICI\)1520-6548\(199607\)11:4<279::AID-GEA1>3.0.CO;2-Z](https://doi.org/10.1002/(SICI)1520-6548(199607)11:4<279::AID-GEA1>3.0.CO;2-Z)
- STINER M. C., ACHYUTHAN H., ARSEBÜK G., HOWELL F. C., JOSEPHSON S. C., JUELL K. E., PIGATI J. & QUADE J. 1998. — Reconstructing cave bear paleoecology from skeletons: a cross-disciplinary study of middle Pleistocene bears from Yarımburgaz Cave, Turkey. *Paleobiology* 24: 74-98. <https://doi.org/10.1017/S0094837300019989>
- STINER M. C., MUNRO N. D. & SANZ M. 2012. — Carcass damage and digested bone from mountain lions (*Felis concolor*): implications for carcass persistence on landscapes as a function of prey age. *Journal of Archaeological Science* 39: 896-907. <https://doi.org/10.1016/j.jas.2011.10.020>
- STRAUS L. G. 2013. — Iberian Archaeofaunas and Hominin Subsistence during Marine Isotope Stages 4 and 3, in CLARK J. L. & SPETH J. D. (eds), *Zooarchaeology and Modern Human Origins: Human Hunting Behavior during the later Pleistocene*. Springer Netherlands, Dordrecht: 97-128. https://doi.org/10.1007/978-94-007-6766-9_7
- SUTCLIFFE A. J. 1970. — Spotted Hyaena: Crusher, Gnawer, Digester and Collector of Bones. *Nature* 227: 1110-1113. <https://doi.org/10.1038/2271110a0>
- TAGLIACCOZZO A., ROMANDINI M., FIORE I., GALA M. & PERESANI M. 2013. — Animal Exploitation Strategies during the Uluzzian at Grotta di Fumane (Verona, Italy), in CLARK J. L. & SPETH J. D. (eds), *Zooarchaeology and Modern Human Origins: Human Hunting Behavior during the later Pleistocene*. Springer Netherlands, Dordrecht: 129-150. https://doi.org/10.1007/978-94-007-6766-9_8
- TAVOSO A. 1987a. — Le remplissage de la grotte Tournal à Bize-Minervois (Aude). *Cypselà Revista de Prehistòria Protohistòria*: 23-35.
- TAVOSO A. 1987b. — Le Moustérien de la grotte Tournal. *Cypselà Revista de Prehistòria Protohistòria*: 161-173.
- TOURNAL P. 1827. — Note sur deux cavernes à ossements (sic), découvertes à Bize, dans les environs de Narbonne. *Annales des Sciences Naturelles* 12: 78-82.
- TOURNAL P. 1828. — Note sur la caverne de Bize près de Narbonne. *Annales des Sciences Naturelles* 15: 348-349.
- TOURNAL P. 1829. — Considérations théoriques sur les cavernes à ossements (sic) de Bize, près de Narbonne (Aude) et sur les ossements (sic) humains confondus avec des restes d'animaux appartenant à des espèces perdues. *Bulletin des sciences naturelles et de géologie* 19: 18-28.
- VALENSI P. 2000. — The archaeozoology of Lazaret Cave (Nice, France). *International Journal of Osteoarchaeology* 10: 357-367. [https://doi.org/10.1002/1099-1212\(200009/10\)10:5<357::AID-OA561>3.0.CO;2-W](https://doi.org/10.1002/1099-1212(200009/10)10:5<357::AID-OA561>3.0.CO;2-W)
- VILLA P. & MAHIEU E. 1991. — Breakage patterns of human long bones. *Journal of Human Evolution* 21: 27-48. [https://doi.org/10.1016/0047-2484\(91\)90034-S](https://doi.org/10.1016/0047-2484(91)90034-S)
- YOKOYAMA Y., & NGUYEN H.-V., QUAEGBEUR J.-P., LE HASIF G. & ROMAIN O. 1987. — Datation par la spectrométrie gamma non destructive et la résonance de spin électronique (E.S.R.) du remplissage de la grotte Tournal à Bize (Aude). *Cypselà Revista de Prehistòria Protohistòria* 6: 145-149.
- YRAVEDRA J., LAGOS L. & BÀRCENA F. 2011. — A taphonomic study of wild wolf (*Canis lupus*) modification of horse bones in northwestern Spain. *Journal of Taphonomy* 9 (1): 37-65.
- YRAVEDRA J., LAGOS L. & BÀRCENA F. 2012. — The wild wolf (*Canis lupus*) as a dispersal agent of animal carcasses in northwestern Spain. *Journal of Taphonomy* 10 (3-4): 227-248.

Submitted on 30 September 2019;
accepted on 3 December 2019;
published on 14 December 2020.

APPENDICES

APPENDIX 1. — Loading scores (decomposition of inertia) for the variables (taphotypes and carnivore) for femur. Princ coords, std devs; rep and ctr (per mil); 2-d rep (per mil).

Rows:

	Axis 1	StDev	Rep	Ctr	Axis 2	StDev	Rep	Ctr	Quality
fd0	−0.385	0.174	949	44	0.064	0.280	27	1	975
fd1	−0.594	0.000	613	5	0.471	0.000	385	4	998
fd1_2	1.362	0.000	883	28	0.422	0.000	85	3	968
fd1_2_3_4	0.579	0.528	912	25	0.064	0.120	11	0	923
fd1_2_3_4_5_6	−0.594	0.000	613	5	0.471	0.000	385	4	998
fd1_3	−0.594	0.000	613	11	0.471	0.000	385	7	998
fd1_5	−0.594	0.000	613	11	0.471	0.000	385	7	998
fd2	−0.594	0.000	613	16	0.471	0.000	385	11	998
fd2_3	−0.594	0.000	613	5	0.471	0.000	385	4	998
fd2_3_4	−0.594	0.000	613	5	0.471	0.000	385	4	998
fd2_3_4_5_6	−2.270	0.000	172	77	−4.984	0.000	828	403	1000
fd2_3_5_6	−0.594	0.000	613	5	0.471	0.000	385	4	998
fd2_4	1.362	0.000	883	28	−0.422	0.000	85	3	968
fd2_5	−0.594	0.000	613	5	0.471	0.000	385	4	998
fd3	−0.594	0.000	613	16	0.471	0.000	385	11	998
fd3_4_5_6_7_8	1.362	0.000	883	28	−0.422	0.000	85	3	968
fd3_5	−0.594	0.000	613	11	0.471	0.000	385	7	998
fd5	−0.594	0.000	613	95	0.471	0.000	385	65	998
fd5_6	−2.270	0.000	172	77	−4.984	0.000	828	403	1000
fd5_6_7_8	0.741	0.346	463	82	−0.131	0.138	15	3	477
fd5_7	−0.594	0.000	613	5	0.471	0.000	385	4	998
fd9	−0.594	0.000	613	5	0.471	0.000	385	4	998
fp0	1.362	0.000	883	110	−0.422	0.000	85	12	968
fp1_2	1.362	0.000	883	28	−0.422	0.000	85	3	968
fp1_2_3_4	1.362	0.000	883	110	−0.422	0.000	85	12	968
fp2	1.362	0.000	883	28	−0.422	0.000	85	3	968
fp2_4	1.362	0.000	883	28	−0.422	0.000	85	3	968
fp4	1.362	0.000	883	28	−0.422	0.000	85	3	968
fp5_6_7_8	1.362	0.000	883	83	−0.422	0.000	85	9	968

Columns:

	Axis 1	StDev	Rep	Ctr	Axis 2	StDev	Rep	Ctr	Quality
C_hyenas	0.872	0.000	92	11	−0.161	0.000	3	0	95
C_lions	−1.931	0.319	185	166	−4.057	2.049	815	801	1000
T_lions	−0.505	0.064	635	224	0.383	0.054	365	141	1000
U.II	1.158	0.139	916	598	−0.343	0.079	80	57	996

APPENDIX 2. — Loading scores (decomposition of inertia) for the variables (taphotypes and carnivore) for humerus. Princ coords, std devs; rep and ctr (per mil); 2-d rep (per mil).

Rows:

	Axis 1	StDev	Rep	Ctr	Axis 2	StDev	Rep	Ctr	Quality
hd0	−0.213	0.098	837	31	−0.076	0.116	106	6	943
hd1	−0.398	0.000	366	2	−0.343	0.000	271	2	637
hd1_2_3_4_6	−0.398	0.000	366	2	−0.343	0.000	271	2	637
hd1_3_4	−0.398	0.000	366	2	−0.343	0.000	271	2	637
hd1_6_8	−0.398	0.000	366	2	−0.343	0.000	271	2	637
hd2	−0.129	0.245	152	1	0.067	0.425	42	0	194
hd3	−0.398	0.000	366	11	−0.343	0.000	271	12	637
hd3_4	−0.432	0.000	15	3	−0.545	0.000	24	6	39
hd3_4_6	−0.398	0.000	366	2	−0.343	0.000	271	2	637
hd3_4_6_7_8	6.047	0.000	703	505	−3.926	0.000	296	315	1000
hd3_6	−0.398	0.000	366	2	−0.343	0.000	271	2	637
hd4	−0.398	0.000	366	7	−0.343	0.000	271	7	637
hd4_6	−0.398	0.000	366	2	−0.343	0.000	271	2	637
hd5_6_7_8	2.221	1.564	982	272	0.299	0.786	18	7	1000
hd6	−0.398	0.000	366	9	−0.343	0.000	271	10	637
hd6_7	−0.398	0.000	366	2	−0.343	0.000	271	2	637
hd6_7_8	−0.398	0.000	366	2	−0.343	0.000	271	2	637
hd8	−0.398	0.000	366	2	−0.343	0.000	271	2	637
hp0	−0.276	0.117	340	12	−0.156	0.190	109	5	449
hp1_3	0.946	0.000	234	12	1.707	0.000	763	60	997
hp5_6_7	0.946	0.000	234	12	1.707	0.000	763	60	997
hp5_6_7_8	0.946	0.000	234	37	1.707	0.000	763	179	997
hp5_6_8	0.946	0.000	234	12	1.707	0.000	763	60	997
hp6	0.946	0.000	234	25	1.707	0.000	763	119	997
hp7	0.946	0.000	234	12	1.707	0.000	763	60	997
hp7_6	0.946	0.000	234	12	1.707	0.000	763	60	997

Columns:

	Axis 1	StDev	Rep	Ctr	Axis 2	StDev	Rep	Ctr	Quality
C_hyenas	5.000	1.877	778	690	−2.668	0.856	222	291	1000
C_lions	−0.357	0.436	27	14	−0.370	0.203	29	22	55
T_lions	−0.329	0.035	486	111	−0.233	0.041	243	82	729
U.II	0.782	0.306	312	186	1.160	0.285	686	605	998

APPENDIX 3. — Loading scores (decomposition of inertia) for the variables (taphotypes and carnivore) for radius. Princ coords, std devs; rep and ctr (per mil); 2-d rep (per mil).

Rows:

	Axis 1	StDev	Rep	Ctr	Axis 2	StDev	Rep	Ctr	Quality
rd0	−0.135	0.142	1000	6	−0.002	0.194	0	0	1000
rd1	−0.135	0.406	186	1	0.282	0.515	814	18	1000
rd1_2	−0.135	0.000	20	0	0.955	0.000	980	69	1000
rd3	−0.135	0.000	16	0	−1.066	0.000	984	86	1000
rd4	−0.135	0.000	20	0	0.955	0.000	980	69	1000
rd5	−0.135	0.000	16	0	−1.066	0.000	984	86	1000
rd5_6_7_8	−0.135	0.000	16	0	−1.066	0.000	984	86	1000
rp0	−0.135	0.145	999	6	0.004	0.189	1	0	1000
rp1	−0.135	0.191	45	2	0.619	0.262	955	174	1000
rp12345678	7.416	0.000	1000	982	0.000	0.000	0	0	1000
rp2	−0.135	0.000	20	0	0.955	0.000	980	69	1000
rp3	−0.135	0.000	16	0	−1.066	0.000	984	86	1000
rp5	−0.135	0.000	16	0	−1.066	0.000	984	86	1000
rp5_6_7_8	−0.135	0.000	16	0	−1.066	0.000	984	86	1000
rp7	−0.135	0.000	16	0	−1.066	0.000	984	86	1000

Columns:

	Axis 1	StDev	Rep	Ctr	Axis 2	StDev	Rep	Ctr	Quality
C_hyenas	7.416	0.000	1000	982	0.000	0.000	0	0	1000
C_lions	−0.135	0.123	78	9	0.464	0.136	922	473	1000
U.II	−0.135	0.198	63	8	−0.518	0.189	937	527	1000

APPENDIX 4. — Loading scores (decomposition of inertia) for the variables (taphotypes and carnivore) for tibia. Princ coords, std devs; rep and ctr (per mil); 2-d rep (per mil).

Rows:

	Axis 1	StDev	Rep	Ctr	Axis 2	StDev	Rep	Ctr	Quality
td0	−0.368	0.057	606	62	−0.009	0.134	0	0	606
td1_2	1.350	1.242	570	58	1.168	0.721	426	63	996
td1_2_3	1.898	1.503	859	77	0.692	0.915	114	15	973
td1_2_3_4_5_6	3.545	0.000	890	268	−0.737	0.000	38	17	929
td1_2_3_4_7	3.545	0.000	890	134	−0.737	0.000	38	8	929
td1_2_4	−0.058	0.000	2	0	−0.666	0.000	212	14	214
td1_4	0.252	0.000	14	1	2.120	0.000	963	69	976
td12345678	3.545	0.000	890	134	−0.737	0.000	38	8	929
td2	−0.058	0.000	2	0	−0.666	0.000	212	7	214
td2_3	−0.600	0.000	276	4	−0.253	0.000	49	1	325
td2_4	−0.058	0.000	2	0	−0.666	0.000	212	7	214
td4	−0.038	0.242	2	0	0.830	0.724	914	42	916
td5_6_7_8	0.457	0.506	132	16	−0.676	0.152	289	49	421
td5_6_8	3.545	0.000	890	134	−0.737	0.000	38	8	929
td8	−0.058	0.000	2	0	−0.666	0.000	212	14	214
tp0	−0.282	0.083	323	15	−0.328	0.165	437	30	760
tp1	−0.540	0.066	339	28	−0.299	0.087	104	12	443
tp1_2	−0.239	0.195	90	2	−0.528	0.255	443	13	533
tp1_2_3	0.097	0.295	8	0	0.727	1.016	444	16	452
tp1_2_3_4_5_6	0.252	0.000	14	1	2.120	0.000	963	69	976
tp1_2_3_5	0.252	0.000	14	1	2.120	0.000	963	138	976
tp1_2_4_5	0.252	0.000	14	1	2.120	0.000	963	69	976
tp1_3	−0.600	0.000	276	8	−0.253	0.000	49	2	325
tp1_3_4	−0.600	0.000	276	8	−0.253	0.000	49	2	325
tp1_3_4_5	0.252	0.000	14	1	2.120	0.000	963	69	976
tp1_5	−0.600	0.000	276	4	−0.253	0.000	49	1	325
tp2	−0.600	0.000	276	4	−0.253	0.000	49	1	325
tp2_3_5_8	0.252	0.000	14	1	2.120	0.000	963	69	976
tp2_4	−0.058	0.000	2	0	−0.666	0.000	212	7	214
tp2_5	0.252	0.000	14	1	2.120	0.000	963	69	976
tp3	0.097	0.280	8	0	0.727	0.996	444	16	452
tp3_4	−0.600	0.000	276	4	−0.253	0.000	49	1	325
tp4_8	−0.600	0.000	276	4	−0.253	0.000	49	1	325
tp5	−0.038	0.241	2	0	0.830	0.709	914	42	916
tp5_6_7	−0.600	0.000	276	8	−0.253	0.000	49	2	325
tp5_6_7_8	0.543	0.610	188	19	−0.677	0.184	293	42	148
tp5_7	−0.600	0.000	276	4	−0.253	0.000	49	1	325
tp6_8	−0.058	0.000	2	0	−0.666	0.000	212	7	214

Columns:

	Axis 1	StDev	Rep	Ctr	Axis 2	StDev	Rep	Ctr	Quality
C_hyenas	2.942	0.777	929	831	−0.510	0.376	28	36	957
C_lions	0.209	0.247	20	11	1.467	0.264	961	793	980
T_lions	−0.498	0.033	393	156	−0.175	0.067	49	28	442
U.II	−0.048	0.106	3	1	−0.461	0.125	244	143	246