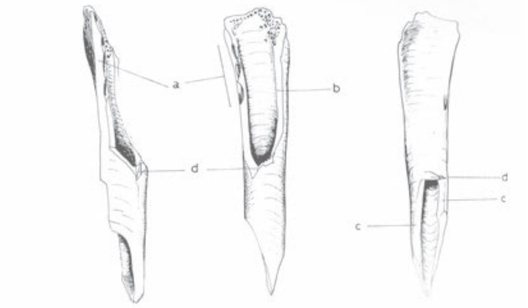


QUATERNARY CLIFF-DWELLING BOVIDS (*CAPRA*, *RUPICAPRA*, *HEMITRAGUS*, *OVIS*): SITE'S TYPOLOGY AND TAPHONOMIC REMARKS

PHILIPPE FOSSE[1], JEAN PHILIP BRUGAL[1], JEAN BAPTISTE FOURVEL[1], STEPHANE MADELAINE[2]

(1) Aix Marseille Université. CNRS, Minist. Culture, UMR 7269 LAMPEA. fosse@mmsh.univ-aix.fr (https://orcid.org/0000-0002-7993-533X), brugal@mmsh.univ-aix.fr (https://orcid.org/0000-0002-5138-3545), fourvel@mmsh.univ-aix.fr (https://orcid.org/0000-0002-1061-4642)
(2) Musée National de Préhistoire & Université Bordeaux, UMR 5199 PACEA. stephane.madelaine@culture.gouv.fr

---

QUATERNARY CLIFF-DWELLING BOVIDS (*CAPRA, RUPICAPRA, HEMITRAGUS, OVIS*): SITE'S TYPOLOGY AND TAPHONOMIC REMARKS

*In Europe, Quaternary karstic deposits yield commonly remains of Caprinae (*Capra, Rupicapra, Hemitragus, Ovis*). A database is elaborated on rich-caprine sites, especially from France and Spain. Based on data dealing with topography and morphology of karstic settings (sinkholes, horizontal galleries), and quantification of faunal remains (NISP, skeletal elements) as well as taphonomic observations (age classes, sex-ratio, carnivore activity), a typology of caprine sites is proposed. Questions are raised about deposit formation and agents of such accumulations. Preliminary data suggest the importance of medium-sized felids (leopard) and canids (wolf) as main predators of cliff-dwelling bovids and/or canids as a systematic secondary bone modifier. Other types of sites concern natural traps and anthropogenic bone accumulations (rock shelters and caves) mainly dated of Late Paleolithic.*

Key words: *Caprids, taphonomy, digested bones, site function, carnivore activity.*

1. INTRODUCTION

Mountain ecosystems are characterized by a relatively low diversity of mammalian species (including both predator and preys). Cliff-dwelling bovids (ibex, chamois, thar, argali and blue sheep in Eurasia, mountain goat and bighorn sheep in N America) are the main ungulate species of these particular environments. During the Holocene, intensified anthropogenic processes highly reduced the geographical range of wild Ungulates and human pressure conducts to establish protected areas as well as action plan such as management, species reintroduction and conservancy zone. During Pleistocene times, cliff-dwelling bovids had a significantly wider geographical range (over almost all northern Hemisphere) occupying more diverse ecosystems, both in plains, hills and mountains. Bone assemblage's formation should be similar to the other ungulates (including cervids, equids and large-sized bovids), as follows: i) naturally died animals; preyed and accumulated in ii) carnivore dens/lairs or iii) anthropic sites. The present paper aims to characterize these 'caprine assemblages' according to their typology and taphonomic criteria.

2. THE CLIFF-DWELLING BOVIDS OF W EUROPE: A BRIEF CHRONO-TAXONOMIC FRAME

In western Europe, several small/medium-sized species of cliff-dwelling bovids have been identified all along Pleistocene times, within numerous archeo- and paleontological sites. So far, four genera have been recognized (Crégut-Bonnoure 1992). In France, the extinct argali *Ovis ammon antiqua*, has been identified in a few Middle Pleistocene sites (Caune de l'Arago: Crégut-Bonnoure 1979; Monchot 1996a; Rivals 2002; Camp de Peyre Delpech *et al*. 1978; Madelaine, unpublished). Thars, belonging to the genus *Hemitragus*, are represented by important populations of Middle Pleistocene *H. bonali* at L'Escale in SE (Bonifay 1974-75; Coumont 2006) and Les Rameaux in SW France (Rouzaud *et al*. 1990; Coumont ibid) and the Late Pleistocene *H. cedrensis* in SE french sites (Les Cèdres: Crégut-Bonnoure 1985). The genus *Capra* concerns several species/sub-species recognized from Early Pleistocene (*Capra alba* in Spain: Calero *et al*. 2006) followed by the appearence of *Capra ibex* and *Capra pyrenaica* during the MIS 7/6, still present in European mountains (Altuna 1972; Crégut-Bonnoure 2002; 2005). Finally, various species and sub-species belonging to the genus *Rupicapra* (*R. rupicapra*, *R. pyrenaica*) are found all along the Pleistocene. The biochronological implication of the chamois is regularly discussed (Masini 1982; Clot and Marsan 1986; Masini and Lovari 1988; Masseti and Salari 2012). The two later genera, *Capra* and *Rupicapra*, are particularly abundant in palaeontological and archaeological record during the Late Pleistocene (*cf. infra*).

3. MATERIAL AND METHODS

In this paper, Quaternary deposits containing mainly ibex and chamois are considered, these two species being the most frequent and often found associated. In SW and SE France as well as in the Pyrenees (both French and Spanish), a survey of 806 sites/levels containing *Capra* (675 Pleistocene and 131 Holocene deposits) has been recently established (Fosse *et al*. in press). According to the collected data (including topography, palaeontology and taphonomy), we could discuss the typological classification and taphonomic characterization of these caprine bone assemblages (figs. 1-3 and references therein). Ecological and taphonomic data were also provided for the main modern and Pleistocene large carnivores (felids, canids and hyenids) dealing with their predation and consumption patterns of medium-sized ungulates (mainly cervids). Our dataset consists: 1) in contextual information (site topography); 2) caprid skeletal part distribution and all damage associated (fig. 4); 3) on data from extant african leopard (Pickering 2001), mountain lion (Stiner *et al*. 2012), gray wolf (Klippel *et al*. 1987; Chase 1990; Esteban *et al*. 2010; Fosse *et al*. 2012) and (spotted) hyena (Carlson and Pickering 2003) scat contents. We will consider in the latter criteria both the scat contents *s.s.* and bone modification produced by gastric juices; we will add direct observations provided by the current authors on modern and Pleistocene samples resulting from red fox (Cardal), wolf/cuon (Combe Grenal, Vaufrey) and cave hyena activities (Lunel-Viel, Fouvent) on cervid bones. Such analysis will allow to discuss specific consumption and digestion patterns observed on different medium-sized ungulate acropodials.

Note: most of the site with bibliography references can be found in the figures 1-4, as they are not systematically quoted in the text.

4. TYPOLOGY OF CLIFF-DWELLING BOVID'S SITES (fig. 5)

Although cliff-dwelling bovids (Capra) have been recognized in Late Pleistocene open-air sites from plain landscapes in N Europe (Couturier 1962; Mol 1992), a majority of the record concerns karstic cavities from mountainous regions in Southern and Central Europe. These are directely connected to their ecomorphologic adaption to rocky environments. Caprine bone accumulations are found in three main site categories according to the morphology and topography of cavities (fig. 5): A) vertical entrance or sinkholes directly open to the outside, B) cavities with horizontal or descending gallery leading to a pitfall, and C) strictly horizontal cavities without any topographic hindrances (like a pit). This global typology could be developed following chronology (Pleistocene, Holocene) and other factors (biotic and abiotic) implying site functions

4.1 TYPE A SITES (fig. 1 and references therein)

Holocene type A sites characterized as pits and sinkholes are found in moutainous areas (e.g., Pyrenees, Alps). These geographical areas constitute the last refugia for numerous wild species. The ibex appears the most common species found in these natural traps, chamois remains being scarce. The traps yield frequently one or two individuals (AN-015, PT 10, Les Bouquetins), sometimes more (16 in Coulet des Roches) and up to 50 individuals (Giévroz Devant). Ibex are mainly identified by fairly complete skeletons and males are the most abundant (AN-015, Bouquetins, PT10) compared to females (SO-4). Carnivore activities (toothmarks) are absent and rodent marks could be observed on unearthed dry bones. Radiometric datings on several indivuals from a single site highlight the diachronic and recurrent trapping processes (Coulet des Roches).

Pleistocene type A corresponds to sinkholes or avens, with narrower chimneys, which contain almost exclusively macro-herbivores (cervids, equids, large bovids) and mega-herbivores (rhinocerotids, proboscideans) and, sometimes containing important caprid samples. They are typical natural traps potentially explored by scavengers (e.g., wolves, cave hyenas) as well as hominids (Brugal and Jaubert 1991; 1996) to exploit the accumulated carcasses. Usually carnivore impact is significantly higher than anthropogenic activities. Although thar remains are scarce at Coudoulous II natural trap, a single fragment of humerus has cutmarks on the distal

Site	Country	Chrono.	Type	Function	Caprid sp.	Caprid NISP	Caprid MNI	Caprid %NISP	other cliff-dw bovids	%NISP all cliff-dw bovids	Reference
AN-015	Spain	Holocene	A	N	*C. pyrenaica*		1				García González 2012
Bouquetins, gouffre	France	Holocene	A	N	*C. pyrenaica*		2				Clot 1988
BSE 21	France	Holocene	A	N	*C. pyrenaica*		1				Clot 1986
Camp de Peyre	France	Middle Pleist.	A ?	N	*O. antiquua*	379					Madelaine unpublished
Coulet des Roches	France	Late Pleist.	A	N	*C. ibex*	529	16		*Rupicapra sp.*		Crégut *et al.* 2018
Escale, ens.2	France	Middle Pleist.	A ?	N	*Hem. bonali*	4072	77	99,7%	none	99,7%	Coumont 2006
Escale, ens.3	France	Middle Pleist.	A ?	N	*Hem. bonali*	254	9	100,0%	none	100,0%	Coumont 2006
Escale, ens.4	France	Middle Pleist.	A ?	N	*Hem. bonali*	212	6	85,8%	none	85,8%	Coumont 2006
Escale, ens.5	France	Middle Pleist.	A ?	N	*Hem. bonali*	79	5	100,0%	none	100,0%	Coumont 2006
Giévroz Devant	Switzer.	Holocene	A	N	*C. ibex*		50				Reynaud-Savioz *et al.* 2018
PT 10	France	Holocene	A	N	*C. pyrenaica*		2		*R. pyrenaica*		Clot 1982; 1984

Fig. 1: Holocene and Pleistocene sinkholes (type A) yielding caprine remains, with quantified data (NISP, %) and taphonomic interpretation. Abbreviations: Pleist. = Pleistocene; H = human activities; K = carnivore modification; N = natural sites.

epiphysis (Brugal *et al.* 2006). The Escale cave could be described as a natural trap as well, although precise topographic context is unclear. The thick stratigraphical filling (20-23 meters thick, Bonifay and Bonifay 1963), belonging to the Middle Pleistocene, contains the largest population of *Hemitragus bonali* in France (Bonifay 1974-75) and has been studied from a taphonomic analysis (Coumont 2006 and see below). The Camp de Peyre site, which yields 379 remains of argali but also abundant remains of reindeer and horse (Delpech *et al.* 1978; Guadelli and Prat 1995) could probably be related to this category. The ungulate bones are complete, without any carnivore toothmarks, and belong mostly to subadult individuals (Madelaine and Fosse pers. obs.). The type A sites yielding caprine remains are not very common, especially for the Pleistocene.

4.2 TYPE B SITES (fig. 2 and references therein)

So far, this type is the most frequent and could be considered as a variant stage of Type A sites, supporting the idea that caprine accumulations result mainly from natural trapping. Although interpretations of some accumulations, especially Holocene ones, can still be explained by ecological (natural living place of ibex) and topographical factors (accidental falls towards the deep sectors of the cavities), the function of Pleistocene sites is more complex due to various taphonomic histories, greatly influenced by the presence of both predators (felids, canids, hyenids) and humans (mainly during the Middle Palaeolithic).

Holocene and Late Glacial deposits provide an interesting source of ecological and taphonomic information. Some caves contain few individuals (one to five) but can reach until up to 36 individuals (Tempiette). Ibex remains are found about 6 to 10 m away from the entrance at the ‘grotte du Balai’, while the bone remains are located about 16 m inside at Schwalmis cave. These examples support ibex behaviors relating a natural exploration of some galeries next to the entrance feeding salt licks on the walls (Couturier 1962; Moncel *et al.* 2008; Blant *et al.* 2012 and references therein; Griggo *et al.* 2019). Although topographies are not available, several swiss sites can probably be classified as type B because they are described as refuges (Al Segno 1, Bouquetins, GU2) or shelters / galleries leading to pitfalls that have trapped ibexes (Bärenhöhle, Dohlenhöhle 1 & 2, GU13, Kapuzinerhöhle ... in Blant *et al. ibid*).

The diachronic frequentations of this type of cavity by some mammals (ibex, chamois, brown bear) are well highlighted by the direct radiocarbon dates (Edis Loch, R7/057, Tempiette); they can spend several thousand years of bone accumulation (Griggo *et al.* 2019). This long time-span of bone accumulation might be similar in many Holocene deposits not yet directly dated and in which several ibexes have been identified (Bucardos, Chourrugue Ouest, Erbinia). This « diachronic population » should be used as a guideline for Late Pleistocene sites where cliff-dwelling species are abundant. Finally, in this type site, the predominance of males (Barranco Jardin J-1, Barranco Jardin J-5, Bucardos, Erbinia, MS-2, Tempiette) over females (CS-59) as well as subadult individuals over adults seems the rule (Chourrugue Ouest, Los Batanes, Illobi). Carnivore toothmarks on caprine bones are scarce.

This topographical configuration is the most frequent for the Pleistocene period and constitutes the most complex study from a taphonomic point of view. Numerous ibex bones are found in vertical holes cutting karstic horizontal galleries. These accumulations are sometimes considerable with a low carnivore involvement (Observatoire, Repolust, Vallescure). However, the pleistocene rich-caprine sites present a combination of potential natural trapping, consumption by carnivores (felids, canids) and exploitation by humans.

Some type B sites yielding spanish ibex remains have been described as leopard « lairs » (Los Rincones). This cave was used at least two times by different large carnivores; one as a winter denning site by brown bears (MNI=8) and one, later by leopards (MNI=4). The interpretation as a leopard site consumption is mainly provided by the spatial bone distribution within the same gallery (Gallery of Leopard) (*cf. infra*). In other sites, a dual exploitation of alpine ibex by humans and wolf is considered (Les Pêcheurs: Moncel *et al.* 2008) whereas other instance (Soulabé) presents an important sample of caucasian ibex associated with leopard and wolf remains

Fig. 2 (next page): Holocene and Pleistocene caves (type B) yielding caprine remains, with quantified data (NISP, %) and taphonomic interpretation. Abbreviations as in fig. 1.

Site	Country	Chrono.	Type	Function	Caprid sp.	Caprid NISP	Caprid MNI	Caprid %NISP	other cliff-dw bovids	%NISP all cliff-dw bovids	Reference
Artazu VII	Spain	Late Pleist.	B	N	*Rupicapra pyr.*	728	15	100,0%			Castaños *et al.* 2017
B 8	Spain	Holocene	B	N	*Capra pyrenaica*		1				Sauqué *et al.* 2015
Balai	Switzerland	Holocene	B	N	*Capra ibex*		3				Blant and Deriaz 2007
Barranco Jardin J-1	Spain	Holocene	B	N	*Capra pyrenaica*		1				Sauqué *et al.* 2015
Batanes, Los	Spain	Late Pleist.	B	N	*Capra pyrenaica*	1079	9	100,0%	none	100,0%	Sauqué *et al.* 2018
Bucardos	Spain	Holocene	B	N	*Capra pyrenaica*		5				Sauqué *et al.* 2015
C-32	Spain	Holocene	B	N	*Capra pyrenaica*		1				Nebot and Pauné 1996
Chourrugue Ouest	France	Holocene	B	N	*Capra pyrenaica*		6				Cazenave *et al.* 1994
Coume Arrats	France	Holocene	B	N	*Capra pyrenaica*		1				Clot 1984
CS 53	Spain	Holocene	B	N	*Capra pyrenaica*		1				Nebot and Pauné 1995
CS 59	Spain	Holocene	B	N	*Capra pyrenaica*		1				Nebot and Pauné 1995
CS 61	Spain	Holocene	B	N	*Capra pyrenaica*		1				Nebot and Pauné 1995
Edis Loch	Switzerland	Holocene	B	N	*Capra ibex*		4				Trüssel 2018
Erbinia	France	Holocene	B	N	*Capra pyrenaica*		3				Fosse, Besson, Cazenave, Delmasure unp.
Grotta degli Stambecchi	Italy	Late Pleist.	B ?	N	*Capra ibex*	451	4	100,0%	none	100,0%	Boscato 2001
Har Mahagna	France	Holocene	B	N	*Capra pyrenaica*		1				Clot 1984
Hortus, all levels	France	Late Pleist.	B ?	H + K + N ?	*Capra caucasica*	2564	65				Pillard 1972; Lebegue *et al.* 2010
Illobi	Spain	Late Pleist.	B	N	*Capra pyrenaica*	24	3				Villaluenga Martínez 2011
Milchbalm	Switzerland	Holocene	B	N	*Capra ibex*		2				Imhof 2003
MS-2	Spain	Holocene	B	N	*Capra pyrenaica*		1				Gárcia González 2012
Muguet	France	Holocene	B	N	*Capra ibex*	8					Ballésio and Philippe 2018
Observatoire	Monaco	Late Pleist.	B	N + K	*Capra ibex*		100				Boule 1927
Pêcheurs, S4	France	Late Pleist.	B	N + K + H	*Capra ibex*	1585	N/A	97,5%		81,0%	Daujeard 2008; Daujeard *et al.* 2019
Permayou inférieur	France	Holocene	B	N	*Capra pyrenaica*		1				Clot 1984
Pié Lombard	France	Late Pleist.	B	N + K + H	*Capra ibex*	1283		68,0%	*R. rupicapra*	70,5%	Moussous 2014
R7/057	Switzerland	Holocene	B	N	*Capra ibex*		2				Blant et al. 2012
Rameaux, Seq.5	France	Middle Pleist.	B	N + K	*Hemitragus bonali*	81	5	4,9%	none	4,9%	Coumont 2006
Rameaux, Seq.6	France	Middle Pleist.	B	N + K	*Hemitragus bonali*	163	5	29,7%	none	29,7%	Coumont 2006
Repolust, gray layer	Austria	Late Pleist.	B	N ?	*Capra ibex*	833	63				Mottl 1951
Repolust, red brown layer	Austria	Late Pleist.	B	N ?	*Capra ibex*	423	31				Mottl 1951
Rincones	Spain	Late Pleist.	B	K	*Capra pyrenaica*	528	20	86,3%	*R. pyrenaica*	91,0%	Sauqué *et al.* 2014; 2014
Salpêtre de Pompignan	France	Late Pleist.	B	H	*Capra ibex*	314		79,3%	*R. rupicapra*	86,6%	Daujeard 2008
Salzofenhohle	Austria	Pleist./Holocene	B	N + K ?	*Capra ibex*	221	12			N/A	Pacher 2011
Schwalmis	Switzerland	Holocene	B	N	*Capra ibex*		3				Blätter *et al.* 1995
Soulabé	France	Late Pleist.	B	N + K	*Capra ibex*	1025	21	91,0%	*R. rupicapra*	14,5%	Fosse *et al.* 2019
Strumwandhöhle	Austria	Holocene	B	N	*Capra ibex*		1				Pacher *et al.* 2018
Tane della Bricole	Italy	Holocene	B	N	*Capra ibex*		1				Blant and Della Toffola 2005
Tempiette	France	Holocene	A	N	*Capra ibex*	3674	36	72,0%	*R. rupicapra*	34,0%	Griggo *et al.* 2019
Üthürri	France	Holocene	B	N	*Capra pyrenaica*		2				Cazenave *et al.* 1994
Vallescure	France	Late Pleist.	B	N + K ?	*Capra ibex*	745				N/A	Fourvel unpublished
Zazpigagn	France	Holocene	B	N	*Capra pyrenaica*		2				Cazenave *et al.* 1994

Site	Country	Chrono.	Type	Function	Caprid sp.	Caprid NISP	Caprid MNI	Caprid %NISP	other cliff-dw bovids	%NISP all cliff-dw bovids	Reference
Adaouste	France	Late Pleist.	C	H	*Capra caucasica*	100	6	26,8%	*Rupicapra sp.*	28,2%	Defleur *et al.* 1994
Amalda, VII	Spain	Late Pleist.	C	K	*Capra pyrenaica*	61	5	7,1%	*R. rupicapra*	69,7%	Yravedra 2006; 2010
Arago, caune de l'	France	Middle Pleist.	C	H + K	*Ovis antiquua*	6055	163	25,8% (MNI)	*H. bonali*	33,0 % (MNI)	Monchot 1996a; 1996b; Rivals *et al.* 2006
Arche	France	Late Pleist.	?	N ?	*Capra caucasica*	242		93,8%	*R. pyrenaica*	97,7%	Rivals and Testu 2006
Arriutort	France	Holocene	C	N	*Capra pyrenaica*		2				Fosse unpublished
Balazuc, 2-3	France	Late Pleist.	C	H	*Capra pyrenaica*	1000	17	89,8%	*R. rupicapra*	90,4%	Daujeard and Moncel 2010
Balma de Margineda, c10	Andorra	Holocene	C	H	*Capra pyrenaica*	62	2	96,9%	*R. pyrenaica*	96,9%	Gardeisen 2008
Balma de Margineda, c7	Andorra	Holocene	C	H	*Capra pyrenaica*	284	5	96,3%	*R. pyrenaica*	97,6%	Gardeisen 2008
Balma de Margineda, c8+8sup	Andorra	Holocene	C	H	*Capra pyrenaica*	1378	18	93,1%	*R. pyrenaica*	98,1%	Gardeisen 2008
Barasses-Lower	France	Late Pleist.	C	H	*Capra ibex*	79		58,0%	*R. rupicapra*	44,0%	Daujeard *et al.* 2019
Barasses-Upper	France	Late Pleist.	C	H	*Capra ibex*	128		80,0%		57,7%	Daujeard *et al.* 2019
Barranco Jardin J-5	Spain	Holocene	C	N	*Capra pyrenaica*		1				Sauqué *et al.* 2015
Baume des Peyrards, a	France	Late Pleist.	C	H	*Capra ibex*	442		67,6%	*R. rupicapra*	69,4%	Lewis 2011
Baume des Peyrards, b	France	Late Pleist.	C	H	*Capra ibex*	150		63,0%	*R. rupicapra*	66,4%	Daujeard 2008
Baume des Peyrards, c-d	France	Late Pleist.	C	H	*Capra ibex*	777		77,1%	*R. rupicapra*	78,0%	Daujeard 2008
Belvis, l.0-6	France	Late Pleist.	C	H	*Capra pyrenaica*	1515		71,1%	*R. rupicapra*	78,5	Fontana 1998
Bolinkoba, VI	Spain	Late Pleist.	C	H	*Capra pyrenaica*	634					Castaños 1986
Castel 2	France	Late Pleist.	C	N + K ?	*Capra pyrenaica*	204	6	99,0%	*Rupicapra sp.*	100,0%	Pernaud *et al.* 2004
Cova Negra	Spain	Late Pleist.	C	H	*Capra pyrenaica*	260		21,6%	*R. pyrenaica*	22,2%	Perez-Ripoll 1977
Crouzade, Ljinf	France	Late Pleist.	C	H	*Capra ibex*	105		21,5%	*R. pyrenaica*	24,0%	Fontana 1998
Dalmari	Italy	Late Pleist.	C	H	*Capra ibex*	885	59	93,8%	none	93,8%	Fiore *et al.* 1998
Eglises, foyer noir	France	Late Pleist.	C	H	*Capra pyrenaica*	1565					Delpech 1983
Erralla, IV	Spain	Late Pleist.	C	N	*Capra pyrenaica*	227	7	95,0%	none	95,0%	Altuna and Mariezkurrena 1985
Erralla, V	Spain	Late Pleist.	C	H	*Capra pyrenaica*	2375					Altuna and Mariezkurrena 1985
Esquilleu III	Spain	Late Pleist.	C	K + H	*Capra pyrenaica*	115	5	50,7%	*R. pyrenaica*	97,8%	Yravedra 2006; 2010
Gabasa, a+c	Spain	Late Pleist.	C	K + H	*Capra pyrenaica*	265	27	43,7%	*R. rupicapra*	51,2%	Blasco Sancho 1995
Gabasa, d	Spain	Late Pleist.	C	K + H	*Capra pyrenaica*	330	24	52,3%	*R. rupicapra*	59,3%	Blasco Sancho 1995
Gabasa, e	Spain	Late Pleist.	C	K + H	*Capra pyrenaica*	434	29	33,8%	*R. rupicapra*	40,2%	Blasco Sancho 1995
Gabasa, f	Spain	Late Pleist.	C	K + H	*Capra pyrenaica*	399	21	36,5%	*R. rupicapra*	40,9%	Blasco Sancho 1995
Gabasa, g	Spain	Late Pleist.	C	K + H	*Capra pyrenaica*	654	46	39,9%	*R. rupicapra*	42,4%	Blasco Sancho 1995
Gabasa, h	Spain	Late Pleist.	C	K + H	*Capra pyrenaica*	272	14	37,6%	*R. rupicapra*	38,2%	Blasco Sancho 1995
GAP SP	France	Late Pleist.	C	K + H	*Capra ibex*	97	16	18,4%	*Rupicapra sp.*	21,9%	Fourvel unpublished
Imanolen Arrobia	Spain	Late Pleist.	C	K	*Capra pyrenaica*	426	13	77,5%	*R. pyrenaica*	97,6%	Castaños *et al.* 2017
Lazaret, UA 25	France	Middle Pleist.	C	H + K ?	*Capra ibex*	109	6	8,6%	*R. rupicapra*	9,3%	Hassani *et al.* 2017
Lazaret, UA 26	France	Middle Pleist.	C	H + K ?	*Capra ibex*	232	8	13,0%	*R. rupicapra*	15,8%	Hassani *et al.* 2017
Lazaret, UA 28	France	Middle Pleist.	C	H + K ?	*Capra ibex*	323	9	14,6%	*R. rupicapra*	17,4%	Hassani *et al.* 2017
Lazaret, UA A	France	Middle Pleist.	C	H + K ?	*Capra ibex*	366	8	20,1%	*R. rupicapra*	20,2%	Hassani *et al.* 2017

Site	Country	Chrono.	Type	Function	Caprid sp.	Caprid NISP	Caprid MNI	Caprid %NISP	other cliff-dw bovids	%NISP all cliff-dw bovids	Reference
Lazaret, UA B	France	Middle Pleist.	C	H + K ?	*Capra ibex*	268	10	19,3%	*R. rupicapra*	19,4%	Hassani *et al*. 2017
Lazaret, UA C	France	Middle Pleist.	C	H + K ?	*Capra ibex*	297	11	19,3%	*R. rupicapra*	19,5%	Hassani *et al*. 2017
Lazaret, UA D	France	Middle Pleist.	C	H + K ?	*Capra ibex*	230	5	15,2%	*R. rupicapra*	15,5%	Hassani *et al*. 2017
Lazaret, UA E	France	Middle Pleist.	C	H + K ?	*Capra ibex*	91	5	10,1%	*R. rupicapra*	10,4%	Hassani *et al*. 2017
Llonin, VIII Cono Posterior	Spain	Late Pleist.	C	H + K	*Capra pyrenaica*	270	7	21,1%	*R. pyrenaica*	81,0%	Sanchis *et al*. 2019
Noisetier	France	Late Pleist.	C	K + H	*Rupicapra rup.*	1150 ?			*C. caucasica*		Mallye *et al*. 2012
Praileaitz I, Exterior	Spain	Late Pleist.	C	H + K	*Capra pyrenaica*	182	7	34,1%	*R. pyrenaica*	82,0%	Castaños and Castaños 2017
Praileaitz I, Galeria NW	Spain	Late Pleist.	C	H + K	*Capra pyrenaica*	454	11	64,7%	*R. pyrenaica*	79,3%	Castaños and Castaños 2017
Praileaitz I, Pasillo	Spain	Late Pleist.	C	H + K	*Capra pyrenaica*	47		78,3%	*R. pyrenaica*	83,3%	Castaños and Castaños 2017
Praileaitz I, Sala 1	Spain	Late Pleist.	C	H + K	*Capra pyrenaica*	119		65,0%	*R. pyrenaica*	74,9%	Castaños and Castaños 2017
Praileaitz I, Sala 2	Spain	Late Pleist.	C	H + K	*Capra pyrenaica*	366	10	78,9%	*R. pyrenaica*	85,3%	Castaños and Castaños 2017
Praileaitz I, Vestibulo	Spain	Late Pleist.	C	H + K	*Capra pyrenaica*	1115	16	63,8%	*R. pyrenaica*	80,9%	Castaños and Castaños 2017
Prince, foyer B	France	Late Pleist.	C	H	*Capra ibex*	608		73,8%	*R. rupicapra*	74,2%	Daujeard 2008
Raco del Duc, level F-G	Spain	Late Pleist.	C	K	*Capra pyrenaica*	465	9	91,2%	none	91,2%	Sauqué and Sanchis 2017
Rascaño, 1	Spain	Late Pleist.	C	H	*Capra pyrenaica*	577	26	85,9%	*R. rupicapra*	86,8%	Altuna 1981
Rascaño, 2	Spain	Late Pleist.	C	H	*Capra pyrenaica*	557	15	87,0%	*R. rupicapra*	88,1%	Altuna 1981
Rascaño, 3	Spain	Late Pleist.	C	H	*Capra pyrenaica*	510	20	93,9%	*R. rupicapra*	94,3%	Altuna 1981
Rascaño, 4a	Spain	Late Pleist.	C	H	*Capra pyrenaica*	673	23	91,2%	none	91,2%	Altuna 1981
Rascaño, 4b	Spain	Late Pleist.	C	H	*Capra pyrenaica*	1319	36	88,2%	none	88,2%	Altuna 1981
Rascaño, 5	Spain	Late Pleist.	C	H	*Capra pyrenaica*	1313	34	91,6%	none	91,6%	Altuna 1981
Riera, all levels (1-30)	Spain	Late Pleist.	C	H	*Capra pyrenaica*	6906					Altuna 1986
Riparo Mochi	Italy	Late Pleist.	C	H	*Capra ibex*	292	34	17,8%	*R. rupicapra*	21,9%	Tagliacozzo *et al*. 2012
S'Espasa	Spain	Late Pleist.	C	K	*Capra pyrenaica*	760	10	98,6%	none	98,6%	Sauqué *et al*. 2017
Teshik Tash	Tadjikistar	Late Pleist.	C ?	H	*Capra sibirica*	760	38				Movius 1953
Tourasse, 7a	France	Late Pleist.	C	H	*Capra ibex*	262		13,6	*R. rupicapra*	23,1%	Gourdain 2000
Tritons, unit 2	Spain	Late Pleist.	C ?	H + K	*Capra pyrenaica*	1031	22	96,6%	none		Mico *et al*. 2020
Urtiaga	Spain	Late Pleist.	C	H	*Capra pyrenaica*	1099					Altuna 1972
Vache, c1-4	France	Late Pleist.	C	H	*Capra pyrenaica*	71451	1831	87,6%	*R. pyrenaica*	91,6%	Pailhaugue 1995
Zafarraya	Spain	Late Pleist.	C	K + H	*Capra pyrenaica*	2660	140	94,8%	*R. pyrenaica*	96,5%	Barroso Ruiz (coord.) 2003

Fig. 3: Holocene and Pleistocene caves (type C) yielding caprine remains, with quantified data (NISP, %) and taphonomic interpretation. Abbreviations as in fig. 1.

and with a very low evidence of human activities (cutmarks). Ibex bones have been found mainly at the base of a natural pitfall and have been consumed by carnivores (leopard/wolf, *cf. infra*). In Salzofen cave bear site, carnivore toothmarks have been observed on appendicular long bones of alpine ibex. In this high-altitude site (2005 m a.s.l.) other carnivores have been identified: cave lion, wolverine and wolf.

Finally, natural deposits could be as well described for some chamois sites (Aratzu VII) although leopards and large canids were identified among the faunal list. The taphonomic analysis clearly mentionned the lack of any carnivore toothmarks on all pyrenean chamois remains and all species, including both ungulates and carnivores (leopards, cave lion, cuon, red fox). It seems that all these species have fallen down and trapped independently into the pitfall.

4.3 TYPE C SITES (fig. 3 and references therein)

Horizontal karstic cavities (caves) are grouped within Type C sites consisting in natural-death sites dated to Holocene (Arriutort, Barranco Jardin J-5) and Late Pleistocene (Erralla IV). These sites are rare and generally considered as the result of particular events (e.g., accidental death, lightning-strikes). In Erralla IV, age-classes distribution of spanish ibex « population » (MNI=7) shows the prevalence of senile and adult individuals. This mortaliy pattern is, by far, different than those noticed in A and B type sites.

Dealing with modern carnivore sites, we can mention red fox dens. This small canid does oftenly collect ovicaprinae bones in its consumption places (Yravedra *et al*. 2014). A special case (Cardal cave) where both few ibex and chamois bones were found associated with an important marmot sample (Fosse 2010) can be cited. The site is located in the French Pyrenees (2205 m a.s.l.) and caprine long bones ends and phalanges are systematically toothmarked (scores, pits, punctures).

Several Pleistocene small caves (from 4 to 30 m depth) are interpreted as leopard « lairs » (Raco del Duc I, S'Espasa, Tritons). The leopards are regurlarly found in association to secondary carnivore species (scavenger / opportunistic predator?) such as wolf (Pié Lombard), red fox (Imanolen Arrobia) or spotted hyena (Llonin). In some cases, the leopards are associated to human activities (Amalda VII). In other caves, a dual exploitation of ibex and chamois respectively by humans and dhole (*Cuon*) is considered (Noisetier); in this site the chamois bones have been found with a high frequency and degree of surface modification (digestion). A mixed association between ibex and lynx is reported at Buraca Escura (Aubry *et al*. 2001; Arceredillo *et al*. 2018). Caprine seem essentially of natural origin with some limited evidence of lynx exploitation from the Late Paleolithic level. Although Gabasa cave is described as a hyena den, the rich accumulation of spanish ibex remains in all levels is associated to an important population of wolves. Similar to Gabasa, wolves are the main predator at Praileaitz I (Exterior, Galeria NW, Vestibulo?) with a great abundance of spanish ibex and chamois remains. Role of this canid in bone modification is highly suspected in both sites.

Many shelters and horizontal caves are preferred places for human Paleolithic occupation. During Lower and Middle Paleolithic, layers often demonstrate alternate occupancy with carnivores (Arago, Cova Negra, Balazuc, Le Lazaret, Les Peyrards) and caprine accumulations can be caused by all these different predators. In contrast, several Late Paleolithic sites (Solutrean, Magdalenian) yield sometime huge amount of caprine bones (especially ibex: Dalmari, Belvis, Ermittia, Erralla, Bolinkoba, Les Eglises, Rascaño, La Riera, La Vache) and are recognized as specialized ibex hunting sites. This species can represent at least 80-95 % of the total remains per level/site and has been intensively exploited from a food, economic and symbolic perspective.

The proposed typology on caprine bone accumulation highlights the importance of topography, but also of other biological factors (presence of predators, marks on bones, age classes, completness of remains) to infer the functional nature of these Holocene and Pleistocene sites. Vertical karstic cavities (types A and B) constitute the majority of cases, and they can often be interpreted as natural death place for caprines possibly exploited afterward by human and non-human predators. The horizontal galleries (type C) are mainly human habitats and more rarely used by carnivores for denning; in some cases, caprine could naturally occupy caves as a shelter for special event (harsh climatic condition), and died there, secondary exploited, or not, by meat/bone-eaters.

Site	Code	Type	Accumulating processes	Caprid sp.	Cranial NISP	Axial NISP	Append NISP	Total NISP	Cranial %NISP	Axial %NISP	Append %NISP
S'Espasa	1	C	Leopard	*Capra pyrenaica*	16	322	278	**616**	2,60	52,27	45,13
Rincones	2	B	Leopard	*Capra pyrenaica*	35	59	317	**411**	8,52	14,36	77,13
Vache, c2	2	C	Natural trap	*Capra pyrenaica*	1022	173	5645	**6840**	14,94	2,53	82,53
Raco del Duc, level F-G	3	C	Leopard	*Capra pyrenaica*	31	177	225	**433**	7,16	40,88	51,96
Zafarraya	4	C	Leopard / Cuon	*Capra pyrenaica*	526	173	433	**1132**	46,47	15,28	38,25
Pêcheurs, S4	5	B	Wolf ?	*Capra ibex*	73	517	627	**1217**	6,00	42,48	51,52
Gabasa	6	C	Wolf ?	*Capra pyrenaica*	90	182	958	**1230**	7,32	14,80	77,89
GAP SP	7	C	Wolf ?	*Capra ibex*	17	13	49	**79**	21,52	16,46	62,03
Erralla, IV	8	C	Natural trap	*Capra pyrenaica*	23	105	84	**212**	10,85	49,53	39,62
Batanes	9	B	Natural trap	*Capra pyrenaica*	43	558	352	**953**	4,51	58,55	36,94
Coulet des Roches	10	A	Natural trap	*Capra ibex*	63	221	245	**529**	11,91	41,78	46,31
Vallescure	11	B	Natural trap	*Capra ibex*	48	131	566	**745**	6,44	17,58	75,97
Escale, ens.2	12	A	Natural trap	*Hemitragus bonali*	111	710	2769	**3590**	3,09	19,78	77,13
Escale, ens.3	13	A	Natural trap	*Hemitragus bonali*	5	29	176	**210**	2,38	13,81	83,81
Escale, ens.4	14	A	Natural trap	*Hemitragus bonali*	14	19	134	**167**	8,38	11,38	80,24
Escale, ens.5	15	A	Natural trap	*Hemitragus bonali*	4	12	56	**72**	5,56	16,67	77,78
Rameaux, Seq.5	16	B	Natural trap	*Hemitragus bonali*	3	6	58	**67**	4,48	8,96	86,57
Rameaux, Seq.6	17	B	Natural trap	*Hemitragus bonali*	5	12	138	**155**	3,23	7,74	89,03
Castel 2	18	C	Natural trap	*Capra pyrenaica*	20	104	74	**198**	10,10	52,53	37,37
Arche	19	?	Natural trap	*Capra caucasica*	12	51	72	**135**	8,89	37,78	53,33
Balma de Margineda, c7	20	C	Natural trap	*Capra pyrenaica*	52	39	198	**289**	17,99	13,49	68,51
Balma de Margineda, c8+8sup	21	C	Natural trap	*Capra pyrenaica*	84	130	650	**864**	9,72	15,05	75,23
Balma de Margineda, c10	22	C	Human	*Capra pyrenaica*	12	10	39	**61**	19,67	16,39	63,93
Vache, c1	23	C	Natural trap	*Capra pyrenaica*	467	84	3635	**4186**	11,16	2,01	86,84
Vache, c3	25	C	Natural trap	*Capra pyrenaica*	1597	244	8027	**9868**	16,18	2,47	81,34
Vache, c4	26	C	Natural trap	*Capra pyrenaica*	2414	374	10875	**13663**	17,67	2,74	79,59
Barasses	27	B ?	Wolf ?	*Capra* sp.	16	38	42	**96**	16,67	39,58	43,75
Soulabé	28	B	Natural trap	*Capra ibex*	30	62	441	**533**	5,63	11,63	82,74
Adaouste	29	C	Natural trap	*Capra caucasica*	7	7	37	**51**	13,73	13,73	72,55
Grotta degli Stambecchi	30	B ?	Natural trap	*Capra ibex*	10	237	154	**401**	2,49	59,10	38,40
Dalmari	31	C	Human	*Capra ibex*	63	96	406	**565**	11,15	16,99	71,86
Arago	32	C	Human	*Ovis antiquua*	263	398	2084	**2745**	9,58	14,50	75,92
Salzofenhohle	33	B	Natural trap	*Capra ibex*	25	102	90	**217**	11,52	47,00	41,47
Riparo Mochi	34	C	Natural trap	*Capra ibex*	106	7	147	**260**	40,77	2,69	56,54
Amalda VII	35	C	Leopard / Lynx ?	*Capra pyrenaica*	16	192	258	**466**	3,43	41,20	55,36
Esquilleu III	36	C	Leopard	*Capra pyrenaica*	13	15	81	**109**	11,93	13,76	74,31
Rascaño, 5	37	C	Human	*Capra pyrenaica*	159	70	437	**666**	23,87	10,51	65,62
Rascaño, 4a	38	C	Human	*Capra pyrenaica*	161	120	536	**817**	19,71	14,69	65,61
Rascaño, 4b	39	C	Human	*Capra pyrenaica*	67	69	298	**434**	15,44	15,90	68,66
Rascaño, 3	40	C	Human	*Capra pyrenaica*	40	78	146	**264**	15,15	29,55	55,30
Rascaño, 2	41	C	Human	*Capra pyrenaica*	55	78	185	**318**	17,30	24,53	58,18
Rascaño, 1	42	C	Human	*Capra pyrenaica*	70	104	169	**343**	20,41	30,32	49,27
Imanolen Arrobia	43	C	Leopard / Fox ?	*Capra pyrenaica*	277	37	90	**404**	68,56	9,16	22,28
Noisetier	44	C	Dhole ?	*Capra pyrenaica*	11	21	116	**148**	7,43	14,18	78,37
Rinoceront	45	A ?	Canid ?	Caprinae	40	311	215	**566**	7,07	54,95	37,98

Fig. 4: Skeletal part distribution (%NISP) for Capra and Rupicapra remains in the 3 categorized caprine sites. Source as in figs. 1-3.

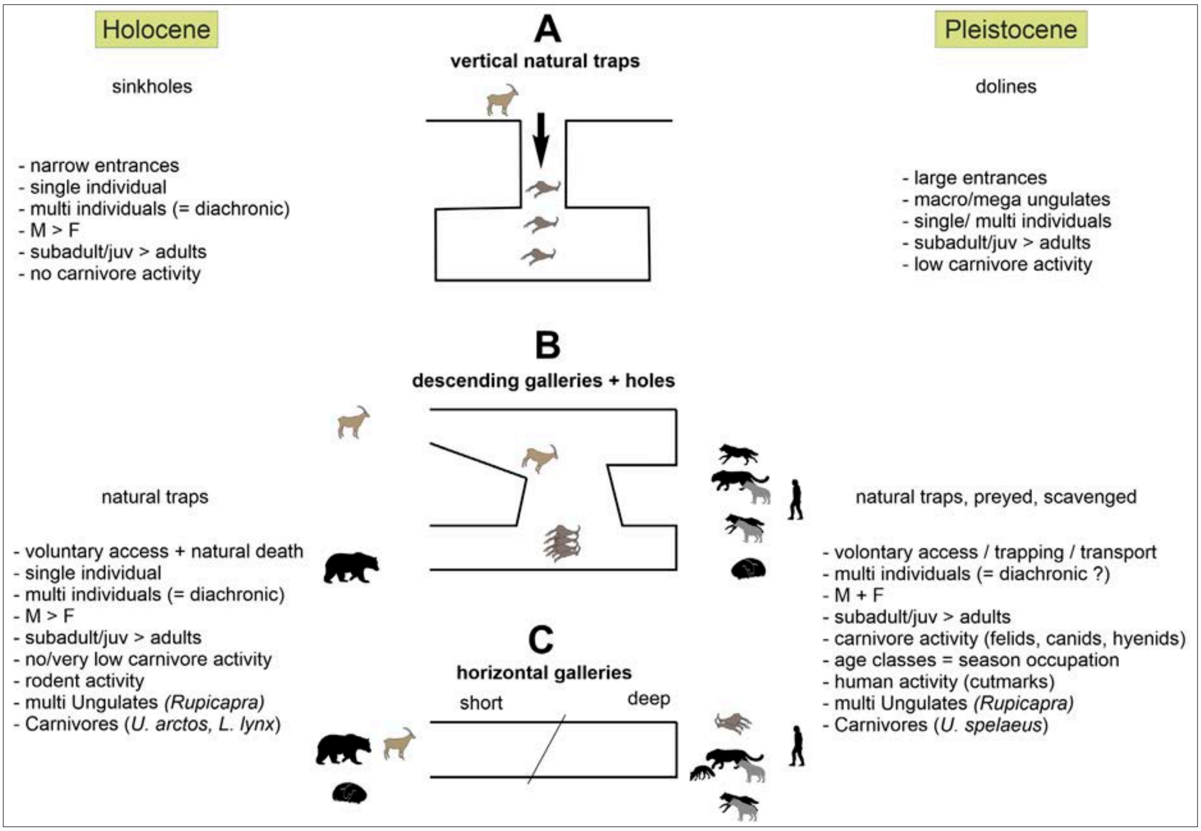


Fig. 5: Typology of Holocene and Pleistocene European sites yielding caprine remains.

5. ECOLOGY OF EXTANT CAPRINE'S PREDATORS

The specific identification of carnivore's exploitation of ungulate (ranging from 30 to 200 kg), and here on caprine species can be raised by the degree and frequency of association between predators and prey. Ecological data on extant caprine-hunters are not abundant. However, the ibex/argali-medium to large-sized felid trophic relationships is the most frequently observed so far.

5.1 PREDATION BY FELIDS

Excluding lions' social behaviour, felids are solitary hunters. Hunting strategies used by snow leopard (*Panthera uncia*), mountain lion (*Puma concolor*) and african leopard (*Panthera pardus*) consist in ambush huntings focused on a single prey. In Asia, the snow leopard is the main predator of siberian ibex *Capra sibirica* (Shehzad *et al*. 2012; Lyngdoh *et al*. 2014; Johansson *et al*. 2015; Weiskopf *et al*. 2016) and of the blue sheep *Pseudois nayaur* (Oli *et al*. 1993; Wegge *et al*. 2012; in Weiskopf *et al*. op. cit.; Chetri *et al*. 2017). In human-modified areas where carnivore's diet focus mainly on livestock, seasonal consumption of siberian ibex is always higher in the snow leopard than in other carnivores, especially the gray wolf (Anwar *et al*. 2011; Bocci *et al*. 2017). In the Near-East, the Persian leopard (*P. pardus saxicolor*) is the main predator of the urials, *Ovis orientalis* (Farhadinia *et al*. 2018) while in N America, the mountain lion is the main predator of bighorn sheep, *Ovis canadensis* (McKinney *et al*. 2006; Clemenza *et al*. 2009; Rominger 2017; Beale 2019). Feeding experiments on captive pumas suggest a wintering scavenging behaviour of this species over deer carcasses (Bauer *et al*. 2005), eating up to 50% of edible tissues (but no bones?). The Himalayan thar *Hemitragus jemlahicus* may be seasonally preyed on by the snow leopard (Shrestha 2008). The European lynx (*Lynx lynx*) is considered as an efficient hunter of chamois and roe deer and even reindeer populations (Breitenmoser and Haller 1993; Molinari-Jobin *et al*. 2002; Nieminen and Leppaluoto 1988). Predation on calves is important (Nybakk *et al*. 2002). The Iberian lynx (*Lynx pardinus*), smaller than the european species, is a highly specialized rabbit-hunter (> 80% of diet) and very rarely (< 5%) on fallow deer, red deer (Delibes 1980; Gil-Sanchez *et al*. 2006). Ungulate identification is based on hairs whereas bones identified in scats belong always to lagomorph size vertebrates (Lloveras *et al*. 2008).

5.2 PREDATION BY CANIDS

Large canids are social predators, huntig by packs. The main prey of wolves are deers (roe deer, fallow deer, red deer, reindeer, elk, moose: Zlatanova *et al*. 2014) and wild boars (Nores *et al*. 2008; Sin *et al*. 2019) from plain or forested regions. In N America, the mountain goat *Oreamnos americanus*, smaller than eurasian ibex, is preyed upon mainly by brown bear and then by gray wolf and mountain lion (Côté and Festa-Bianchet 2003). Argalis are sometimes preyed on by wolves in W Europe (Poulle *et al*. 1997; Capitani *et al*. 2004; Gazzola *et al*. 2007; Stahlberg *et al*. 2017). The arid highlands of central Asia, with very low mammalian diversity, are a rare place where all large carnivores (canids, felids) predate, in equivalent proportions, on argali and siberian ibex (Jumabay-Uulu *et al*. 2014). In Europe, chamois is also mentioned to be a significant prey of wolf, but no precise details are available. Finally, extant foxes (and eagles) prey upon neonate/very young ibex in W Europe (Crampe 1991). Even though wolf scats (genetically identified) are regularly found at snow leopard kill-sites (suggesting scavenging activity by canids), no direct observations on scavenging behavior in wolves on ibex, thar or chamois carcasses has been recorded. Most of the above-mentioned studies are based on scat contents (hair analysis and genetics), while no detailed taphonomic data on prey carcasses are available (skeletal parts, bone scattering, toothmarks etc). However, feeding experiments on captive wolves reveal heavy bone modification pattern on ovicaprinae remains (Castel 2004).

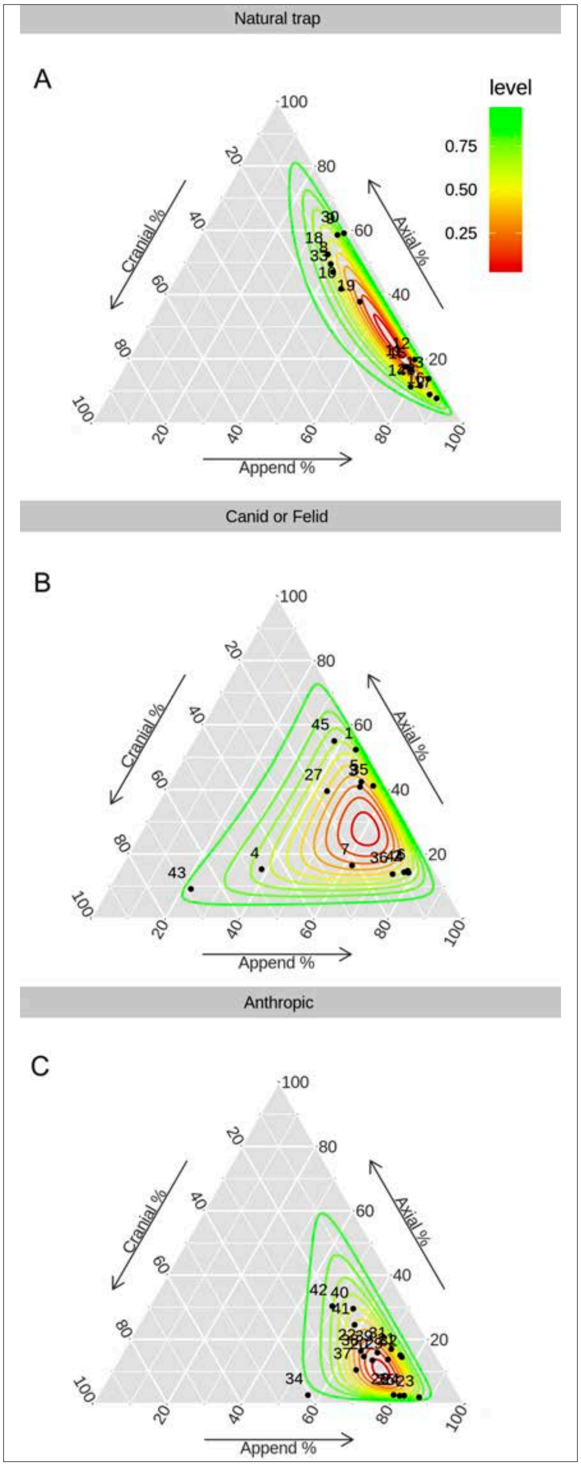
Eco-ethological data highlight this highly frequent trophic relationship between adult caprine – large felids (*Panthera*, *Puma*) in diverse ecosystems whereas wolf's main prey are often gregarious ungulates (cervids, large bovids).

6. TAPHONOMY OF CAPRINE'S PREDATORS/SITES

Skeletal part distribution has been recorded according to the site typology (fig. 6, fig. 4 for data and figs. 1-3 for references); isolated teeth were systematically excluded of the counts as they over-biased the samples. Data from scat contents or regurgitations are also mentioned. Ingestion is both related to regurgitation of undigestable items (plants, hairs, horns, hooves, chitin …) as well as defecation accompanying each other by chemical dissolution processes. Main analyses on carnivore scat contents concern the morphological or genetic identification of organic remains (ex. hair, bone, pollen, etc.) from a taxonomic or ecological perspective (prey, diet, season …) (e.g., Bon *et al*. 2012; Utge *et al*. 2020 and ref. herein). Recently, a morphometric approach of coprolites has been carried out in order to identify carnivore species and to match ungulate gnawed remains to the identified predators found in a site (Sanz *et al*. 2016). Most of the taphonomic coproscopic data concern small/medium carnivores (red fox) and their main prey (lagomorphs, rodents) (Andrews and Nesbit-Evans 1983).

6.1 NATURAL SITES

Natural sites (Type A and B) are characterized by a balanced frequency of all skeletal parts (fig. 6, A). However, two groups can be distinguished: 1) sites where axial skeletal elements are very abundant, as a result of caprine naturally dying into the traps that have not been carrion-fed by carnivores (L'Observatoire, Grotta delli Stambecchi, Erralla IV, Coulet des Roches, Salzofen?); 2) sites where vertebrae and ribs are much less frequent (Escale, Rameaux). In these Middle Pleistocene sites, low-density paleontological remains are much less well frequent than in recent natural traps, presumably due to differential conservation effects. Sediment compression is high and the % survival can be correlated with


Natural trap

Canid or Felid

Anthropic

Fig. 6: Skeletal part distribution (%NISP) for *Capra* and *Rupicapra* remains in the 3 categorized caprine sites. Colours/grades = various confidence ellipses. Isolated teeth not considered. Site numbers and data in fig. 4.

bone density for each skeletal element. Fragmentation *in situ* is often important (Coumont 2006). Very moderate consumption by carnivores is observed (L'Escale).

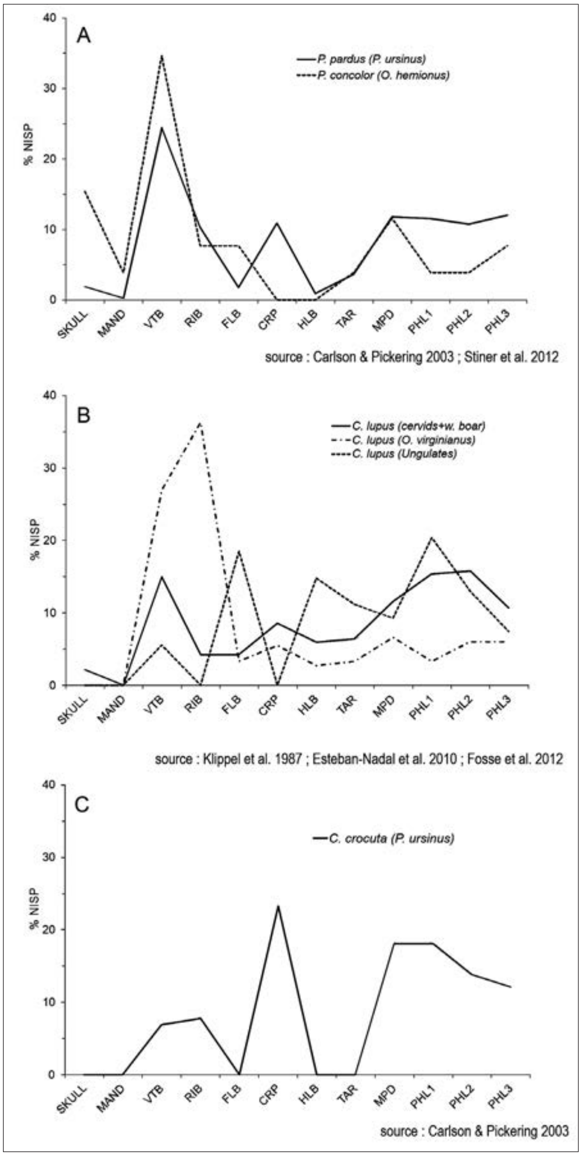
6.2 FELID (LEOPARD) SITES

Felids are meat/flesh-eaters and hunt preys of different size. There is no undoubtedly observation on food regurgitation by lions or leopards in Africa, neither by the snow leopard in Asia nor the mountain lion/puma in America. There is no detailed description of the small bones ingested by the mountain lion. Taphonomic studies on scat contents are scanty for the felid species (Stiner *et al.* 2012 for the puma; Carlson and Pickering 2003 for the african leopard). Main skeletal elements identified in scats are vertebrae, ribs and phalanges (fig. 7, A). In the Pleistocene european record, the leopard (*P. pardus* sp.) has been described as the main predator of ibex (Imanolen Arrobia, S'Espasa, Llonin, Los Rincones, Soulabé, Tritons unit 2, Zafarraya). In leopard lairs, the distribution of skeletal parts is close to that found in natural sites (S'Espasa), with the exception of axial skeletal elements, which are sometimes less abundant (Imanolen Arobia). The frequency of complete bones is high (37% in S'Espasa, 50% in Imanolen Arrobia, 64% in Llonin) whereas bone modification is low (5% at S'Espasa, 8% at Tritons, 16% at Imanolen Arrobia), with few toothmarks per bone and, moreover, no identifiable digested bone (Imanolen Arrobia, Raco del Duc, Los Rincones, S'Espasa). This is undoubtedly the main taphonomic feature of bone accumulations produced by fossil leopards and it is also an important difference with the modern record. In Tritons cave, there are only five ibex digested bones, scavenged by canids (Mico *et al.* 2020). In Llonin, 10% of the chamois bones and some ibex bones were digested but have been found with numerous coprolites attributed both to the leopard and also to the cave hyena.

6.3 CANID (WOLF) SITES

Extant canids (wolf, dog) only regurgitate meat to feed upon weaning pups (Malm and Jensen 1993); (identifiable) bone fragments can only be found in scats, staying several days in the stomach (pH of about 3). The scat contents are mostly composed of vertebrae and rib fragments and the proportion of phalanges is greater than in felid scats (fig. 7, B). In Poland (Biezszcady), where the diet of wolves is mainly based on predation of red deer, roe deer and wild boar, a sample of 800 scats has been carried out. The scats were cleaned and prepared (separation of hair, plant and bone fragments). Less than 8% of scats yield bone remains and, overall, there was a clear paucity of bones per scat. Identified bones are mainly small fragments of vertebrae and ribs as well as phalanges. Carpals, tarsals, patellae and a few isolated teeth complete these samples. The skeletal distribution is comparable to other observations made on other wolf scats (Klippel *et al.* 1987; Barja and Corona 2007; Esteban-Nadal *et al.* 2010) or even on leopard scats (Pickering 2001), by the abundance of phalanges (fig. 7, A-B). A feeding experiment also highlighted the large quantity of small (< 1cm) unidentifiable fragments in wolf scats (Esteban-Nadal *et al.* 2010).

The gray wolf appears to be the main (cervid) bone accumulator in some N American caves (Granite Quarry cave: Klippel *et al.* 1987; Lower Rampart cave 1: Sattler ibid; Moses Coulee cave: Darwent and Lyman 2002). In Europe, the wolf could be considered as a predator of alpine (Sant Agostino X: Stiner 2004) and of pyrenan ibex (Praileaitz I Exterior/Galeria NW/Vestibulo: Castaños and Castaños 2017). In these two samples, long bones belong mainly to subadult individuals (non-epiphyseal bones) and are complete. Appendicular bones are the most abundant elements whereas vertebrae and ribs are under-represented. Toothmarks seem to be frequent; no information is recorded of the presence of digested bone. In Granite Quarry cave, mule deer remains belong mainly to fawns (< 1 year old) and show chemical alterations characteristic of digestion (corrsion, acid-etching). In Pleistocene natural deposits scavenged by wolves (Gral), the frequency of gnawed bones is less than 10%, for all ungulate size classes; some digested bones have been found but no coprolite has been identified (Castel *et al.* 2010). In the hyena (and wolf?) den of Gabasa, 3% of the bones are gnawed; no indication of the presence of identifiable digested bones is given. Nevertheless, several first phalanges show toothmarks (mainly punctures and furrows). The systematic presence of crushed acropods in carnivore sites has, for more than a century, been discussed and correctly attributed to the action of canids, through actualistic observations (Martin 1906; Peï 1938 (plates VII & XXI); Chase 1990; 2001). Identification of large canid activity is based both on similar sized/morphological circular holes on opposite sides (usually punctures on cranial and caudal faces) and as well on the presence of these bones in modern canid scats (coyote, *Canis latrans*: Chase 1990). The gray wolf is also an active scavenger of



source : Carlson & Pickering 2003 ; Stiner et al. 2012

source : Klippel et al. 1987 ; Esteban-Nadal et al. 2010 ; Fosse et al. 2012

source : Carlson & Pickering 2003

Fig. 7: Comparative frequency (%NISP) of identified bones in modern gray wolf, african leopard, mountain lion and spotted hyena scats.

cervid remains in natural traps (Igue du Gral: Castel *et al*. 2010; Cova del Rinoceront layer I: Sanz and Daura 2018) and on cave bear skeletons (Grosse Grotte: Weinstock 1999), reindeer and ibex remains (left by humans?) as well (Balazuc: Daujeard 2008; Combe Grenal : Chase 1986; 2001; Gamssulzenhöhle: Kühtreiber and Kunst 1995; Schusterlucke: Galik 1997; Divje Babe I: Toskan 2007; Vergisson II: Fabre 2010). The second large canid involved with a carnivore activity on caprine bones is the dhole (*Cuon alpinus*). Gnawed small bones have been observed on a few thar and red deer remains (patellae) at Vaufrey cave (Binford 1988; Fosse pers. obs.) whereas at Noisetier cave, numerous and strongly digested bones belonging to the pyrenan chamois were found, with coprolites (Mallye *et al*. 2012). Overall, bone modification by wolf is stronger than those noticed for leopard sites. In wolf lairs (GAP) and cave hyena dens (Gabasa), the skeletal distribution shows an under-representation of ribs and vertebrae in comparison with one found in leopard sites (fig. 6, B).

6.4 HYENID (FOSSIL SPOTTED HYENA) SITES

Hyenids regurgitate animal remains (hair, meat, bone, horn, hoof) after having eaten too much food too quickly (Kruuk 1972). Regurgitated bones of large unguealtes such as buffalo can be found on kill sites (Fosse, Fourvel, Brugal, pers. obs.). High concentration of hydrochroric acid in their stomach (pH lower than 2) allow a much more efficient absorption of organic remains than for any other large carnivore; deposits of phosphatic scats (white) are characteristic of a scent marking behavior. Despite numerous neotaphonomic analyses on all extant hyena species, there are few studies on hyenid scat contents related to the presence of ungulate remains (Kolska Horwitz 1990). One experimental study has been carried out with small primates (Carlson and Pickering 2003) and shows a significant difference in the skeletal part distribution, compared to canid and felid scats, through the abundance of carpals, tarsals and phalanges and a lower frequency of vertebrae and long bones as well (fig. 7, C). The different modes of prey transport between felids (whole carcasse) and canids/hyenids (head, legs …) or the context of bone assemblages (primary consumption site vs scavenging site) could explain the variations observed.

In cave hyena dens, (small) fragments of long bones, perforated with various stages of intensity, have been correctly attributed to acid-etching phenomena (Zapfe 1966; Villa *et al*. 2010; Bourdillat 2008). These pieces are typical of a consumption by this predator/scavenger. Furthermore, the highest frequency of ingested bones is only found in Late Pleistocene hyena dens (20% in cueva del Buho: Sala Burgos 2012; 12% in Fouvent: Fourvel 2012). However, caprine remains are rarely found in Pleistocene hyena dens. At Gerde cave (Clot 1987) and grotte Marie (Crochet *et al*. 2007), a few ibex bones have been identified while only a few chamois remains have been recovered from Unikoté cave (NISP=11; Michel 2005). Even though ibex and chamois are particularly abundant in Gabasa cave (Blasco Sancho 1995) recognized as a hyena den, the relative abundance of wolf remains in each levels supports the fact that caprines could not be considered only as the result of hyena depredation but rather as an important taphonomic agent in accumulation/modification of ungulate bones. Most of data from Pleistocene hyena dens involve with cervids (red deer, reindeer) as well as with equids and large-sized bovids.

6.5 A COMPARATIVE FRAMEWORK OF DIGESTED BONES

The question of the degree small bones (carpals, tarsals, patella, phalanx) crushing, ingestion and digestion recovered from the scat contents constitutes one of the most consistent aspect of feeding behaviour in different Pleistocene top predators. These particular remains should be considered as significant indicators in the identification of the carnivore species/zoologicalgroup which could be involved in the bone accumulation processes. Despite their remarkable interest in understanding the feeding behaviour of different Pleistocene top predators, most of the above-mentioned works have provided little data on digested identifiable bones.

A comparison between modern wolf scat contents (Poland), *Hemitragus*/*Capra* from L'Escale and Soulabé, reindeer from Combe Grenal (wolf activity) and cervids from Lunel-Viel (hyena den) as well as a few chamois sample found in modern red fox den allows us to propose differences in the degree of crushing and digesting small bones by canids and hyenids. This comparison concerns the first phalanges on the one hand (fig. 8, A-B, fig 9) as this is the bone most frequently consumed by all carnivore species and other small bones (carpals, tarsals) on the other hand (fig. 10). Wolf scats contain seldom identifiable bones, including phalanges. The first phalanges are sometimes found complete but are much more frequently reduced to their distal part (fig. 8, A-1). Proximal ends are also present, but in few number. Complete phalanges are ingested either after being bitten (punctures) or not. In the first case, circular hole could break totally the cortical bone and penetrate into the marrow cavity under proximal articular epiphysis on medial/lateral side. Then, very small bone fragments resulting from breakage linked to the teeth pressure can be found inside of this hole. Puncture circular shape differs mainly from acid-etched holes which are much more elongated and shapeless. First phalanges exhibit commonly holes close to the distal articular epiphysis, on their cranial side. Distal ends do present sharpened edges around articular surfaces and a thinned cortical extremity on the opposite side (shaft).

Ungulate phalanges (*Rupicapra*, *Ovis*) are also found in red fox dens (Cardal, French Pyrenees). These particular remains result from a collecting behavior by the small canid and were brought back into the dens as isolated skeletal part or still in anatomical association with other phalanges and hooves. The phalanges may be nibbled at both epiphyses and sometimes punctured in their distal part, on the cranial side (fig. 8, A-2). Although red fox does not swallow complete ungulate bone pieces as long as phalanges are, digested phalanges coud be found in dens, coming from collecting around bird of prey nests, mainly the bearded vulture (*Gypaetus barbatus*). Rodents also contribute to the modification of phalanges left by red foxes.

In Escale cave (natural trap), scavenging of *Hemitragus* bones by carnivores are really scanty (Coumont 2006), probably due to the inaccessibility of too deep deposits by any carnivores. However, few first phalanges exhibit toothmarks (pitting) and a distal end has been gnawed and probably ingested (fig. 8, A-3). This kind of bone modification can be attributed to small canids, probably red/arctic foxes which are abundant in the adjacent levels.

In Soulabé cave, about a hundred first phalanges of *Capra caucasica* have been identified with 75% of them being complete and showing no carnivore traces. Modified phalanges present either isolated punctures on their shaft or, more frequently, punctures in the distal part of the cranial side and scores on medial and lateral sides (fig. 8, A-4). Phalanges were gnawed from the proximal end, then reduced to their distal half. Only one complete phalanx is digested (fig. 8, A-4). Corrosion, exposing medular cavities, is quite important on cranial side, below the proximal articular epiphysis and at the distal one as well. The low/moderate frequency of toothmarks on ibex bones and the presence of leopard as the main large predator had led to suggest this carnivore as the main ibex carcasses accumulator, the wolf being much less abundant (Fosse *et al.* 2019). A rapid examination of Raco del Duc bone assemblage by one of the authors (PF) on one hand and a comparative approach on first phalanges (and other small bones) ravaged by different carnivores on other hand allow us to consider bone at Soulabé to be greater than in the leopard sample (Sauqué and Sanchis 2017) and significantly less than or comparable to that of Combe Grenal where the wolf is described as an important taphonomic agent in several levels (Chase 1986; 2001). In this cave, an important sedimentary filling has been excavated and corresponds to intense mousterian human occupations involved with reindeer exploitation. In several levels (e.g. 59, 27, 23), reindeer phalanges show isolated puncture (Chase 2001) as well as multiple abrasive areas resulting from digestion by the wolf. Combe Grenal sample contains more fragmented (proximal and especially distal ends) than complete phalanges (fig. 9). Punctures are rare, especially on complete phalanges and are found near to the proximal epiphyseal joint, on cranial and medial/ lateral sides but are also found more oftenly on distal fragments. On complete phalanges, cortical bone surface is altered by acid-etching, starting as a circular hole and then a wider and deeper horizontal area near the epiphyses on the cranial side, and with a large scooping out cluster on the caudal side. Bone surfaces are regularly polished and the sharpening of the shaft is well marked (fig. 8, B-5). These destructions constitute a significantly stronger step than those observed on the Soulabé samples.

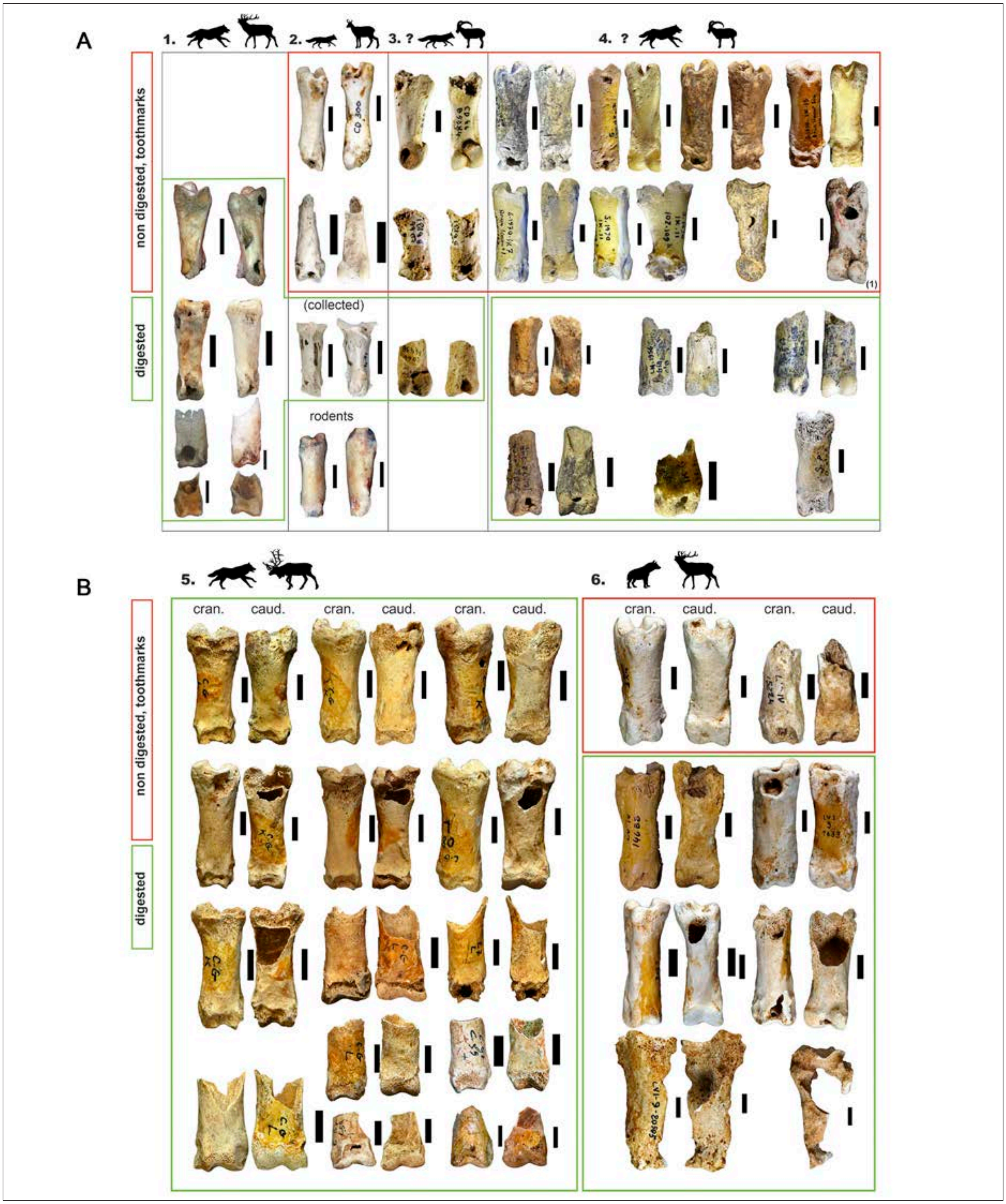


Fig. 8 (A+B): Carnivore modification on caprid and cervid first phalanges by modern and Late Pleistocene red fox, gray wolf and hyenas: 1. modern wolf scat contents (Poland, Biezszcady); 2. modern red fox den (Cardal); 3. natural trap + small carnivores (*V. vulpes*) activity (L'Escale); 4. natural trap + mainly wolf activity? (Soulabé), (1) Les Pêcheurs (wolf activity); 5. wolf activity on reindeer phalanges (anthropogenic refuses? Combe Grenal); 6. hyena den (Lunel-Viel 1+IV).
Bar scale = 1cm. All pictures by Ph. Fosse, except L'Escale (Ph. Jugie, MNP) and Les Pêcheurs (J.B. Fourvel). Cranial (cran) and caudal (caud) views for each element.

			C. lupus	natural + small canids ?	natural + *C. lupus* ?	~*C. lupus*	*C. c. spelaea*
			scats (n=62) Poland	Escale	Soulabé	Combe Grenal, 59, 29, 27, 24, 23, 22, 21, 14	Lunel-Viel 1+IV
			Ungulates	*H. bonali*	*C. caucasica*	*R. tarandus*	cervids
phalanges I	cpt	nt		451	73	32	19
		TM		2	10	1	2
		D	1	1	3	4	6
		TMD	2			2	
	prox	nt			5	52	
		TM				3	
		D	8		1	1	
	dist	nt			2	35	
		TM			4	11	
		D	19	3	2	3	
		TMD	2				
	fgt	nt			3		2
		D	2				
phalanges II	cpt	nt		293	56	45	21
		TM		2	1		
		D	5		4	12	3
	prox	nt			3	34	
		D	5				
	dist	nt			1	21	
		D	7				
	fgt	nt			1		
phalanges III	cpt	nt		189	51	22	22
		TM		1	3		
		D	11			3	26
	prox	D	7				
			69	**942**	**223**	**281**	**101**

Fig. 9: Frequency (NISP) and modification patterns on middle sized ungulate first phalanges found in different types of carnivore modern and Pleistocene sites. Abbreviations: nt = no traces; D = digested; TM = toothmarks; TMD = toothmarks + digestion.

The last predatory species considered is the cave hyena. Known for its capacity to accumulate prey remains in caves, this carnivore has a mixed diet, based on the consumption of meat and bones. In Pleistocene hyena dens, gnawed bones are abundant, as are digested identifiable bones, this latter being under-studied from a taphonomic perspective. In Lunel-Viel, all cervid phalanges were swallowed when complete, without prior crushing stage (fig. 8, B-6). The circular depressions generally correspond to chemical dissolution cups with rounded edges. Although phalanges can be heavily modified by chemical dissolution, these bones appear to be less destroyed overall than in previous wolf samples. A probable explanation would be due to the ingestion of complete lower legs (carpals/tarsals-hooves) by hyenas (Fosse and Fourvel pers. obs.), the wolf ingesting one phalanx at a time. Undigested phalanges show scores and furrows on medial and lateral sides. This comparison of bone modification on first phalanges allows to suggest that the wolf's taphonomic characterization is mainly observed on fragmentary phalanges, reduced to their distal part. For complete phalanges, the destruction produced by wolves is more marked on edging parts, whereas it is constant on all sides in the case of ingestion by

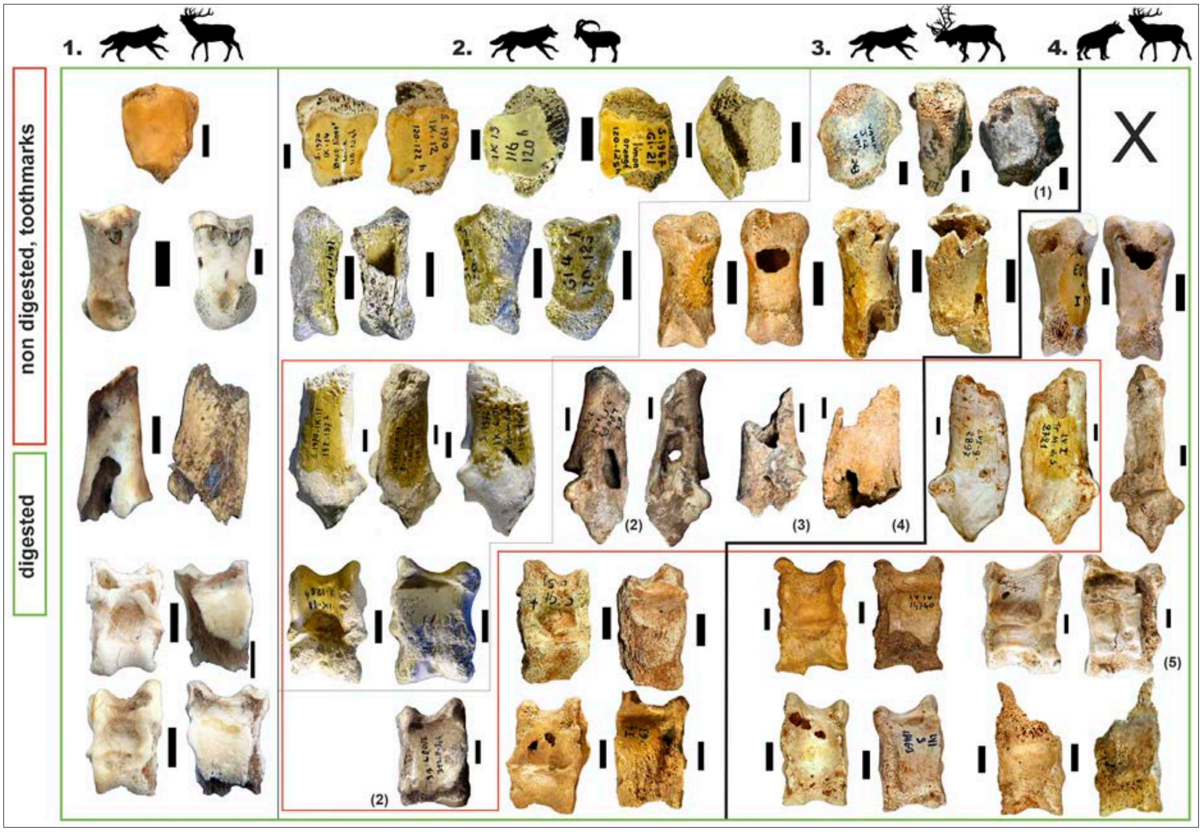


Fig. 10: Comparative modification of small bones by gray wolves and cave hyenas: 1. modern wolf scat contents (Poland, Biezszcady); 2. natural trap + mainly wolf activity? (Soulabé); 3. wolf activity on middle-sized ungulate small bones (anthropogenic refuses? Combe Grenal), (1) red deer (Vaufrey), (2), reindeer (Le Portel) (3) ibex (Les Pêcheurs), (4) cervid (Grotte aux Puces); 4. hyena den (Lunel-Viel 1+IV) (5) reindeer (Fouvent).
Bar scale = 1cm. All pictures by Ph. Fosse, except Fouvent, Grotte aux Puces, Les Pêcheurs and Le Portel samples (J.B. Fourvel). Cranial and caudal views for each element.

hyenas. These first distinguishing criteria can be completed by observations on the other small bones consumed by these two carnivores (fig. 10).

Bone modification by ingestion does concern other small bones (patellae, carpals, tarsals, sesamoids, phalanges). The patella is a moderately compact bone, of a shape easily grasped by carnivores. Nibbling of the upper and lower extremities or ingestion of whole bone has been recorded for extant gray wolf (fig. 10, 1). At Vaufrey cave, in layer VIII described as a cuon denning level (Binford, 1988), red deer patellae are bones mostly modified by carnivores, the other small bones (carpals, tarsals and phalanges) have almost never been toothmarked (pits, scores). Systematic destruction of upper and lower extremities of patellae as a carnivore breakage pattern could be difficult to be distinguished from a natural sedimentary abrasion (fig. 10, 3(1)). Due to the scarcity of modified bones by carnivores, and the absence of coprolites as well, the layer VIII may not reflect a primary accumulation by canids, but rather a very moderate scavenging of carcasses from already dead animals (natural cause? anthropogenic?). In Soulabé cave, ibex patellae have almost all (n=12) been digested by carnivores. Upper and lower extremities are ravaged and gastric juices sometimes have eroded deeply medial and lateral sides, whereas cranial and caudal articular sides remain undamaged. Absence of middle sized ungulate gnawed patellae in Pleistocene hyena dens can presumably be explained by the selecting transport of ungulate legs by this carnivore or by the total consumption of these bones on the kill-site. Evidence of carnivore modification on this bone is common in canid deposits and could also be a good diagnostic taphonomic criterion.

Phalanges are also altered by gastric juices. In wolf scats, these bones are rather complete when belonging to subadult or adult individuals and are reduced to distal portions when unfused (young individuals); in this latter case, phalanges are therefore punctured before ingestion. The effects of gastric juices produce circular holes on shafts and also modify edging areas of articular surfaces (fig. 10, 2). Modification of bone surface due to the digestive effects is common on reindeer phalanges consumed by Pleistocene wolves (Combe Grenal), with a scooping out on the caudal side, as it was observed on first phalanges. In Soulabé, the second phalanges are complete, with eroded surfaces on all four sides and a scooping out area on the caudal side as well. Digestion/regurgitation by cave hyena can produce damage on cervid second phalanges. Punctures are present on proximal and distal ends, as well as scooping out of the caudal side. General morphology of these phalanges is modified from undigested pieces, with a sharpened edges and rounded extremeties. Tarsals, especially calcaneus and astragalus, are compact bones. These bones are modified by large carnivores, although there are significant differences in the degree of alteration between digested tarsals by canids and hyenids. In modern wolf scats only the calcaneus of (very) young cervids have been found. Pieces from adult individuals are too big to be swallowed. Digested calcaneus is fragmented, corresponding to the supra-articular portion (fig. 10, 1). These bones could be slightly gnawed (tuber calcanei) before ingestion. The same morphotype is found in Pleistocene wolf dens, on alpine ibex and cervid calacenus at grotte des Pêcheurs and Grand Abri aux Puces respectively (fig. 10, 3(3)(4)). The other characteristic of consumption by wolves is the presence of a contiguous series of punctures on the caudal side of complete non-ingested calcaneus. These successive punctures can form a line of perforations. This particular morphology of toothmarks, found at the Portel cave (fig. 10, 3(2)), has been observed on modern kill sites as well (Prucca 2003). Calcaneus eaten by cave hyenas do not present this damage pattern and rather systematically show the proximal extremity nibbled, with a progression towards the articular part. Some pieces show a single toothmark on the caudal face, this part of the bone being usually covered with scores (fig. 10, 4). Whole calcaneus can be digested. The spotted hyena (fossil) is the only carnivore species able of ingesting such large bones. On astragalus, differences between canid and hyenid sites can also be described. Wolves can ingest complete ungulate (i.e. small cervid) astragali and chemical destruction due to gastric juices mainly concern caudal and lateral surfaces. The cranial surface shows moderate alteration (fig.10, 1). In Pleistocene wolf sites, astragals are nibbled (posterior surface) or ingested, sometimes with significant disappearance of cortical bone on the posterior and anterior sides (Combe Grenal). The number of astragals so severely modified is low in a bone assemblage. On the contrary, in cave hyena dens, frequency of cervid ingested astragals is very high (11/60 pieces in Lunel-Viel; Fosse, unpublished), with a very high degree of dissolution on all sides, up to the fragmentation of this bone in smaller pieces. The cranial side may be severely damaged and presents large areas of exposure of the medular cavities and holes (fig. 10, 4). These differences recorded in modern and Pleistocene samples could be noticed on most small bones. The intensity of destruction is greater and more frequent in hyena dens than in wolf lairs. Moreover, cave hyena does not only ingest bones and teeth of medium-sized ungulates but also swallows most of the much more robust bones of larger ungulates such as equids and large bovids. In a hyena's den, most prey bones (ungulates and carnivores) show the characteristics of acid-etching modification. This is also a significant difference from Pleistocene wolf dens.

This comparative work on digestion effects produced by large carnivores should be continued and could be a useful tool to distinguish between canid and hyenid bone accumulations in Pleistocene sites.

7. ENDING REMARKS

Caprines are the emblematic species in the rocky regions and they are present in all mountains ecosytems. Their well adapted cliff-dwelling behavior implies specific hunting techniques different from plains or forested large ungulates (horse, deer, bison…). A detailed survey from southern Europe have been elaborated allowing to propose a first site typology of sites rich in caprine remains. Three type of sites have been distinguished based at first on the site karstic mappings but also combined with faunal associations and some taphonomic features found in the bone assemblages. Although present in three types of sites, from their distinct topographies, these cliff-dwelling bovids are above all abundant in type B deposits. This type is characterized by voluntary and natural frequentations by these ungulates in cavities as well as their potential predators/scavengers. While ecological data favour the trophic relationship between caprines and felids (*Panthera*, *Puma*), faunal analyses of Pleistocene record seem to suggest a more frequent association between caprines and canids, mainly wolves. However, this hypothesis may result of the lack of comparative data from modern leopard, and raises the problem to identify bone assemblage slightly modified by felids. Nevertheless, the pattern observed in the fossil record about the frequency of toothmarks and digestion on small bones (carpals, tarsals, and phalanx) could favor a greater wolf activity in many karstic caves, as hunter or scavenger than any other large carnivore species.

ACKNOWLEDGEMENTS

Professor Manuel Perez-Ripoll's works have significantly contributed to a better knowledge on Pleistocene/Holocene caprine deposits. This contribution is made in his honour. The authors would like to thank Cristina Real Margalef and Alfred Sanchis for inviting us to participate in this volume and allowing us to have a quick look at Raco del Duc's bone sample as well. The authors also thank Pedro Castaños (Bilbao), Jean Jacques Cleyet-Merle and Philippe Jugie of the National Museum of Prehistory in Les Eyzies (France) and Henryk Okarma and Wojtek Smietana of the Institute for Nature Conservation in Krakow (Poland). This article is part of a work on digested bones in different french Pleistocene sites currently being carried out by the present authors of this article. Some observations presented in this paper take place in a working group on Caprine sites led by the « Groupement de Recherches en Taphonomie 'TaphEnA' », GDR 3591 of the CNRS-INEE (resp. J.-Ph. Brugal).

REFERENCES

ALTUNA, J. (1972): Fauna de mamiferos de los yacimientos prehistoricos de Guipuzcoa, *Munibe* 24 (1-4), 1-464.

ALTUNA, J. (1981): Restos oseos del yacimiento prehistorico del Rascaño, *El Paleolitico Superior de la Cueva del Rascaño (Santander)* (J. Gonzalez Echegaray, I. Barandiaran, coords.), Centro de Investigacion y Museo de Altamira Monografias 3, 223-269.

ALTUNA, J. (1986): The mammalian faunas from the prehistoric site of la Riera, La Riera cave, (L. G. Straus, G. Clark, coords.), *Anthropological Research* 237-274, 421-480.

ALTUNA, J.; MARIEZKURRENA, K. (1985): Bases de subsistencia de los pobladores de Erralla : macromamiferos, *Munibe* 37, 87-117.

ANDREWS, P., NESBIT EVANS, E. M. (1983): Small mammal bone accumulations produced by mammalian carnivores, Paleobiology 9 (3), 289-307.

ANWAR, M.; JACKSON, R.; NADEEM, M., JANECKA, J.; HUSSAIN, S.; BEG, M. A.; MUHAMMAD, G.; QAYYUM, M. (2011): Food habits of the snow leopard Panthera uncia (Schreber, 1775) in Baltistan, Northern Pakistan, *Eur. J. Wildl. Res.* 57, 1077-1083.

ARCEREDILLO, D.; BRUGAL, J. P.; PEYROUSE, J. B.; AUBRY, T. (2018): Paléolithique moyen et supérieur à Buraca Escura (Redinha, Pombal, Portugal): comparaisons taphonomique et archéozoologique, *Quaternaire* 29 (1), 53-60.

AUBRY, T.; BRUGAL, J. P.; CHAUVIERE, F. X.; FIGUERAL, I.; MOURA, M. H.; PLISSON, H. (2001): Modalités d'occupations au Paléolithique supérieur dans la grotte de Buraca Escura (Redinha, Pombal, Portugal), *Revista Portuguesa de Arqueologia*, 4 (2), 19-46.

BALLÉSIO, R.; PHILIPPE M. (2018): L'ours brun holocène du réseau du Muguet à Samoëns (Haute-Savoie), *Bull. mens. Soc. linn. Lyon* 87 (1-2), 3-29.

BARJA, I.; CORONA M. E. (2007): El análisis de excretas desde la etología y la arqueozoología: el caso del lobo ibérico, *Human and Faunal Relationships Reviewed: An Archaeozoological Approach* (E. Corona, M. J. Arroyo-Cabrales, coords.), B.A.R.-i.s. 1627, Oxford, 113-121.

BARROSO RUIZ, C.; RIQUELME CANTAL, J. A.; MOIGNE, A. M.; BANES, L. (2003): Las faunas de grandes mamíferos del Pleistoceno superior de la cueva del boquete de Zafarraya. Estudio paleontológico y paleoecológico, *El Pleistoceno superior de la cueva del Boquete de Zafarraya*, Arqueologia, Monografias, 169-222.

BAUER, J. K.; LOGAN, K. A.; SWEARNOR, L. L.; BOYCE, W. M. (2005): Scavenging behavior in puma, *The Southwestern Naturalist* 50 (4), 466-471.

BEALE, M. (2019): *Cougar habitat and prey selection on reclaimed coal mines in west-central Alberta*, Ms University of Alberta.

BINFORD, L. R. (1988): Etude taphonomique des restes fauniques de la Grotte Vaufrey, couche VIII, *La Grotte Vaufrey, paléoenvironnement, chronologie, activités humaines* (J. P. Rigaud, coord.), Mémoires de la Société Préhistorique Française 19, 535-563.

BLANT, M.; DELLA TOFOLLA, R. (2005): Découvertes des ossements subfossiles d'un bouquetin (*Capra ibex*) et d'un ours (*Ursus arctos*) datés de la fin du Pléistocène supérieur – début de l'Holocène à la grotte "Tana delle Bricolle" (Arogno, TI), 1-2.

BLANT, M.; DERIAZ, P. (2007): Le gisement paléontologique datant du Pléistocène supérieur de la grotte du Balai (Sainte-Croix, Vaud), *Actes du 12' Congrès national de Spéléologie*, Vallée de Joux, 155-158.

BLANT, M.; IMHOF, W.; OPPLIGER, J.; CASTEL, J. C. (2012): Analyse chronologique des données d'occupation de bouquetins (*Capra ibex*) dans les grottes des Alpes suisses, *Actes du 13' Congrès national de Spéléologie*, 231-236.

BLASCO SANCHO, F. (1995): *Hombres, fieras y presas. Estudio arqueozoológico y tafonómico del yacimiento del Paleolítico Medio de la cueva de Gabasa 1 (Huesca)*, Monografías Arqueológicas 38.

BLÄTTER, H.; MOREL, P.; TRÜSSEL, M.; TRÜSSEL, P. (1995): Holozäne Bären-, Steinbock- und Kleinwirbeltierefunde in einer Höhle der Nidwaldner Voralpen: Paläontologie und Ichnologie, *Mitteilungen der Naturforschenden Gesellschaft Luzern* 34, 139-157.

BOCCI, A.; LOVARI, S.; KHAN, M. Z.; MORI, E. (2017): Sympatric snow leopards and tibetan wolves: coexistence of large carnivores with human-driven potential competition, *European Journal of Wildlife Research* 63, 1-9.

BON, C.; BERTHONAUD, V.; MAKSUD, F.; LABADIE, K., POULAIN, J.; ARTIGUENAVE, F.; WINCKER, P.; AURY, J. M.; ELALOUF, J. M. (2012): Coprolites as a source of information on the genome and diet of the cave hyena, *Proc. R. Soc. B* 279,
DOI: https://doi.org/10.1098/rspb.2012.0358

BONIFAY, E.; BONIFAY, M. F. (1963): Un gisement à faune épi-villafranchienne à Saint-Estève-Janson (Bouches-du-Rhône), *Comptes-Rendus de l'Académie des Sciences* 256, 1136-1138.

BONIFAY, M. F. (1974-1975): "*Hemitragus bonali*" Harlé et Stehlin Caprinae de la grotte de l'Escale (Saint Estève-Janson, Bouches-du–Rhône), *Quaternaria* 18, 215-302.

BOSCATO, P. (2001): Grotta degli Stambecchi (Valdastico -VI): Considerazioni tafonomiche su resti fossili di *Capra ibex* L. 1758, *Studi Trentini di Scienze Naturali - Acta Geologica* 76, 107-119.

BOULE, M. (1927): *La grotte de l'Observatoire à Monaco*, Archives de l'Institut de Paléontologie humaine 1.

BOURDILLAT, V. (2008): *Hommes – Carnivores ? Caractériser l'action de l'hyène des cavernes : de l'utilisation des données fossiles pour l'interprétation des sites mixtes*, phD M.N.H.N. Paris.

BREITENMOSER, U.; HALLER H. (1993): Patterns of predation by reintroduced european lynx in the Swiss Alps, *The Journal of Wildlife Management* 57 (1), 135-144.

BRUGAL, J. P.; JAUBERT J. (1991): Les gisements paléontologiques pléistocènes à indices de fréquentation humaine : un nouveau type de comportement de prédation ?, *Paléo* 3, 15-41.

BRUGAL, J. P.; JAUBERT, J. (1996): Stratégie d'exploitation et mode de vie des populations du Paléolithique moyen: exemple des sites du Sud de la France, *La vie préhistorique* (J. P. Mohen, P. Chaunu, Y. Coppens, coords.), París, 148-155.

BRUGAL, J. P.; DIEZ FERNANDEZ-LOMANA, J. C.; HUGUET PAMIES, R.; MICHEL, P.; ROSELL ARDEVOL, J. (2006): Karstic cavities, natural bone accumulations and discrete human activities in the European paleolithic: some case studies, *Paleolithic zooarchaeology in practice* (J. A. Haws, B. S. Hockett, J. P. Brugal, coords.), Oxford, 1-12.

CALERO, J. A. C.; VAN DER MADE, J.; MANCHEÑO, M. A.; MONTOYA, P.; ROMERO, G. (2006): *Capra alba* Moyà-Solà, 1987 del Pleistoceno Inferior de la Sierra de Quibas (Albanilla, Murcia, España), *Estudios Geológicos* 62 (1), 571-578.

CAPITANI, C.; VARUZZA, I. B.; SCANDURA, M.; APPOLLONIO, M. (2004): A comparative analysis of wolf (*Canis lupus*) diet in three different italian ecosystems, *Mamm. Biol.* 69 (1), 1-10.

CARLSON, K. J.; PICKERING, T. R. (2003): Intrinsic qualities of primate bones as predictors of skeletal element representation in modern and fossil carnivore feeding assemblages, *Journal of Human Evolution* 44, 431-450.

CASTAÑOS, J.; CASTAÑOS, P.; MURELAGA, X. (2017): Imanolen Arrobia: a new Late Pleistocene carnivore den from the north of the iberian peninsula (Deba, Spain), *Ameghiniana* 54 (4), 370-389.

CASTAÑOS, J.; CASTAÑOS, P.; SUAREZ-BILBAO, A.; IRIARTE-CHIAPUSSO, M. J.; ARRIZABALAGA, A.; MURELAGA, X. (2017): A large mammal assemblage during MIS 5c: Artazu VII (Arrasate, northern Iberian Peninsula), *Historical Biology*, 1-17.

CASTAÑOS, P. (1986): *Los macromamiferos del Pleistoceno y Holoceno de Vizcaya*, phD San Sebastian.

CASTAÑOS, P.; CASTAÑOS J. (2017): Estudio de la fauna de macromamíferos del yacimiento de Praileaitz I (Deba, Gipuzkoa), *Munibe Monographs. Anthropology and Archaeology Series* 1, 221-265.

CASTEL, J. C. (2004): L'influence des canidés sur la formation des ensembles archéologiques. Caractérisation des destructions dues au loup, *Revue de Paléobiologie* 23 (2), 675-693.

CASTEL, J. C.; COUMONT, M. P.; BOUDADI-MALINE, M.; PRUCCA, A. (2010): Rôle et origine des grands carnivores dans les accumulations naturelles. Le cas des loups (*Canis lupus*) de l'Igue du Gral (Sauliac-sur-Célé, Lot, France), *Revue de Paléobiologie* 29 (2), 411-425.

CAZENAVE, G.; BESSON, J. P.; DE VALICOURT, E. (1994): Trouvailles préhistoriques et paléontologiques de la SSPPO, *Bulletin de la SSPPO Quarantenaire de Ia SSPPO* 1952-1992, 224-232.

CHASE, P. G. (1986): *The hunters of Combe Grenal. Approaches to Middle Paleolithic subsistence in Europe*, B.A.R.-i.s. 286, Oxford.

CHASE, P. G. (1990): Sifflets du Paléolithique moyen (?). Les implications d'un coprolithe de coyote actuel, *Bulletin de la Société préhistorique française* 87 (6), 165-167.

CHASE, P.G. (2001): Punctured reindeer phalanxs from the Mousterian of Combe Grenal (France), *Arheološki vestnik (Arh. vest.)* 52, 17-23.

CHETRI, M.; ODDEN, M.; WEGGE, P. (2017): Snow leopard and Himalayan wolf: food habits and prey selection in the Central Himalayas, Nepal, *PLoS ONE* 12 (2), e0170549.

CLEMENZA, S. M.; RUBIN, E. S.; JOHNSON, C. K.; BOTTA, R. A.; BOYCE, W. M. (2009): Puma predation on radiocollared and uncollared bighorn sheep, *BMC Research Notes* 2(1), 230, 1-6.
DOI: https://doi.org/10.1186/1756-0500-2-230

CLOT, A. (1982): Les bouquetins fossiles des Pyrenées occidentales et centrales, *Grande faune sauvage des montagnes d'Europe et écosystèmes d'altitude* (C. Dendaletche coord.), *Acta biol. Mont.* 1, 251-265.

CLOT, A. (1984): Grands mammifères piégés dans les cavités des Pyrénées Occidentales. Premières datations au Carbone 14, *Acta biol. mont.* IV, 389-395.

CLOT, A. (1986): Déterminations de paléontologie quaternaire dans le bassin de L'Adour (troìsième série, Pyrénées-Atlantiques), *Archéologie des Pyrénées occidentales* 6, 141-166.

CLOT, A. (1987): *La grotte de Gerde (Hautes Pyrénées), site préhistorique et paléontologique*, Bagnères-de-Bigorre.

CLOT, A. (1988): Bouquetins quaternaires dans les Pyrénées. 1. Restes osseux du gouffre des Bouquetins (Accous, Pyrénées-Atlantiques), *Revue de Comminges* CI (1er trimestre), 5-13.

CLOT, A.; MARSAN G. (1986): La Grotte du Cap de la Bielle à Nestier (Hautes-Pyrénées). Fouilles M. Debeaux 1960, *Gallia Préhistoire* 29 (1), 63-141.

COTE, S. D.; FESTA-BIANCHET M. (2003): Mountain goat *Oreamnos americanus*, *Wild Mammals of North America: Biology, Management, Conservation* (G.A. Feldhamer, B. Thompson, J. Chapman coords.), The John Hopkins University Press, 1061-1075.

COUMONT, M. P. (2006): *Taphonomie préhistorique: mammifères fossiles en contexte naturel, les avens-pièges, apport pour l'étude des archéofaunes*, phD Aix-Marseille I.

COUTURIER, M. A. J. (1962): *Le bouquetin des Alpes*, Grenoble.

CRAMPE, J. P. (1991): *Le bouquetin ibérique. Eléments pour une réintroduction au versant Nord des Pyrénées Occidentales*, Parc National des Pyrénées Documents scientifiques 26.

CRÉGUT-BONNOURE, E. (1979): *La faune des Mammifères du Pléistocène moyen de la Caune de l'Arago à Tautavel (Pyrénées orientales)*, phD Marseille.

CRÉGUT-BONNOURE, E. (1985): Un nouveau Caprinae, *Hemitragus cedrensis* nov. sp. (Mammalia, Bovidae) des niveaux pléistocènes moyens de la grotte des Cèdres (Le Plan d'Aups, Var). Intérêt biogéographique, *Geobios* 22 (5), 653-663.

CRÉGUT-BONNOURE, E. (1992): Les *Caprinae* (Mammalia, Bovidae) du Pleistocene d'Europe : intérêt biostratigraphique, paléoécologique et archéozoologique, *Mémoire de la Société géologique de France* 160, 85-93.

CRÉGUT-BONNOURE, E. (2002): *Les* Ovibovini *et* Caprini *(Mammalia, Artiodactyla, Bovidae, Caprinae) du Plio-Pléistocène d'Europe: systématique, évolution et biochronologie*, Doctorat d'Etat Université Lyon 1, 2 vols.

CRÉGUT-BONNOURE, E. (2005): Nouvelles données paléogéographiques et chronologiques sur les Caprinae (Mammalia, Bovidae) du Pléistocène moyen et supérieur d'Europe, Munibe 57, 205-219.

CRÉGUT-BONNOURE, E.; BOULBES, N.; DESCLAUX, E.; MARCISZAK, A. (2018): New insights into the LGM and LG in southern France (Vaucluse): the mustelids, micromammals and horses from Coulet des Roches, *Quaternary* 1 (19), 1-47.

CROCHET, J. Y.; GENCE, J.; BOULBES, N.; BOUTIE, P.; CRETIN, C.; CREGUT, E.; DUZER, D.; JOLLY, D.; LAUDET, F.; LEFEVRE, D.; MOURER-CHAUVIRE, C.; ROUSSELIERES, F.; THOUAND, E. (2007): Nouvelles données paléoenvironnementales dans le Sud de la France vers 30000 ans 14C BP : le cas de la grotte Marie (Hérault), *Comptes Rendus Palevol* 6(4), 241-251.

DARWENT, C. M.; LYMAN R. L. (2002): Detecting the postburial fragmentation of carpals, tarsals and phalanxs, *Advances in forensic taphonomy: method, theory and archaeological perspectives* (W. D. Haglund, M. H. Sorg, coords.), CRC Press, 355-377.

DAUJEARD, C. (2008): *Exploitation du milieu animal par les Néandertaliens dans le Sud-Est de la France,* phD Lyon 2.

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(3), 368-391.

DAUJEARD, C.; BRUGAL, J. P.; MONCEL, M. H.; FERNANDES, P.; DELVIGNE, V.; LAFARGE, A.; LE PAPE, J. M.; RAYNAL, J. P. (2019): Neanderthals, carnivores and caprines in two Upper Pleistocene sites of south-eastern France, *Hommes et Caprinés. De la montagne à la steppe, de la chasse à l'élevage* (L. Gourichou, C. Daujeard, J.-P. Brugal, coords.), XXXIX^{ème} rencontres internationales d'archéologie et d'histoire d'Antibes, 77-98.

DELIBES, M. (1980): El lince ibérico. Ecologia y comportamiento alimenticios en el Coto Doñana, Huelva, Doñana, *Acta Vertebrata*, 7, 1-128

DEFLEUR, A.; BEZ, J. F.; CREGUT-BONNOURE, E.; DESCLAUX, E.; ONORATINI, G.; RADULESCU, C.; THINON, M.; VILETTE, P. (1994): Le niveau moustérien de la grotte de l'Adaouste (Jouques, Bouches-du-Rhône). Approche culturelle et paléoenvironnement, *Mus. Anthropol. préhist. Monaco* 37, 11-48.

DELPECH, F. (1983): *Les faunes du Paléolithique supérieur dans le Sud-Ouest de la France*, CNRS Cahiers du Quaternaire 6.

DELPECH, F.; LE TENSORER, J.M.; PRAT, F.; PINEDA R. (1978): Un nouveau gisement du Pléistocène moyen : Camp de Peyre à Sauveterre-la-Lémance (Lot-et-Garonne), *Comptes Rendus de l'Académie des Sciences, Paris* 286 (série D), 1101-1103.

ESTEBAN-NADAL, M.; CACERES, I.; FOSSE, P. (2010): Characterization of a current coprogenic sample originated by *Canis lupus* as a tool for identifying a taphonomic agent, *Journal of Archaeological Science* 37 (12), 2959-2970.

FABRE, M. (2010): *Environnement et subsistance au Pléistocène supérieur dans l'est de la France et au Luxembourg : étude ostéologique des gisements de la Baume de Gigny (Jura), Vergisson II (Saône-et-Loire) et Oetrange (Luxembourg)*, phD Université Aix-Marseille I.

FARHADINIA, M.; JOHNSON, P.; HUNTER, L.; MACDONALD, D. W. (2018): Persian leopard predation patterns and kill rates in the Iran-Turkmenistan borderland, *Journal of Mammalogy*, 99 (3), 713-723.

FIORE, I.; TAGLIACOZZO, A.; CASSOLI, P. F. (1998): Ibex exploitation at Dalmeri rockshelter (TN) and "specialized hunting" in the sites of the Eastern Alps during the Tardiglacial and the Early Holocene, *Preistoria Alpina* 34, 173-183.

FONTANA, L. (1998): *Mobilité et subsistance au Magdalénien dans le Languedoc occidental et le Roussillon*, phD Université Paris I, Paris.

FOSSE, P. (2010): La marmotte dans les Pyrénées : données paléontologiques et écologiques livrées par des découvertes de restes osseux, Tais, *Bulletin de liaison des Mammalogistes de Midi-Pyrénées* 4, 75-90.

FOSSE, P.; SELVA, N.; SMIETANA, W.; OKARMA, H.; WAJRAK, A.; FOURVEL, J. B.; MADELAINE, S.; ESTEBAN-NADAL, M.; CACERES, I.; YRAVEDRA, J.; BRUGAL, J. P.; PRUCCA, A.; HAYNES, G. (2012): Bone modification by modern wolf (*Canis lupus*) : a taphonomic study from their natural feeding places, *Journal of Taphonomy* 10 (3-4), 197-217.

FOSSE, P.; ALTUNA, J.; CASTAÑOS, P.; CREGUT-BONNOURE, E.; FOURVEL, J. B.; MADELAINE, S.; MAGNIEZ, P.; NADAL, J.; VIGNE, J. D. (in press): Le bouquetin dans la Préhistoire, *Recueil en hommage à J. Clottes* (A. Averbouh, V. Feruglio, coords) in press.

FOSSE, P.; FOURVEL, J. B.; LATEUR, N.; MADELAINE, S.; MAGNIEZ, P. (2019): La grotte de Soulabé (Ariège, France): une association bouquetin - léopard? Considérations taphonomiques sur la prédation des caprinés par les Carnivores au Pléistocène, *Hommes et Caprinés. De la montagne à la steppe, de la chasse à l'élevage* (L. Gourichou, C. Daujeard, J.-P. Brugal coords.), XXXIX^{ème} rencontres internationales d'archéologie et d'histoire d'Antibes, 17-41.

FOURVEL, J. B. (2012): *Hyénidés modernes et fossiles d'Europe et d'Afrique ; taphonomie comparée de leurs assemblages osseux*, phD Université Toulouse 2.

GALIK, A. (1997): Die Ungulata aus der Schusterlucke im Kremstal (Wald vier tel, Niederösterreich), *Wiss. Mitt. Niederösterr. Landesmuseum* 10, 83-103.

GARCÍA-GONZÁLEZ, R. (2012): New Holocene *Capra pyrenaica* (Mammalia, Artiodactyla, Bovidae) skulls from the southern Pyrenees, *Comptes Rendus Palevol* 11 (4), 241-249.

GARDEISEN, A. (2008): La fauna de mamifers dels nivells azilians de la balma de la Margineda, *Les excavacions a la balma de la Margineda (1979-1991), vol. IV* (J. Guilaine, M. Barbaza, M. Martzluff, coords.), Andorra la Vella, 492-522.

GAZZOLA, A.; AVANZINELLI, E.; BERTELLI, I.; TOLOSANO, A.; BERTOTTO, P.; MUSSO, R.; APOLLONIO, M. (2007): The role of the wolf in shaping a multi-species ungulate community in the Italian western Alps, *Italian Journal of Zoology* 74(3), 297-307.

GIL-SANCHEZ, J. M., BALLESTEROS-DUPERON, E., BUENO-SEGURA, J.F. (2006): Feeding ecology of the iberian lynx *Lynx pardinus* in eastern Sierra Morena (southern Spain), *Acta Theriologica* 51, 85-90.

GOURDAIN, L. (2000): *Étude de la faune de l'ensemble D de la Tourasse (Saint-Martory, Haute-Garonne): perspectives environnementales*, DEA Université de Paris I.

GRIGGO, C.; GAY, I.; ARGANT, A.; ARGANT, J.; DODELIN, C.; FABBRO, E.; HOBLEA, F.; LEBRETON, L.; PHILIPPE, M. (2019): Tempiette cave (Entremont-le-Vieux, Savoie, France) : paleoecology, seasonality and taphonomy of an ibex and chamois trap-cave, *Hommes et Caprinés. De la montagne à la steppe, de la chasse à l'élevage* (L. Gourichou, C. Daujeard, J.-P. Brugal, coords.), XXXIX^{ème} rencontres internationales d'archéologie et d'histoire d'Antibes, 43-59.

GUADELLI, J.L.; PRAT, F. (1995): Le cheval du gisement pléistocène moyen de Camp-de-Peyre (Sauveterre-la-Lémance, Lot-et-Garonne). *Equus mosbachensis campdepeyri* nov. ssp, *Paléo* 7, 85-122.

HASSANI, M.; VALENSI, P.; VISWESWARA, S.; MICHEL, V.; EL GUENNOUNI, K.; DE LUMLEY, H. (2017): Les petits ongulés de la grotte acheuléano-moustérienne du Lazaret (Nice, France) – Origine anthropique ou carnivore ?, *L'anthropologie* 121 (5), 367-393.

IMHOF, W. (2003): Milchbalm-Höhle. Holozäne knochen von rothirsch, steinbock und braunbär (Muotathal, SZ), *Stalactite* 53 (1), 26-30.

JOHANSSON, A.; MCCARTHY, T.; SAMELIUS, G.; ANDREN, H.; TUMURSUKH, L.; MISHRA, C. (2015): Snow leopard predation in a livestock dominated landscape in Mongolia, *Biological Conservation* 184, 251-258.

JUMABAY-UULU, K.; WEGGE, P.; MISHRA, C.; SHARMA, K. (2014): Large carnivores and low diversity of optimal prey: a comparison of the diets of snow leopards *Panthera uncia* and wolves *Canis lupus* in Sarychat-Ertash Reserve in Kyrgyzstan, *Oryx* 48 (4), 529-535.

KOLSKA HORWITZ, L. (1990): The origin of partially digested bones recevered from archaeological contexts in Israel, *Paléorient* 16 (1), 97-106.

KLIPPEL, W. E.; SNYDER, L. M.; PARMALEE, P. W. (1987): Taphonomy and archaeologically recovered mammal bone from southeast Missouri, *Journal of Ethnobiology* 7 (2), 155-169.

KRUUK, H. (1972): *The spotted hyena: a study of predation and social behavior*, Chicago University Press.

KÜHTREIBER, T.; KUNST, K. (1995): Das spätglazial in der Gamssulzenhöhle im Toten Gebirge (Oberösterreich) - Artefakte, tierreste, fundschichtbildung, *Die Gamssulzenhöhle im Toten Gebirge* (G. Rabeder, G. Withalm, coords.), Mitteilungen der Kommission für Quartärforschung 9, 83-120.

LEBEGUE, F.; BOULBES, N.; GREGOIRE, S.; MOIGNE, A. M. (2010): Systèmes d'occupation, exploitation des ressources et mobilité des Néandertaliens de l'Hortus (Hérault, France), *XVI^{ème} Congrès UISPP, Session C34: Système d'habitat du paléolithique moyen*, Vol. III, Kerns Verlag. Tubingen, 455-483.

LEWIS, J. (2011): *Taphonomy and zooarchaeology of the Middle Pleistocene site of Orgnac 3 (Ardèche Valley, Southeastern France)*, phD, Stanford University.

LLOVERAS, L.; MORENO-GARCIA, M.; NADAL, J. (2008): Taphonomic analysis of leporid remains obtained from modern Iberian lynx (*Lynx pardinus*) scats, *Journal of Archaeological Science* 35 (1), 1-13.

LYNGDOH, S.; SHROTRIYA, S.; GOYAL, S. P.; CLEMENTS, H.; HAYWARD, M. W.; HABIB, B. (2014): Prey preferences of the snow leopard (*Panthera uncia*): regional diet specificity holds global significance for conservation, *PLoS ONE* 9 (2), e88349.

MALLYE, J. B.; COSTAMAGNO, S.; BOUDADI-MALIGNE, M.; PRUCCA, A.; LAROULANDIE, V.; THIEBAUT, 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.

MALM, K.; JENSEN, P. (1993): Regurgitation as a weaning strategy - a selective review on an old subject in a new light, *Applied Animal Behaviour Science* 36 (1), 47-64.

MARTIN, H. (1906): Présentation d'ossements de renne portant des lésions d'origine humaine et animale, *Bulletin de la Société préhistorique française* 3, 385-397.

MASINI, F. (1982). *I Camosci subfossili del Monte Sumbra (Alpi Apuane)*, phD Florence.

MASINI, F.; LOVARI, S. (1988): Systematics, phylogenetic relationships and dispersal of the chamois (*Rupicapra* spp.), *Quaternary Research* 30, 339-349.

MASSETI, M.; SALARI, L. (2012): The Late Pleistocene and Holocene chamois in central-southern Italy, *Archaeofauna* 21, 37-51.

MCKINNEY, T.; SMITH, T. W.; DEVOS JR., J. C. (2006): Evaluation of factors potentially influencing a desert bighorn sheep population, *Wildlife Monographs* 164, 1-36.

MICHEL, P. (2005): Un repaire würmien d'hyénes des cavernes: La grotte d'Unikoté (Iholdy, Pyrénées- Atlantiques, France), *Museo de Altamira monografia* 20: 131-150.

MICO, C. M ARILLA, M.; ROSELL, J.; VILLALBA, M.; SANTOS, E.; RIVALS, F.; PICIN, A.; TALAMO, S.; BLASCO, R. (2020): Among goats and bears: A taphonomic study of the faunal accumulation from Tritons Cave (Lleida, Spain), *Journal of Archaeological Science: Reports* 30, 102194.
DOI: https://doi.org/10.1016/j.jasrep.2020.102194

MOL, D. (1992): Een Pleistocene steenbok in de laagvlakte van de Beneden-Rijn, *Grondboor en Hamer* 4/5/6, 93-98.

MOLINARI-JOBIN, A.; MOLINARI, P.; BREITENMOSER-WÜRSTEN, C.; BREITENMOSER, U. (2002): Significance of lynx *Lynx lynx* predation for roe deer

Capreolus capreolus and chamois *Rupicapra rupicapra* mortality in the Swiss Jura mountains, *Wildlife Biology* 8 (2), 109-115.

MONCEL, M. H.; BRUGAL, J. P.; PRUCCA, A.; LHOMME, G. (2008): Mixed occupation during the Middle Palaeolithic: Case study of a small pit-cave-site of Les Pêcheurs (Ardèche, south-eastern France), *Journal of Anthropological Archaeology* 27, 382-398.

MONCHOT, H. (1996a): *Les petits bovidés (genres Ovis, Hemitragus, Capra et Rupicapra) de la Caune de l'Arago (Tautavel, Pyrénées orientales)*, phD Marseille.

MONCHOT, H. (1996b): La consommation du mouflon (*Ovis antiqua*, Pommerol 1879) au Pléistocène moyen de la Caune de l'Arago (Tautavel, Pyrénées-Orientales), *Géologie Méditerranéenne* XXIII (2), 101-115.

MOTTL M. (1951): Die Repolust-Höhle bei Peggau (Steiermark) und ihre eiszeitlichen Bewohner, *Archaeologia austriaca* 8, 1-79.

MOUSSOUS, A. (2014): *Approche biostratigraphique et évolution des paléoenvironnements au cours du Pléistocène supérieur, d'après l'étude des grands mammifères des grottes de Balzi Rossi (Ligurie, Italie)*, phD, Université Perpignan.

MOVIUS, H. L. (1953): The mousterian cave of Teshik-Tash, southeastern Uzbekistan, central Asia, *American School of Prehistoric Research* 17, 11-71.

NEBOT, M.; PAUNE, F. (1995): 5.- Nous jaciments de *Capra pyrenaica pyrenaica* i altres vertebrats en cavernes de la vall d'Ordesa, *Memoria de la campanya de Ordesa 1994 Grup espeleologic Pedraforca*, 60-73.

NEBOT, M.; PAUNÉ, F. (1996): Avanç a l'inventari de noves restes de *Capra pyrenaica* i d'altres vertebrats trobats a cavitats del P.N.O.M.P., *Memoria de la campanya Ordesa 1996. G. E. Pedraforca*, 56-59.

NIEMINEN, M.; LEPPALUOTO, J. (1988): Predation in the reindeer husbandry area in Finland during 1976-86, *Rangifer* 8 (1), 25-34.

NORES, C.; LLANEZA, L.; ÁLVAREZ, M. Á. (2008): Wild boar *Sus scrofa* mortality by hunting and wolf *Canis lupus* predation: an example in northern Spain, *Wildl. Biol.* 14, 44-51.

OLI, M. K.; TAYLOR, I. R.; ROGERS, M. E. (1993): Diet of the snow leopard (Panthera uncia) in the Annapurna Conservation Area, Nepal, *J. Zool., Lond.* 231, 365-370.

PACHER, M. (2011): Fossil and subfossil remains of *Capra ibex*, L. from Salzofenhöhle (upper Austria) and the eastern alpine region, *Fragments from the Ice Age environments. Proceedings in honour of Ivan Turk's jubilee* (B. Toskan, coord.), Opera Instituti Archaeologici Sloveniae 21, 35-50.

PACHER, M.; ERLER, R.; SPÖTL, C. (2018): Funde von Holozänen braunbären und steinböcken in höhlen des Tuxertales (Tirol), *Die Höhle* 69 (1-4), 90-99.

PAILHAUGUE, N. (1995): La faune de la salle Monique, Grotte de la vache (Alliat, Ariège), *Bulletin de la Société Préhistorique de l'Ariège* L, 225-289.

PEÏ, W. C. (1938): Le rôle des animaux et des causes naturelles dans la cassure des os, *Paleontologia sinica* (n.s. D) 7.

PEREZ-RIPOLL, M. (1977): *Los Mamiferos del yacimiento musteriense de Cova Negra (Jativa, Valencia)*, Trabajos Varios. S.I.P. 53, València.

PERNAUD, J.; QUILES, J.; RIVALS, F. (2004): *La faune de la fin du Pléistocène dans la haute vallée de l'Aude: l'exemple de la grotte de Castel 2 a Bessède-de-Sault (Aude, France)*, B.A.R.-i.s. S1271, Oxford, 31-37.

PICKERING, T.R. (2001) : Taphonomy of the Swartkrans hominid postcrania and its bearing on issues of meat-eating and fire management, *Meat-eating and human evolution* (G. B. Stanford, H.T. Bunn, coord.), Oxford, 33-51.

PILLARD, B. (1972): La faune des grands mammifères du Würmien II de la grotte de l'Hortus (Valflaunès, Hérault), *Etudes Quaternaires mémoire* 1, 163-205.

POULLE, M. L.; CARLES, L.; LEQUETTE, B. (1997): Significance of ungulates in the diet of recently settled wolves in the Mercantour mountains (southeastern France), *Revue d'Ecologie* 52, 357-368.

PRUCCA, A. (2003): *Caractérisation de l'impact des loups sur des ossements d'herbivores (cerfs de Virginie, orignaux, bisons): étude des modifications infligées par les loups captifs et sauvages nord-américains*, DEA Université Aix-Marseille.

REYNAUD-SAVIOZ, N.; BLANT, M.; WENGER, R. (2018): Découvertes paléontologiques au gouffre de Giétroz Devant dans le vallon de Susanfe (commune d'Evionnaz, Valais), *Bull. Murithienne* 136, 21-30.

RIVALS, F. (2002): *Les petits bovidés (Caprini et Rupicaprini) pléistocènes dans le bassin méditerranéen et le Caucase. Étude paléontologique, biostratigraphique, archéozoologique et paléoécologique*, phD Perpignan.

RIVALS, F.; TESTU A. (2006): Un nouveau gisement paléontologique à *Capra caucasica praepyrenaica*: la grotte de l'Arche à Bugarach (Aude, France), *Comptes Rendus Palevol* 5 (5), 711-719.

RIVALS, F.; TESTU, A.; MOIGNE, A. M.; LUMLEY DE, H. (2006): The Middle Pleistocene argali (Ovis ammon antiqua) assemblages at the Caune de l'Arago (Tautavel, Pyrénées-Orientales, France): were prehistoric hunters or carnivores responsible for their accumulation?, *International Journal of Osteoarchaeology* 16, 249-268.

ROMINGER, E.M. (2017): The Gordian Knot of mountain lion predation and bighorn sheep, *The Journal of Wildlife Management* 82(1), 19-31.
DOI: https://doi.org/10.1002/jwmg.21396

ROUZAUD, F.; SOULIE, M.; BRUGAL, J.P.; JAUBERT, J. (1990): L'Igue des Rameaux (St-Antonin-Noble-Val, Tarn et Garonne). Un nouveau gisement du Pléistocène moyen. Premiers résultats, *Paléo* 2, 89-106.

SALA BURGOS, N. (2012): *Tafonomia de yacimientos karsticos de carnivoros en el Pleistoceno*, phD Universidad Madrid.

SANCHIS, A.; REAL, C.; SAUQUÉ, V.; NÚÑEZ-LAHUERTA, C.; ÉGÜEZ, N.; TORMO, C.; PEREZ RIPOLL, M.; CARRIÓN MARCO, Y.; DUARTE, E.; DE LA RASILLA, M. (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.

SANZ, M.; DAURA, J.; ALVAREZ, N.; BRUGAL, J. P. (2016): Not only hyenids: a multi-scale analysis of Upper Pleistocene carnivore coprolites in Cova del Coll Verdaguer (NE Iberian Peninsula), *Palaeogeography, Palaeoclimatology, Palaeoecology* 443, 249-262.

SANZ, M.; DAURA, J. (2018): Taphonomic analysis of an ungulate-dominated accumulation at the Pleistocene Cova del Rinoceront site near Barcelona, Spain (northeastern Iberian Peninsula), *Palaeogeography, Palaeoclimatology, Palaeoecology* 498, 24-38.

SATTLER, R. A. (1997): Large mammals in Lower Rampart cave 1, Alaska: interspecific utilization of an eastern Beringian cave, *Geoarchaeolgy* 12(6), 657-688.

SAUQUÉ, V. (2014): *Tafonomía, sistemática y aproximación paleoambiental de los macromamíferos del Pleistoceno Superior del Moncayo (Zaragoza)*, phD Zaragoza.

SAUQUÉ, V.; RABAL-GARCES, R.; SOLA-ALMAGRO, C.; CUENCA-BESCOS, G. (2014): Bone accumulation by leopards in the Late Pleistocene in the Moncayo massif (Zaragoza, NE Spain), *PLoS ONE* 9 (3), e92144.

SAUQUÉ, V.; RABAL GARCES, R.; GARCIA-GONZALEZ, R.; GISBERT, M. (2015): Bucardos y osos fósiles del Pirineo: recuperación de restos paleontológicos, catalogación y datación de los yacimientos del Pleistoceno-Holoceno de las cavidades del Pirineo oscense, *Lucas Mallada* 17, 247-289.

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.

SAUQUÉ, V.; SANCHIS, A.; MADURELL-MALAPEIRA, J. (2017): Late Pleistocene leopards as a bone accumulator: taphonomic results from S'Espasa cave and other Iberian key sites, *Historical Biology* 30 (6), 821-834.

SAUQUÉ, V.; GARCÍA-GONZÁLEZ, R.; RABAL-GARCES, R.; GALAN, J.; NÚÑEZ-LAHUERTA, C.; GISBERT, M.; CUENCA-BESCOS, G. (2018): Los Batanes: a trap for the pyrenean wild goat during the Late Pleistocene (Spain), *Quaternary International* 481, 75-90.

SHEHZAD, W.; MCCARTHY, T. M.; POMPANON, F.; PUREVJAV, L.; COISSAC, E.; RIAZ, T.; TABERLET, P. (2012): Prey preference of snow leopard (*Panthera uncia*) in South Gobi, Mongolia, *PLoS ONE* 7 (2), e32104.

SHRESTHA, B. (2008): *Prey abundance and prey selection by snow leopard (*Uncia uncia*) in the Sagarmatha (Mt. Everest) national park, Nepal*, S.L.C. Report for International Snow Leopard Trust, Snow Leopard Network.

SIN, T.; GAZZOLA, A.; CHIRIAC, S.; RISNOVEANU, G. (2019): Wolf diet and prey selection in the southeastern Carpathian mountains, Romania, *PLoS ONE* 14 (11), e0225424.

STÅHLBERG, S. M BASSI, E.; VIVIANI, V.; APOLLONIO, M. (2017): Quantifying prey selection of northern and southern european wolves (*Canis lupus*), *Mammalian Biology* 83, 34-43.

STINER, M. C. (2004): Comparative ecology and taphonomy of spotted hyenas, humans, and wolves in Pleistocene Italy, *Revue de Paléobiologie* 23 (2), 771-785.

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 (4), 896-907.

TAGLIACOZZO, A.; ZEPPIERI, F.; FIORE, I., SPINAPOLICE, E.; DEL LUCCHESE, A. (2012): Archaeozoological evidence of subsistence strategies during the Gravettian at Riparo Mochi (Balzi Rossi, Ventimiglia, Imperia - Italy), *Quaternary International* 252, 142-154.

TOSKAN, B. (2007): 11. Remains of large mammals from Divje babe I - Stratigraphy, taxonomy and biometry, *Divje Babe I. Upper Pleistocene Palaeolithic site in Slovenia* (I. Turk, coord.), Opera Instituti Archaeologici Sloveniae 13, 221-278.

TRÜSSEL, M. (2018): Jahrtausende alte steinbock-skelette entdeckt, *Licht und Schatten entlebucher brattig*, 74-78.

UTGE, J.; SÉVÊQUE, N.; LARTIGOT-CAMPIN, A. S.; TESTU, A.; MOIGNE, A. M.; VEZIAN, R.; MAKSUD, F.; BEGOUËN, R.; VERNA, C.; SORIANO, S.; ELALOUF, J. M. (2020): A mobile laboratory for ancient DNA analysis, *PLoS ONE* 15(3), e0230496.
DOI: https://doi.org/10.1371/journal.pone.0230496.

VILLA, P.; SANCHEZ GOÑI, M. F.; BESCOS, G. C.; GRÜN, R.; AJAS, A.; GARCIA PIMIENTA, J. C.; LEES, W. (2010): The archaeology and paleoenvironment of an Upper Pleistocene hyena den: an integrated approach, *Journal of Archaeological Science* 37 (5): 919-935.

VILLALUENGA MARTÍNEZ, A. (2011): Sima de Illobi (Aralar, Navarra), yacimiento de oso pardo (*U. arctos* Linnaeus, 1758): estudio taxonómico y tafonómico, *Munibe Antropologia-Arkeologia* 62, 145-174.

WEGGE, P.; SHRESTHA, R.; FLAGSTAD, O. (2012): Snow leopard *Panthera uncia* predation on livestock and wild prey in a mountain valley in northern Nepal: implications for conservation management, *Wildlife Biology* 18, 131-141.

WEINSTOCK, J. (1999): The Upper Pleistocene mammalian fauna from the Grosse Grotte near Blaubeuren (southwestern Germany), *Stuttgarter Beiträge zur Naturkunde. Serie B (Geologie und Paläontologie)* 277, 1-49.

WEISKOPF, S. R.; KACHEL, S. M.; MCCARTHY, K. P. (2016): What are snow leopards really eating? Identifying bias in food-habit studies, *Wildlife Society Bulletin* 1-8.
DOI: https://doi.org/10.1002/wsb.640

YRAVEDRA, J. (2006): Acumulaciones biológicas en yacimientos arqueológicos: Amalda VII y Esquilleu III-IV, *Trabajos de Prehistoria* 63 (2), 55-78.

YRAVEDRA, J. (2010): Tafonomía en la Cueva de Amalda: La intervención de carnívoros, *Zona Arqueológica* 13, 174-184.

YRAVEDRA, J.; FOSSE, P.; ANDRES, M.; BESSON, J. P. (2014): Taphonomic analysis of small ungulates modified by fox (*Vulpes vulpes*) in Southwestern Europe, *Journal of Taphonomy* 12, 37-67.

ZAPFE, H. (1966): Lebensspuren, *Die Teufels- oder Fuchsenlucken bei Eggenburg (N.O.)* (K. Ehrenberg, coord.), Österreische Akademie der Wissenschaften Mathematisch-naturwissenschaftliche Klasse, Denkschriften 112, 109-122.

ZLATANOVA, D.; AHMED, A.; VALASSEVA, A.; GENOV, P. (2014): Adaptive diet strategy of the wolf (*Canis lupus* L.) in Europe: a review, *Acta zool. bulg.* 66 (4), 439-452.