



HAL
open science

Bone modification by modern wolf (*Canis lupus*): a taphonomic study from their natural feeding places

Philippe Fosse, Nuria Selva, Adam Wajrak, Jean-Baptiste Fourvel, Stéphane Madelaine, Montserrat Esteban-Nadal, José Yravedra, Jean-Philip Brugal, Audrey Prucca, Gary Haynes

► To cite this version:

Philippe Fosse, Nuria Selva, Adam Wajrak, Jean-Baptiste Fourvel, Stéphane Madelaine, et al.. Bone modification by modern wolf (*Canis lupus*): a taphonomic study from their natural feeding places. *Journal of Taphonomy*, 2012, 10 (3-4), pp.197-217. hal-01842851

HAL Id: hal-01842851

<https://hal.science/hal-01842851>

Submitted on 24 Nov 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Bone Modification by Modern Wolf (*Canis lupus*): A Taphonomic Study From their Natural Feeding Places

Philippe Fosse*

*Université de Toulouse le Mirail, UMR 5608 (TRACES)
5 allées Antonio-Machado, 31058 Toulouse cedex, France*

Nuria Selva, Wojciech Smietana, Henryk Okarma
Institute of Nature Conservation, Mickiewicza 33, 31-120 Cracow, Poland

Adam Wajrak

Gazeta Wyborcza, ul. Czerska 8/10, 00-732 Warsaw, Poland

Jean Baptiste Fourvel

*Université de Toulouse le Mirail, UMR 5608 (TRACES)
5 allées Antonio-Machado, 31058 Toulouse cedex, France*

Stéphane Madelaine

*Musée National de Préhistoire, 24620 Les Eyzies de Tayac, France
PACEA UMR 5199, Université Bordeaux 1, 33405 Talence, France*

Montserrat Esteban-Nadal, Isabel Cáceres

*Institut Català de Paleoeologia Humana i Evolució Social (IPHES), Universitat Rovira i
Virgili (URV), Campus Catalunya, Avinguda de Catalunya 35, 43002 Tarragona, Spain*

José Yravedra

*Universidad Complutense de Madrid, Facultad de Geografía e Historia
c/Profesor Aranguren s/n, Ciudad Universitaria, 28040 Madrid, Spain*

Jean Philip Brugal

Aix Marseille Université, CNRS, UMR 7269 LAMPEA, 13094 Aix-en-Provence, France

Audrey Prucca

Les Loups du Gévaudan, Sainte-Lucie, 48100 Saint-Léger de Peyre

Gary Haynes

Anthropology Department (096), University of Nevada, Reno, Nevada 89557-0096, USA

Journal of Taphonomy 10 (3-4) (2012), 197-217.

Manuscript received 15 March 2012, revised manuscript accepted 15 November 2012.

Large carnivore neotaphonomy is used to provide guidelines for understanding fossil bone assemblages. However, few studies have been carried out on the taphonomic signatures of wolves (*Canis lupus*) in their natural settings. From 2001 to 2007, 56 wolf feeding places were studied in 2 geographic areas of Poland (Bialowieza, Bieszczady). We recorded ecological aspects such as prey selection, time span of carcasses use, scavengers' activity and the identification of prey from ungulate hairs found in scats, and taphonomic considerations, such as the number and type of bone remains, intensity of tooth modification on carcasses and the effect of digestion on skeletal elements observed in scats. Localities studied included kill sites (4 *C. capreolus* and 20 *C. elaphus* in Bialowieza, 29 *C. elaphus* in Bieszczady) and scavenging sites (10 *B. bonasus* carcasses in Bialowieza). In order to characterize taphonomically impact of wolf on medium- and large-size ungulates, the general bone modifications recorded in this study are compared with data from North American and Iberian wolf feeding sites as well as from other large carnivore (*Crocuta*) den contents.

Keywords: TAPHONOMY, WOLF, BONE DESTRUCTIONS, SCATS

Introduction

Although modern wolf (*Canis lupus*) kill-sites from North America have been used to characterize the general taphonomic signature for all large carnivores (skeletal parts, toothmarks...: Binford, 1981; Haynes, 1981), neotaphonomic studies developed for the last thirty years have mainly focused on hyenids. It could be explained by a conjunction of ecological (hyenids are terrestrial mammals whose diet is balanced from meat and bone consumption), paleobiological (fossil hyena dens have been identified from early XIXth century in Europe) or even ideological considerations (reconstruction on subsistence during Plio-Pleistocene times in Africa). However, in Eurasian open air and cave sites, large Canids (and especially *Canis*) are systematically identified among Carnivora taxa and might therefore be considered as potential taphonomic agents in ungulate bone accumulations. Influence of (large) canids in fossil bone assemblage formation/

modification is still difficult to establish, due to lack of comparative modern data from natural contexts.

From direct field observations mainly achieved in Poland (Fosse *et al.*, 2004, 2011), the United States (Haynes, 1981; Prucca, 2003) and Spain (Esteban-Nadal *et al.*, 2010; Yravedra *et al.*, 2011), the present paper attempts to make a survey on 1) taphonomic status of pleistocene wolf, 2) bone damages noticed on modern ungulates carcasses (red deer, bison) and 3) wolf scat contents in Poland. Those taphonomic considerations should provide interesting data in order to identify the fossil wolf as a bone accumulator and to distinguish its bone modification from typical meat/bone eaters (hyenids).

Pleistocene and Holocene sites with wolf remains: a taphonomic survey

From ecological, paleontological and zooarchaeological records, Quaternary sites

yielding wolf remains could be ranked into two main categories (Figure 1), that can be described as follows: sites in which occurrences of wolf are involuntary and sites in which these presence is voluntary. In former sites, wolf has been naturally trapped (complete skeletons) or consumed by Humans (cutmarks) or, much more commonly, by Hyenids (toothmarks); in the latter ones, wolf could be considered as a partial taphonomic agent having contributed to the modification of a bone assemblage. Classification of sites could be deduced either from bone contexts or from ichnological ones (identified footprints on paleofloors; see Figure 2). Scavenging available flesh and bones from carcasses left by Humans and other non anthropogenic Mammals (natural traps yielding reindeer, moose or bison bones, cave bear sites) might be relatively common. The latest case, true ungulate bone accumulations made by wolf, are suspected in a few cases but it remains unclear, mainly because of presence from other Carnivore species. Based on these observations, wolf could appear more as a scavenger than as an important bone accumulator.

Modern wolf: neotaphonomic consideration on denning

Although interesting information on the characteristics of modern wolf dens can be found in works in biology or ecology, no precise record is exploitable in a taphonomic perspective. Even if use of dens by males should be specified, it is however proved that females look for shelters to give birth in (late) spring. The occupation of rock shelters seems rare, majority of studies highlighting use of sandy (or clayed) enlarged dens. These tunnels present a small entrance (40x50 cm on average) for a depth about 3m (Trapp, 2004; Trapp *et al.*, 2008; Kowaleski, 2009). The duration of occupation is correlated with latitude and altitude in which wolf packs live. Of short duration (approximately 44 days on average) in temperate zones (Fuller, 1989; Ciucci & Mech, 1992; Cluff *et al.*, 2002; Alfredeen, 2006), the occupation of a den can spread out over several months, covering spring and summer, in the most northern regions of the northern Hemisphere (Mech & Merrill, 1998). In

	Bialowieza <i>C. elaphus</i>	Bieszczady <i>C. elaphus</i>	<i>T</i>	Bialowieza <i>B. bonasus</i>	TOTAL
humerus (MNE)	16	20	36	9	45
humerus (NISP)	16	29	45	9	54
radio-ulna (MNE=NISP)	3	18	21	11	32
radius (MNE=NISP)	10	8	18		18
metacarpal (MNE=NISP)	11	24	35	8	43
femur (MNE)	13	15	28	9	37
femur (NISP)	13	19	32	9	41
tibia (MNE)	14	33	47	8	55
tibia (NISP)	14	36	50	8	58
metatarsal (MNE=NISP)	19	26	45	7	52
TOTAL (MNE)	86	144	230	52	282
TOTAL (NISP)	86	160	246	52	298

Table 1. Number of bones identified on wolf kill-sites in Poland. MNE = minimum number of elements; NISP = number of identified skeletal parts.

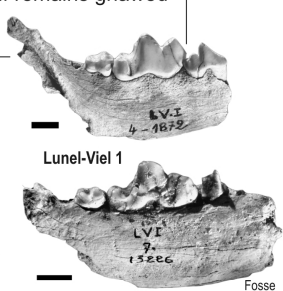
A - involuntary occurrences			
1	2	3	
natural traps	anthropic sites	hyena dens	
trapped	prey	prey	
wolf skeletons (with seldom other large Carnivores trapped)	wolf remains with anthropogenic marks (cutmarks, burnt bones)	wolf remains gnawed	
1- Gargas-Oublottes (Gaudry & Boule, 1892), La Berbie (Madelaine, unpublished), La Bouhadère (Clot, 1970) ...	2- Divje Babe I (Toskan, 2007), Fumane (Romandini, 2011), Krems-Wachberg (Fladerer, 2003), Riparo Tagliente (Alhaique <i>et al.</i> , 2004) ...	3- open air sites : Châtillon St Jean (Chauviré, 1962), caves : Bockstein, H (Webb, 1988), Fontéchévade, E (Paletta, 2005), Fouvent (Fourvel, unpublished), Furninha (Brugal, 2010), Gabasa (Blasco-Sancho, 1997), Gerde (Clot, 1987), La Roche aux Chats (Joffroy <i>et al.</i> , 1959), Lunel-Viel (Fosse, 1994), Pin Hole (Turner, 1981), Teufelslucke (Zapfe, 1966), Tornewton (Turner, 1981), Villa Seckendorf (Ziegler, 1996), Wezmeh (Mashkour <i>et al.</i> , 2009) ...	
B - voluntary occurrences			
4	5	6	7
natural traps (mass death sites, isolated skeletons) from open air or karstic sites	anthropic sites	Ursidae dens	wolf lairs
scavenger	scavenger	scavenger	predator
Ungulate remains with wolf tooth marks	Ungulate bones from anthropogenic levels with wolf tooth marks	<i>U. spelaeus/U. arctos</i> bones with (suspected) wolf tooth marks	accumulation of ungulate remains, wolf scats, wolf remains ...
4- open air (mass death) sites : Berelekh (Baryshnikov <i>et al.</i> , 2009), Bottrop (von Koenigswald <i>et al.</i> , 1995), Mokhovo (Foronova, 1999), Tourville, D (Descombes, 1980), open air (isolated skeletons) : Blue Babe (Guthrie, 1992), Miesenheim 4 (Baales & Street, 1996), Saltville (Mc Donald & Bartlett, 1983), cave (mass death) sites : Igue du Gral (Castel <i>et al.</i> , 2010) ... Jaurens (Ballésio, 1979), Joint Mitnor (Sutcliffe, 1960), Le Quéroy-Gare (Suire, 1969), Les Rameaux (Coumont, 2006), Moses Colee (Darwent & Lyman, 2002), Villereversure (Martin, 1968), cave (isolated skeletons) : Eichlöchl (Blant, 2004), Gamssulzen, 2 (Kühtreiber & Kunst, 1995), Réseau des Lagopèdes (Morel, 1984) ...	5- open air sites : Predmost (Soergel, 1922), Boxgrove (Parfitt, 1999 ; Smith, 2010) ; caves : Lazaret- entrée-locus VIII-Centre (Valensi, 1994), Trou Al'Wesse (Miller <i>et al.</i> , 2007), Vergisson II (Chaput, 2001), with presence of C. crocuta : Bourgeois Delaunay (Suire, <i>op. cit.</i>), Furninha (Brugal, 2010), Gabasa (Blasco-Sancho, 1995), Gombe Grenal (Suire, 1969 ; Chase, 1990 ; Madelaine & Fosse, unpublished), Le Portel, F2 (Gardeisen, 1994), Pair non Pair-F' (Suire, <i>op. cit.</i>), Pech de l'Aze, (Suire, <i>op. cit.</i>), Suard (Suire, <i>op. cit.</i>) ...	6- U. spelaeus sites : Brillenhöhle (Boesneck & von den Driesch, 1973), Cotencher (Stehlin, 1933), Dachstein, Salzofen, Schottloch, Tropfstein (Pacher & Döppes, 1997), Deszczowa (Cyrek <i>et al.</i> , 2000), Divje Babe 1 (Toskan, 2007), Gamssulzen (Kühtreiber & Kunst, <i>op. cit.</i>), Grosse Grotte (Weinstock, 1999), La Balme à Collomb (Ballésio & Philippe, 1995), Jama pod Herkovimi (Pohar, 1981), Lezebikiri (Altuna, 1972), Malarnaud (Suire, <i>op. cit.</i> ; Dufour, 1989), Mixnitz (Abel & Kyrle, 1931), Mladec (Pacher, 2008), Sloup, Stadel-VII (Gamble, 1979), Potocka zijalka (Döppes, 2004), Treugol'naya, 5 (Hoffecker <i>et al.</i> , 2003), Velika pecina, Veternija, Vindija (Miracle <i>et al.</i> , 2010), Vertesszöllös 2 (Kretzoi, 1989), Victoria (Lord <i>et al.</i> , 2007) ; U. arctos sites : Lower Rampart I (Sattler, 1997), Victoria cave (Lord <i>et al.</i> , 2007) ...	7- footprints : Grézalo (Méroc, 1956), Chauvet Pont d'Arc (Garcia, 2005 ; this study), bonny contexts : Maldidier, 3, 6c (Suire, 1969 ; Castel, 1991), Sant Agostino, S.X (Stiner, 1991, 2004), Schusterlucke (Galk, 1997), Vaufrey VIII (Cuon, Binford, 1988), Zafarraya (Cuon & P. pardus, Baroso Ruiz <i>et al.</i> , 2003).

Figure 1. Taphonomic status of Pleistocene wolf (*Canis lupus*). Bold=wolf known as a taphonomic agent; normal=probable role of wolf on a bone assemblage.

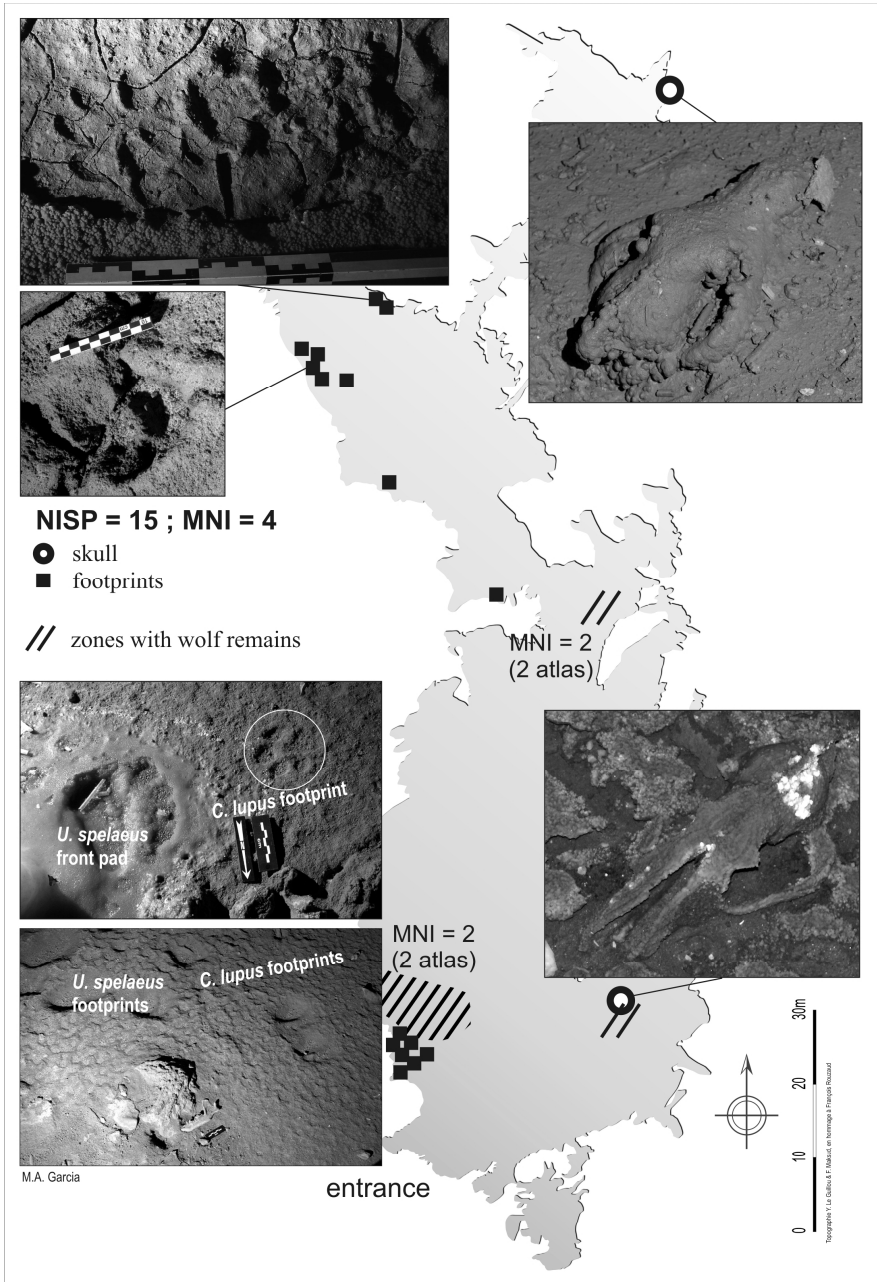


Figure 2. Chauvet Pont s'Arc cave (France): a survey from wolf paleontology and ichnology (field observations with M. Philippe and † M.A. Garcia).

Poland (Bialowieza), dens are occupied between 13 and 74 days, between the middle of May and the end of July (Theuerkauf *et al.*, 2003). Females can re-use the same den over several years, at least 6 years (Czerwertynski, 1997). Inside dens, there seems to be no bone (Peterson, 1977; Kowaleski, *ibid*; Prucca, 2011), feeding of cubs is provided by milky origin or regurgitation of meaty pieces. In rare cases, and following the example of the spotted hyena (*Crocuta*), some bones were found near the entrance. To date, neither accumulation nor concentration of bones has been described. Characterization of bone destruction presented below deals with wolf kill-sites and scat contents, found near Ungulate carcasses or randomly.

Samples from modern wolf: material and methods

As all social carnivores, wolves developed specific foraging behavior (predation and scavenging) allowing them to consume an important spectrum of vertebrates. In Poland (respectively Bialowieza in the northeast and Bieszczady in the southeast), red deer (*Cervus elaphus*) is the main prey (Okarma, 1995; Jedrzejewski *et al.*, 2000, 2001; Smietana & Klimek, 1993; Smietana, 2005); in Bialowieza, the European bison (*Bison bonasus*) is an important additional resource (scavenging of adults' carcasses: Selva, 2004). In North America, a similar spectrum of predation is observed; the white-tailed deer (*O. virginianus*) and the bison (*B. bison*) are the main preys of wolves in Wood Buffalo NP, Isle Royale NP and Forest Lake NP (Haynes, 1981, 1982). The studies undertaken in the two Polish regions allowed to establish important reference collections for the taphonomic characterization of wolf.

In order to obtain information on the rate of bone damage, carcasses were either removed after a few hours of exposure or left exposed during two or three weeks (in winter); this differential time span of food availability for carnivores constitutes the main condition in the skeletal representation and bone scattering (especially appendicular elements). The whole Polish sample (Bialowieza and Bieszczady) concerns 55 deers and 10 bisons (Fosse *et al.*, 2004, 2011), the North American sample 10 white-tailed deer and 9 bisons (Haynes, 1981; Prucca, 2003). In Bieszczady, 1200 scats, prepared (without sieving) for specific identification of preys (W. Smietana), were also analyzed in a taphonomic perspective. Data resulting from these two collections were compared between them, then with a sample recently achieved in Spain (Yravedra *et al.*, 2011). Also, scat contents from Bieszczady were compared with a coproscopic analysis (sieved) of wolf scats in Spain (Esteban-Nadal *et al.*, 2010) and then compared with cervid and large bovid bones, most probably regurgitated by fossil spotted hyena (*Crocuta crocuta spelaea*). Principal aim of this research is to identify the taphonomic signature of fossil wolf in European karstic deposits.

Results

Osteological composition of wolf kill-sites (or scavenging sites) is closely linked to several biological parameters concerning predators (number of wolves consuming, time span of carcass consumption), prey (age, weight, sanitary state) and climatic context (temperature, number of days with snow cover, high summer temperatures, activities of arthropods and other invertebrate scavengers). Carcasses located and then removed quickly

for trace analysis are quite logically less damaged by wolves than those exposed to other taphonomic processes more than a week. In the first case, carcasses often present a low number of anatomical units (*sensu* Haynes, 1981), confined in a few square meters area; appendicular segments are still articulated with axial skeleton and long bones are globally intact (only meat was consumed). In the second case, hierarchical and repeated consumption by wolves pulls an important dislocation of a carcass and a bone scattering up to 500 meters from the kill-site; in that case, carcasses consist mainly in axial skeleton (head, vertebrae, innominates, ribs). Nevertheless, a certain variability of skeletal distribution can be observed, related to biological and taphonomic factors mentioned above; there is consequently no typical pattern (*sensu* Binford) of abandoned elements by wolves (or by other large carnivores).

The bison

Although two skeletons of young bisons (< 6 months old each) were collected and yielded numerous wolf toothmarks, the sample presented here concerns only adult individuals (n=10). In Bialowieza, consumption of adult bison is quite common during winter (Selva, 2004). The climatic context (number of freezing days, frozen intensity, time and thickness of snow cover, decay... (*cf.* Guthrie, 1992) and see Figure 3A) and also cause of animal death (natural *vs* predation) induce variations in meat/bone exploitation by wolves.

Some carcasses were visited for several consecutive weeks. Bison bodymass (more than 400 kg for adult females and 600 kg for males respectively, Krasinska & Krasinski, 2002) does provide an important

food supply (meat). The consumption begins with opening of belly until the rib cage and then continues by shredding of skin and some meat of rear legs. This consumption sequence, unvarying in its general stages (*i.e.* Blumenschine, 1986), affects only few bones. On fresh carcasses, destructions concern mainly distal extremities of ribs (chewings, pittings, punctures) and vertebral spines (punctures essentially). Damage on long bones appears limited, both in term of toothmark diversity and intensity (Table 2, Figure 3B): only one humerus and a femora (belonging to the same carcass) present typical *scooping out* of cancellous bone (*sensu* Sutcliffe, 1970) on their proximal end (Figure 3C). Cortical parts of these bones present some scores on their metaphysis and shaft. The most intense destructions (isolated punctures) concern essentially thin parts of postcranial elements (cranial part of scapulae, extremities of innominates (ilium); Figure 3C). Globally, bones remain intact on the ground and are exposed to weathering over several years. A carcass, exposed over at least 6,5 years (during 1980 days, see Fosse *et al.*, 2004:fig. 3), presents, compared with Behrensmeyer (1978)'s model, an important chronological gap of deterioration (effect of the substratum? forest context?); indeed, although annual climatic variations are very important in Poland, modification of osseous surfaces seem "delayed" in comparison with the African model, bones remaining well preserved better and longer (Figure 3D).

The red deer

In spite of cyclic fluctuations (Kamler *et al.*, 2007), red deer is the main prey of wolves, both in Bialowieza and in Bieszczady. From

Table 2. Frequency and type of damages produced by wolf on bison long bones in Poland.

	<i>Bison bonasus</i>										
	NISP Białowieża	%	% conservation	% survival	T gnawed	% gnawed	% gnawed/bones	T scooping out	T scores	T pits	T punctures
humerus prox											
humerus shaft (fgt)											
humerus dist + shaft	1										
humerus complete	8				1		1	1	1	1	1
T humerus	9		20.0	9.2	4	1.6	8.9	1	1	1	1
radius-ulna complete	11								2		
T radius-ulnae	11								2		
mtcp complete	8										
T metacarpals	8										
femur prox											
femur shaft (fgt)											
femur cylinder											
femur prox + shaft									1		1
femur dist + shaft	1										
femur complete	8							2	2	2	2
T femurs	9	3.7	28.1	9.2	10	4.1	31.3	2	3	2	3
tibia shaft (fgt)											
tibia dist + shaft											
tibia complete	8								2		1
T tibiae	8	3.3	16.0	8.2	3	1.2	6.0		2		1
mtt prox + shaft											
mtt complete	7							1	1	1	1
T metatarsals	7	2.8	15.6		4	1.6	8.9	1	1	1	1
TOTAL	44				21			4	9	4	6

tooth wear stages raised on 14 complete carcasses, it seems that 6 individuals were fawns (based on the eruption phase from lower first molars), 3 individuals were adults (with slightly worn permanent teeth) and 5 were senile males or females (very worn upper and lower molars). Although hunting

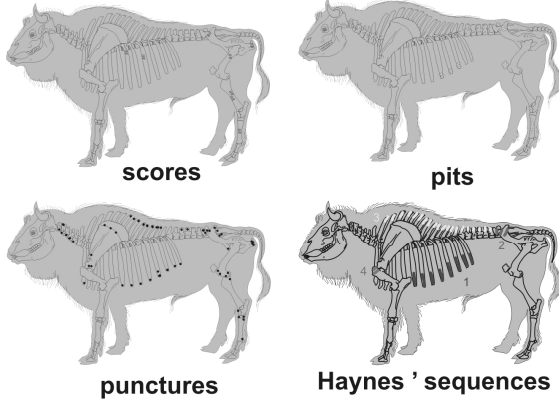
strategy allows wolf packs to hunt deers of any ages, predominance of the most vulnerable individuals (young and old adults) seem to prevail. Other hunted ungulates are respectively the wild boar (*S. scrofa*) and the roe deer (*C. capreolus*). These two species are quite common both on kill-sites and in

A - Bialowieza (Poland) : European bison (*B. bonasus*) carcasses killed/scavenged by wolf (*C. lupus*)

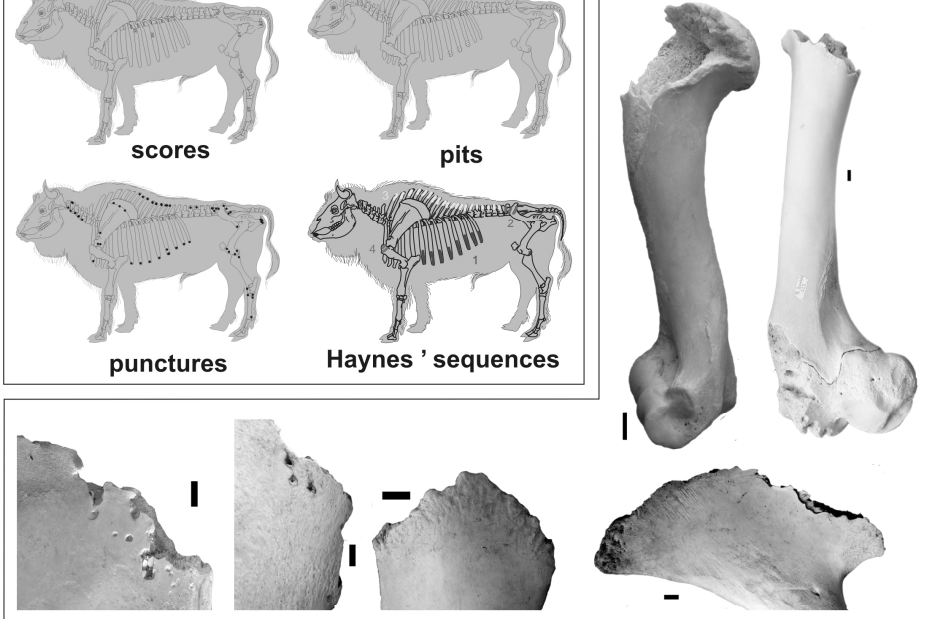


courtesy : N. Selva (IOP-Krakow)

B - Location of wolf toothmarks on European bison carcasses (cumulative data from 10 skeletons)



C - examples of wolf toothmarks on European bison postcranial bones (bar scale = 1cm)



D - weathering stages on bison bones

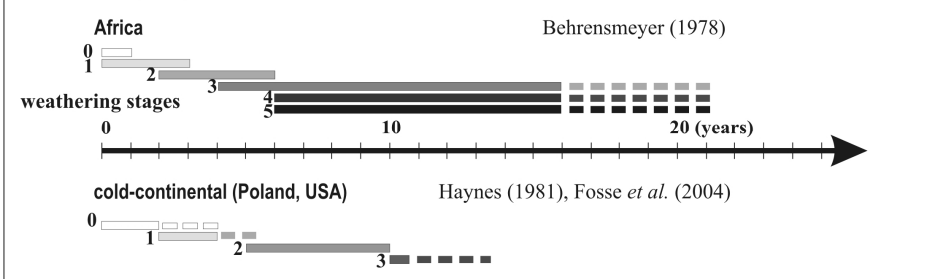


Figure 3. Taphonomic data from bisons scavenged/killed by wolf in Bialowieza (Poland).

scat contents (*cf.* below). Meaty long bones (humerus, femorae) present destructions, mainly localized on their proximal epiphysis (Figure 4C); the lower segments (radius/tibiae-phalanges) are intact. In these kill-sites, anatomical articulations are frequent.

The bone composition on a kill-site also depends on the number of wolves consuming a carcass and the time span of use (Figure 4A). Important variations were found, according to these parameters and according to the seasons (persistence of edible parts related to the temperature). Although destructions observed on deer bones are more important than those found on bison ones, it is necessary to note the importance of sub-complete elements, in particular distal appendicular segments (radius-ulnae, tibiae, *cf.* Figure 3). Heads (skulls, mandibles) and axial elements (vertebrae, girdles) present more damages (in particular punctures) than appendicular bones (mainly destroyed by scores and pits, *cf.* Figure 4B). Skulls are damaged first of all at the level of their nasal parts and then of their occipital condyles or parietal bones (opening of the braincase). Skulls reduced to the state of palatal fragments are rare. Complete mandibles are numerous; partial destructions are found on the base of the horizontal ramus either on condyles or extremity of the ascending one. Vertebrae are systematically toothmarked (punctures on apophyses and spines). Scapulae and innominates, often sub-complete, present deteriorations only at their extremities (separation of the legs from the carcass towards secondary feeding areas). Scapulae are damaged at their cranial extremities, and exceptionally around glenoid cavities; innominates provide all toothmarks (scores, pittings, punctures), concentrated on iliums, ischiums and sciatic parts. No damage was observed near their acetabular cavities.

Digested bones

In Bieszczady, wolf scats were collected and prepared to identify specifically the prey. Analysis of 1200 scats allowed to collect 60 samples (i.e. 5 %) containing determinable bone fragments, belonging to the red deer then to the wild boar and roe deer. A total of 292 bones was identified, anatomically and specifically (Figure 5). The red deer is the most common species (n=136) and it is represented only by unfused bones, while species of smaller size (wild boar, n=100 and roe deer, n=56) are identified from bones belonging to adult and non adult individuals. The skeletal distribution is similar for each species: isolated vertebral disks (belonging to young individuals), carpals, tarsals, sesamoids and (unfused) phalanxes dominate clearly samples. First phalanxes are abundant and reduced to their half distal part for the red deer or the wild boar, whereas this small bone appears usually complete for the roe deer. Third phalanxes are reduced to their proximal part for the red deer and are complete for other species. The chemical deteriorations are difficult to recognize, these parts being protected by hooves. Portions of long bones (femoral head of roe deer, distal fragments of the unfused tibiae of wild boar) are rare. Modifications of bone surfaces consist of lustring of the articular surfaces or partial dissolution of compact bones (scaphoids, talus). These modifications are slight to moderate. Identification as ingested parts is in many cases only based on the fact of having been found in scats.

Discussion

Analysis of ungulates consumed by wolves in Poland allows to complete field data observed in North America (Binford, 1981; Haynes, 1981;

Magoun & Valkenburg, 2001; Prucca, 2003) dealing with skeletal parts, sequences of bone reduction or consumption data (location of toothmarks, typology, intensity). Binford's model (1981:229, fig. 5.18) presented, from a combination of wolf kill-sites from Alaska and kill-sites of African large carnivores, an over-representation of axial elements (skulls, vertebrae, girdles) in acquisition or hunting sites, whereas appendicular bones are transported to the den (or consumed *in situ*?). This over-simple dichotomy cannot be retained because many modern and fossil case studies present intermediate skeletal distributions whereas their function (denning sites) is clearly attested. Structuring of wolf kill-sites, based on 21 sites in Alaska (data deduced from Binford, 1981:211-213, table 5.01), is globally found in Poland (Figure 6), even if the degree of carcass consumption seems lesser; "soft" elements (humerus prox.) or easily edible parts (extremities of innominates and ribs, articular bones, phalanxes) are less represented than robust bones, usually abandoned.

The North American kill-sites (Binford's samples) and Polish one present a relatively similar cranial/postcranial ratio, deer carcasses being often sub-complete with at least 2 or 3 remaining legs (Haynes, 1981; Fosse *et al.*, 2004). On the other hand, the wolf "model" seems distinct from what was observed in hyena dens (Fosse *et al.*, 2011; Fourvel, 2012) where small ungulates (Caprinae, Antilopinae) are represented by numerous cranial elements and a balance between axial and appendicular elements. Identification of the site function seems difficult based only on skeletal distribution analysis (for a sized-identified species). For larger species (horse in Spain: Yravedra *et al.*, 2011; bison in North America and Poland; Haynes, 1981; Fosse *et al.*, 2004), appendicular skeleton is systematically well represented. Fracturation of bone remains

observed on red deer carcasses in Poland also provides interesting remarks; many long bones are complete and/or slightly damaged. This observation, which prevails as well for rich meaty bones (humerus and especially femur) as for the poorer ones (radius, tibia, metapodials), is also found in some wolf kill-sites (n=22) from northern latitudes (Magoun & Valkenburg, 2001) and seems different from observations made in Forest Lake NP (Haynes, 1981; Prucca, 2003). Inter-predator competition for food access could explain this different pattern of bone destruction. Indeed, for these samples, it was noticed that complete long bones were rare. While low fracturation of long bones seems to be the rule for wolf sites in European natural context, a much stronger destruction was recorded in other samples. In Poland, the absence of long bones consumption could be explained by regular predation of red deers (every wolf pack consumes on average of 0.78 ungulate a day, or a whole animal every 1.32 days, Jedrzejewska & Jedrzejewski, 1998:206), a carcass became unprofitable being therefore quickly left. In North America (Haynes' samples), stronger seasonal constraints as well as a less high biomass could lead to a much more intense consumption of long bones. The influence of prey availability on bone consumption rate was already observed in other predators, such as the spotted hyena (Fourvel & Mwebi, 2011). In Republic of Djibouti, it was noticed that hyenas reduced only few long bones of goat (82 % of these elements are (sub-) complete and 6% are cylinders), mainly because of an important prey availability (abundant domestic livestock and numerous carcasses). On the contrary, in Kenya, hyenas, evolving in natural settings, consume more strongly bones; cylinders were there abundant (23% of total long bones

	<i>Cervus elaphus</i>												
	NISP Bialowieza	NISP Bieszczady	NISP total	%	% conservation	% survival	T gnawed	% gnawed	% gnawed/bones	T scooping out	T scores	T pits	T punctures
humerus prox		3	3	1.2	6.7	3.1	3	1.2	6.7		1	1	1
humerus shaft (fgt)		3	3	1.2	6.7	3.1							
humerus dist + shaft	8	12	20	8.1	44.4	20.4	8	3.3	17.8		1	5	2
humerus complete	8	11	19	7.7	42.2	19.4							
T humerus	16	29	45	18.3	100.0	45.9	11	4.5	24.4		2	6	3
radius-ulna complete	3	18	21	8.5	100.0	21.4	6	2.4	28.6		1	4	1
T radius-ulnae	3	18	21	8.54	100.0	21	6	2.4	29		1	4	1
radius prox	1		1	0.4	5.6	1.0	1	0.4	5.6			1	
radius prox + shaft	1	1	2	0.8	11.1	2.0	1	0.4	5.6			1	
radius dist + shaft	2		2	0.8	11.1	2.0							
radius complete	6	7	13	5.3	72.2	13.3	3	1.2	16.7		2		1
T radius	10	8	18	7.3	100.0	18.4	5	2.0	27.8		2	2	1
mtcp complete	11	24	35	14.2	100.0	35.7	4	1.6	11.4		3	1	
T metacarpals	11	24	35	14.2	100.0	36	4	1.6	11		3	1	
femur prox		1	1	0.4	3.0	1.0							
femur shaft (fgt)		2	2	0.8	6.1	2.0							
femur cylinder	2	2	4	1.6	12.1	4.1							
femur prox + shaft		3	3	1.2	9.1	3.1	1	0.4	3.1	1			
femur dist + shaft		5	5	2.0	15.2	5.1	1	0.4	3.1	1			
femur complete	12	5	17	6.9	51.5	17.3	6	2.4	18.8				6
T femurs	14	19	33	13.4	100.0	33.7	8	3.3	25.0	2			6
tibia shaft (fgt)		3	3	1.2	6.0	3.1							
tibia dist + shaft	3	10	13	5.3	26.0	13.3	5	2.0	10.0		1	4	
tibia complete	11	23	34	13.8	68.0	34.7	3	1.2	6.0			1	2
T tibiae	14	36	50	20.3	100.0	51.0	8	3.3	16.0		1	5	2
mtt prox + shaft	3	3	6	2.4	13.3	6.1							
mtt complete	16	23	39	15.9	86.7	39.8	7	2.8	15.6		3		4
T metatarsals	19	26	45	18.3	100.0		7	2.8	15.6		3		4
TOTAL	87	159	246	100			49			2	12	18	17

Table 3. Frequency and type of damages produced by wolf on red deer long bones in Poland.

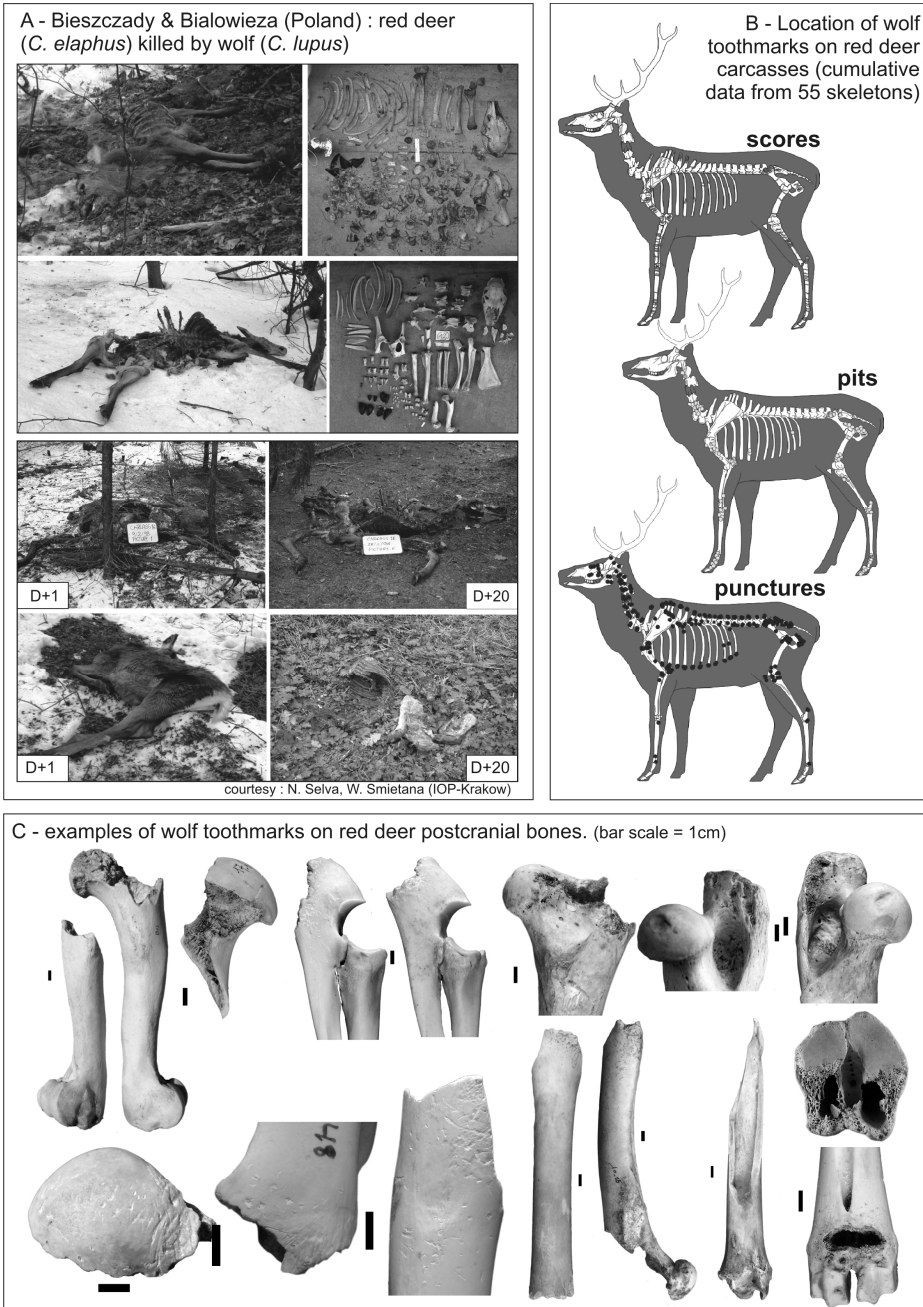


Figure 4. Taphonomic data from red deer killed by wolf in Bialowieza and Bieszczady areas (Poland).

and 19 % belonging to Antelopes) and less than 45 % of bone are (sub-) complete (and 37% belonging to antelopes). In Poland, bone fragmentation (in particular appendicular elements) is low (n of complete bones = 178, 72 % for red deer). Ecological data suggest a ratio of 30 red deers and 5 bisons for 10 km² (from Selva, 2004) or respectively 390 kg and 250 kg of biomass available per square kilometer (considering an average weight of 130 kg for a deer and 500 kg for a bison). This high ratio limits phenomena of food stress and thus the rate of bone reduction.

The comparison of toothmarks resulting from bone consumption by wolves and hyenas allows various comments concerning 1) the tooth mark diversity and localization on

bones, and 2) the consumption mark intensity. Four types were recorded on the Polish bone material: *scooping out*, *scorings/furrowings*, *pittings*, *punctures*. These modifications are relatively uncommon (20% of long bones are gnawed) and principally localized on the extremities. This particular localization could reflect the dislocation of the legs. In hyena dens from Republic of Djibouti, an more important diversification of tooth marks (7 types: *scooping out*, *scorings/furrowings*, *pittings*, *punctures*, *crenulated edges*, *chewing*, *lunate-scars*) was noticed. The tooth mark frequency is also more important on hyenas' kill-sites (from 25 to 30%). These modifications concern each skeletal part (cranial, axial and appendicular skeleton) without any real

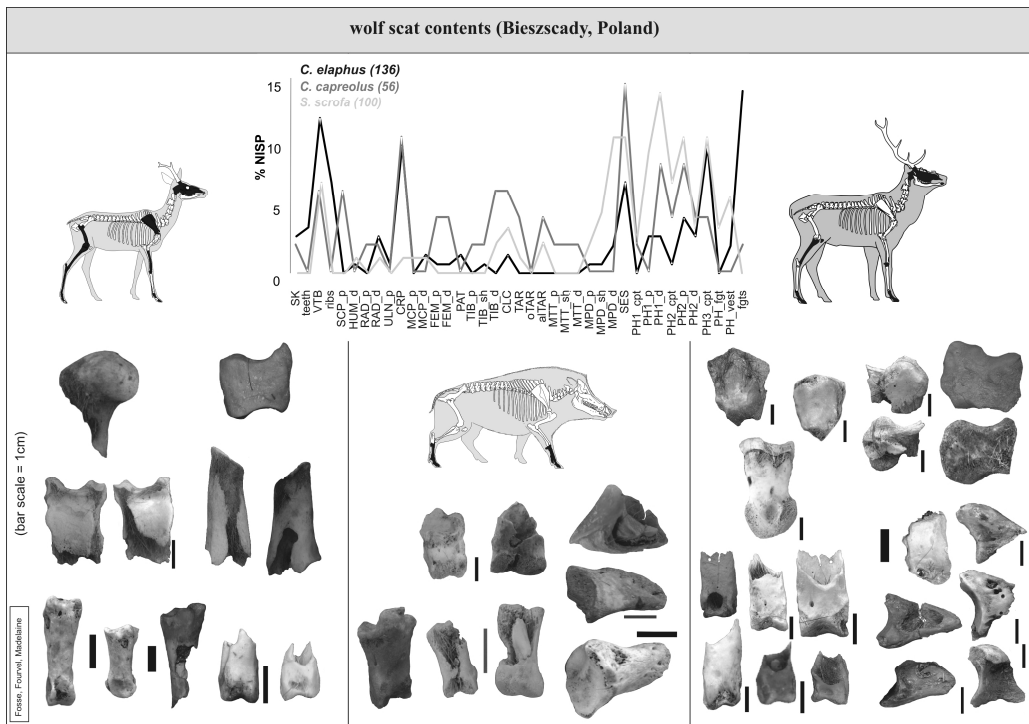


Figure 5. Frequency and morphology of ingested bones by modern wolf from Poland.

distinction (Fourvel, 2012). The specialization of hyena in bone consumption and dentition of canids less adapted to bone crushing could justify these taphonomic differences. The bone consumption by (large) canids provides principally pittings while teeth of hyenas (juvenile?) produce more important and diverse gnawing marks. Nevertheless, this hypothetical distinction must be confirmed with other analysis of various bone samples. The inventory and the analysis of identified bone remains found in scats constitute a new approach in the (neo-) taphonomic studies, for all Carnivores species and especially for the wolf. Indeed, previous works on that point (from extant species) was punctually focused on rare scats contents from both natural and artificial contexts (Klippel *et al.*, 1987 for wolves; Chase, 1990 for coyotes; Kolska Horwitz, 1990 for striped hyenas, dogs and wolves; Martin & Borrero, 1997 or

Stiner *et al.*, 2012 for pumas). These studies were developed in order to establish actualistic models for comparison with palaeontological samples. Recently an exhaustive research on bone remains recovered in scats of extant wild wolves was realized (Esteban-Nadal *et al.*, 2010) but essentially focused on numerous unidentified specimens. The skeletal part distribution observed in scat contents from Bieszczady allows to develop basis of a comparative study of (extant and extinct) large predators' digestion effects on bones. Actually, there is no study focused on cave hyena coprolites contents (only palynological studies were made). Here is presented a first inventory of ingested bones by this predator from two Pleistocene sites (Lunel-Viel and Les Plumettes, respectively dated from Middle and Upper Pleistocene). These bone remains, found within paleontological samples and not directly

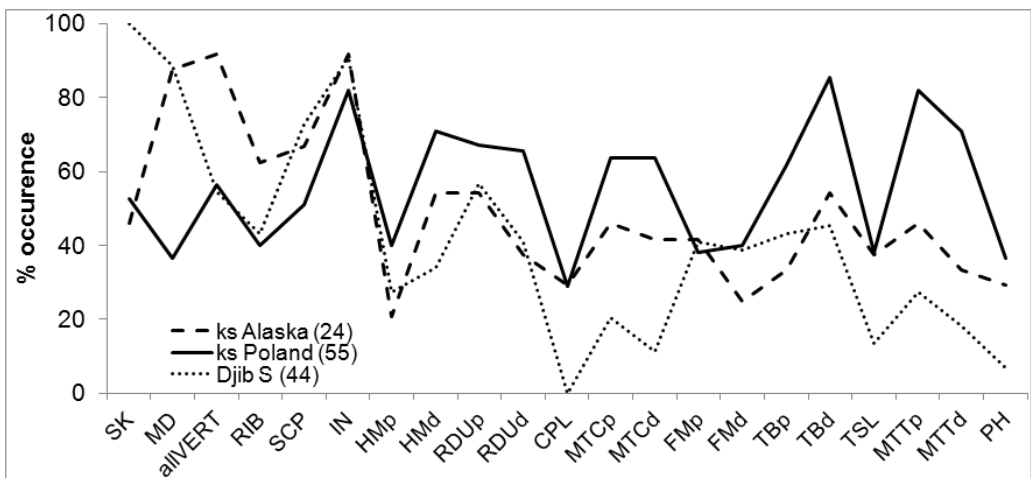


Figure 6. Comparative distribution of Ungulates bones found in Large Carnivore sites (wolf & hyena). SK = skull; MD = mandible; VERT = vertebrae; SCP = scapula; IN = innominate; HM = humerus; RDU = radioulna; CPL = carpals; MTC = metacarpal; FM = femur; TB = tibia; TSL = tarsal; MTT = metatarsal; PH = phalange; p = proximal; d = distal.

from coprolites, suggest that they potentially result from regurgitation. Comparison of the digested elements from these two particular contexts (extant wolves and extinct hyenas; see Figure 7) clearly reveals the differences in inter-specific bone assimilation/ingestion concerning: 1) prey size class and 2) size of ingested bones. Indeed, one bison first phalanx was found in wolf scat (Haynes, pers. obs.; cf. Figure 7) but it is extremely rare and this case is clearly exceptional. In fact, all identified specimens recovered in scats, were attributed small- (adult) and medium-size (juvenile) ungulates. In contrast, ingested bones, coming from fossil spotted hyena dens, belong to medium- (adult cervids) and large-size (adult bovids) ungulates. At this

point, these first observations suggest that only (fossil) hyenas are able to ingest various skeletal remains attributed to medium-size ungulates (cervids: half-complete metapodial, humerus distal ends and principally carpals and tarsals (among which a complete calcaneus) and phalanges). This carnivore could also ingest numerous small bones from large bovids articulations (carpals, tarsals and phalanges) or large carnivores, (half-complete metatarsus IV of *P. spelaea* revealing digestion marks). No other vertebrate groups (neither mammals nor avian) presents such osteophageous capacities. Furthermore, the modifications of bone surfaces resulting of gastric corrosion seem clearly stronger on ingested bones by hyenas than other vertebrate. Even if ingested

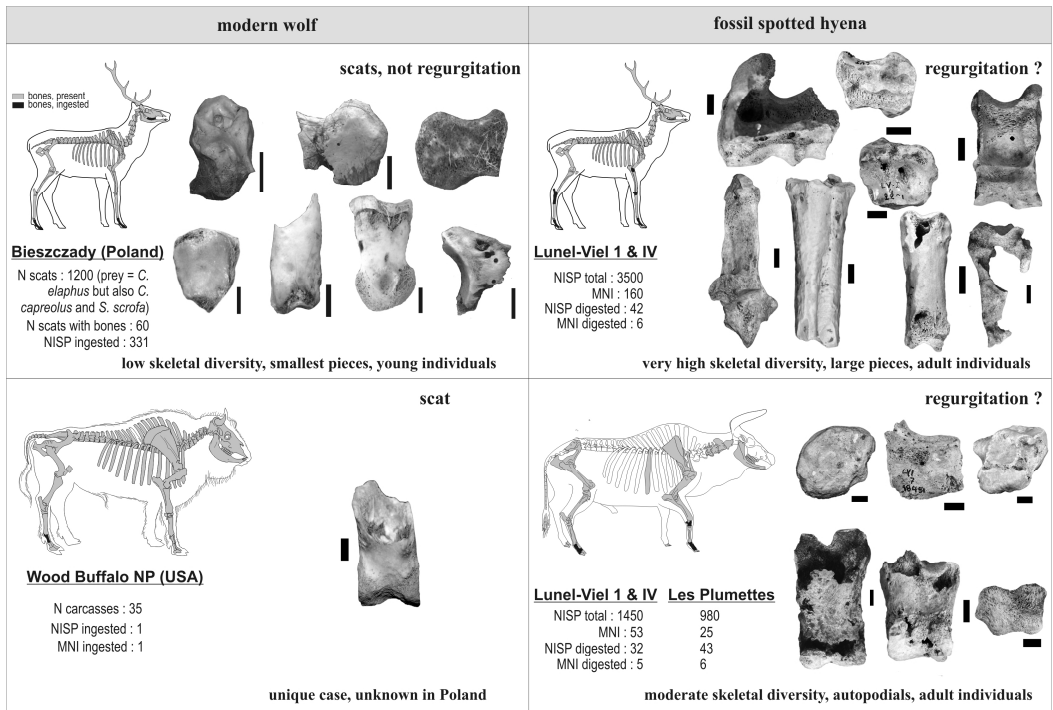


Figura 7. Comparative data on postcranial elements ingested by modern wolf and fossil spotted hyena.

remains represent few bone material from the paleontological samples (less than 1%), these pieces could be considered as the answer of effective identification key to recognize large carnivores groups who have interact with bone accumulations in the Pleistocene deposits.

Conclusions - Perspectives

This work on wolf predation in Poland is a part of global research on taphonomic characterization of large carnivores, both modern and Pleistocene, from Europe and Africa. The analysis of red deer carcasses hunted and consumed by wolves in Bialowieza and Bieszczady highlights complementary data to the previous studies, principally developed in North America. Although toothmarks could be clearly observed, their frequency and intensity on postcranial elements remain low. Bone consumption appears moderate and bone destructions are lower than that was suggested by previous works. The wolf taphonomic signature is difficult to characterize and distinct from other large predators. This first synthesis of published data reveals the great variability in bone samples resulting of activities and consumption by wolves; this particular diversity of taphonomic observations could be the result of behavioral and contextual data (exposition and consumption time span of the carcasses, seasonal availability of prey, degree of inter-carnivores competition, sampling methods...).

Acknowledgments

The authors thank Institutes and people having allowed this study: CNRS (DREI) in

Paris and PAN in Krakow to have financed field researches in Poland (PICS 2571 project). Are very sincerely also thanked Jean Jacques Cleyet-Merle (National Museum of Prehistory, Les Eyzies de Tayac) and Cédric Beauval (Archéosphère) to have facilitated the access to paleontological samples. Very interesting electronic correspondence was made with David Kowaleski (Alfred University, NY) and David Mech (North Central Forest Experiment Station, Minnesota) on modern wolf dens; they are thanked for the relevant information which they delivered us. The authors thank finally very warmly Jordi Rosell and Enrique Baquedano for the organization of this colloquium so innovative and stimulating, their very nice reception to Salou and for their infinite patience.

References

- Abel, O. & Kyrle, G. (1931). *Die Drachenhöhle bei Mixnitz*. Teil 1: Text. Vol. 7-8, Wien.
- Alfredéen, A.C. (2006). Denning behaviour and movement pattern during summer of wolves *Canis lupus* on the Scandinavian Peninsula.
- Alhaique, F., Bisconti, M., Castiglioni, E., Cilli, C., Fasani, L., Giacobini, G., Grifoni, R., Guerreschi, A., Lacopini, A., Malerba, G., Peretto, C., Recchi, A., Rocci Ris, A., Ronchitelli, A., Rottoli, M., Thun Hohenstein, U., Tozzi, C., Visentini, P. & Wilkens, B. (2004). Animal resources and subsistence strategies. *Coll. Antropol.* 28: 23-40.
- Altuna, J. (1972). Fauna de mamíferos de los yacimientos prehistóricos de Guipuzcoa, *Munibe*. 24: 1-464.
- Baales, M. & Street, M. (1996). Hunter-gatherer behavior in a changing late glacial landscape: Allerød late glacial landscape: Allerød Archaeology in the Central Rhineland, Germany. *Journal of Anthropological Research*, 52: 281-316.
- Ballard, W.B. & Dau, J.R. (1983). Characteristics of gray wolf, *Canis lupus*, den and rendezvous sites in southcentral Alaska. *Can. Field-Nat.*, 97: 299-302.
- Ballésio, R. (1979). Le gisement pléistocène supérieur de la grotte de Jaurens à Nespouls, Corrèze, France: les Carnivores (*Mammalia, Carnivora*). 1. *Canidae* et *Hyaenidae*. *Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon*, 17 : 25-55.

- Ballésio, R. & Philippe, M. (1995). Les canidés pléistocènes de La Balme à Collomb (Commune d'Entremont-le-Vieux, Savoie). *Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon*, 33 : 47-68.
- Baroso Ruiz, C. (2003). El Pleistoceno superior de la cueva del Boquete de Zafarraya. *Arqueologia, Monografías*.
- Baryshnikov, G.F., Mol, D. & Tikhonov A.N. (2009). Finding of the Late Pleistocene carnivores in Taimyr Peninsula (Russia, Siberia) with paleoecological context. *Russian Journal of Theriology*, 8: 107-113.
- Behrensmeyer, A.K. (1978). Taphonomic and ecologic information from bone weathering. *Paleobiology*, 4: 150-162.
- Binford, L.R. (1981). *Bones: ancient men and modern myths*. Wiley eds., New York.
- Binford, L.R. (1988). Etude taphonomique des restes fauniques de la Grotte Vaufrey, couche VIII. In (Rigaud, J.P., ed.). *La Grotte Vaufrey, paléoenvironnement, chronologie, activités humaines. Mémoire de la Société Préhistorique Française*, 8: 535-563
- Blant, M. (2004). Die holozäne Fauna der Schratzenfluh. La faune holocène de la Schratzenfluh (Flühli, LU). *Stalactite*, 54: 17-26.
- 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.
- Blumenschine, R.J. (1986). Early hominid scavenging opportunities; implications of carcass availability in the Serengeti and Ngorongoro ecosystems. *B.A.R. i.e.*, 283.
- Boesneck, J. & Driesch von den, A. (1973). Die jungpleistozänen Tierknochenfunde aus der Brillenhöhle. In (Riek, G., ed.) *Das Paläolithikum der Brillenhöhle bei Blaubeuren (Schwäbische Alb)*, Müller & Gräff-Kommissionsverlag, 2: 7-105.
- Brugal, J.P. (2010). Carnivores pléistocènes (Hyénidés, Canidés, Félidés) dans les grottes du Portugal. In (Baquedano, E. & Rosell, J., eds.) *Actas de la 1a reunion de científicos sobre cubiles de hiena (y otros grandes carnívoros) en los yacimientos arqueológicos de la Peninsula Ibérica*. Museo Arqueológico Regional: 92-106.
- Castel, J.C. (1991). *Essai d'étude taphonomique de vestiges osseux paléolithiques; l'exemple de la grotte Maldidier (Dordogne)*. D.E.A. Université de Bordeaux I.
- 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'Igüe du Gral (Sauliac-sur-Célé, Lot, France). *Revue de Paléobiologie*, 29: 411-425.
- Chase, P.G. (1990). Sifflets du Paléolithique moyen (?). Les implications d'un coprolithe de coyote actuel. *Bulletin de la Société préhistorique française*, 87: 165-167.
- Chauviré, C. (1962). *Les gisements fossilifères quaternaires de Châtillon-Saint-Jean (Drôme)*. Thèse 3^{ème} Cycle, Université de Lyon.
- Ciucci, P. & Mech, L.D. (1992). Selection of wolf dens in relation to winter territories in northeastern Minnesota. *Journal of Mammalogy*, 73: 899-905.
- Clot, A. (1987). *La grotte de Gerde (Hautes Pyrénées), site préhistorique et paléontologique*. Société Ramond, Bagnères-de-Bigorre.
- Cluff, H.D., Walton, L.R. & Paquet, P.C. (2002). *Esker habitat studies in the Slave Geological Province: movements and habitat use of wolves denning in the central Arctic, Northwest Territories and Nunavut, Canada*. Final report to the West Kitikmeot/Slave Study Society, Yellowknife, NT Canada.
- Coumont, M.P. (2006). *Taphonomie préhistorique: mammifères fossiles en contexte naturel, les avens-pièges, apport pour l'étude des archéofaunes*. PhD. Université Aix-Marseille I.
- Czertwytynski, S. (1997). *Wolf behavior at the dense and responses to simulated wolf and coyote howls near rendezvous sites*. Canadian thesis, Acadia University.
- Darwent, C.M. & Lyman, R.L. (2002). Detecting the postburial fragmentation of carpals, tarsals and phalanges. In (Haglund, W.D. & Sorg M.H., eds.) *Advances in Forensic Taphonomy: Method, Theory and Archaeological Perspectives*, CRC Press: 355-377.
- Descombes, J.C. (1980). *La première faune rissienne de la basse vallée de la Seine; implications biostratigraphiques et paléocéologiques*. Thèse 3^{ème} Cycle, Université de Poitiers.
- Döppes, D. (2004). Carnivores and Marmots from the Upper Pleistocene sediments of Potocka zijalka (Slovenia). In (Pacher, M., Pohar, V. & Rabeder, G., eds.) *Potocka zijalka - palaeontological and archaeological results of the excavation campaigns 1997-2000*, Mitt. Komm. Quartärforsch. Österr. Akad. Wiss., 67-80
- Dufour, R. (1989). *Les Carnivores pléistocènes de la caverne de Malamaud (Ariège)*. D.E.S.S.N., Université de Bordeaux I.
- Esteban-Nadal, M., Cáceres, 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: 2959-2970.
- Foronova, I.V. (1999). Quaternary mammals and stratigraphy of the Kuznetsk Basin (South-western Siberia). *Antropozoikum / Anthropozoic*, 23: 71-98.
- Fosse, P. (1994). *Taphonomie Paléolithique: les grands mammifères de Soleilhac (Haute-Loire) et*

- de Lunel-Viel 1 (Hérault). Doctorat, Université Aix-Marseille I.
- Fosse, P., Avery, G., Selva, N., Smietana, W., Okarma, H., Wajrak, A., Fourvel, J.B. & Madelaine, S. (2011). Taphonomie comparée des os longs d'Ongulés dévorés par les grands prédateurs modernes d'Europe et d'Afrique (*C. lupus*, *P. brunnea*). In (Brugal, J.P., Gardeisen, A. & Zucker, A., eds.) *Prédateurs dans tous leurs états; évolution, biodiversité, interactions, mythes, symboles*. XXXI rencontres internationales d'archéologie et d'histoire d'Antibes, 127-156
- Fosse, P., Laudet, F. Selva, N. & Wajrak, A. (2004). Premières observations néotaphonomiques sur des assemblages osseux de Bialowieza (N.E. Pologne): intérêts pour les gisements pléistocènes d'Europe. *Paléo*, 16: 91-115.
- Fourvel, J.B. & Mwebi. O. (2011). Hyenas' level of dependence on livestock in pastoralist areas in the Republic of Djibouti and Kenya: relation between prey availability and bone consumption sequence. In (Brugal, J.P., Gardeisen, A. & Zucker, A., eds.) *Prédateurs dans tous leurs états; évolution, biodiversité, interactions, mythes, symboles*. XXXI rencontres internationales d'archéologie et d'histoire d'Antibes, 157-176.
- Fuller, T.K. (1989). Denning behavior of wolves in North-Central Minnesota. *American Midland Naturalist*, 121:184-188.
- Galik, A. (1997). Die Ungulata aus der Schusterlucke im Kremstal (Wald vier tel, Niederösterreich). *Wiss. Mitt. Niederösterr. Landesmuseum*, 10: 83-103.
- Gamble, C. (1979). Hunting strategies in the Central European Palaeolithic. *Proceedings of the Prehistoric Society*, 45: 35-52.
- Gardeisen, A. (1994). *Restes fauniques et stratégies de chasse dans le Pléistocène supérieur de la grotte ouest du Portel (Ariège, France)*. Doctorat, Université de Montpellier III.
- Gaudry, A. & Boule, M. (1892). Les Oubliettes de Gargas. *Matériaux pour l'Histoire des Temps Quaternaires*, 105-130.
- Guthrie, R.D. (1992). *Frozen fauna of the Mammoth Steppe; the story of Blue Babe*. Univ. of Chicago Press, Chicago.
- Haynes, G. (1981). *Bone modifications and skeletal disturbances by natural agencies: studies in North America*. PhD, Catholic University of America.
- Haynes, G. (1982). Utilization and skeletal disturbances of North American prey carcasses. *Arctic*, 35: 266-281.
- Hoffecker, J.F., Baryshnikov, G.F. Doronichev V.B. (2003). Large mammal taphonomy of the Middle Pleistocene hominid occupation at Treugol'naya Cave (Northern Caucasus). *Quaternary Science Reviews*, 22: 595-607.
- Jedrzejewska, B. & Jedrzejewski, W. (1998). *Predation in Vertebrate Communities. The Bialowieza Primeval Forest as a Case Study*. Ecological Studies. Analysis and Synthesis. Springer. 135.
- Jedrzejewski, W., Jedrzejewska, B., Okarma, H., Schmidt, K., Zub, K. & Musiani. M. (2000). Prey selection and predation by wolves in Bialowieza primeval forest, Poland. *Journal of Mammalogy*, 81: 197-212.
- Jedrzejewski, W., Schmidt, K., Theuerkauf, J., Jedrzejewska, B. & Okarma. H. (2001). Daily movements and territory use by radio-collared wolves (*Canis lupus*) in Bialowieza Primeval Forest in Poland. *Can. J. Zoology*, 79: 1993-2004.
- Joffroy, R., Paris, R. & Mouton P. (1959). La grotte de la Roche-aux-Chats à Bâlot (Côte-d'Or). *Bulletin de la Société préhistorique française*, 56: 205-209.
- Kamler, J.F., Jedrzejewski, W. & Jedrzejewska, B. (2007). Survival and cause-specific mortality of red deer *Cervus elaphus* in Bialowieza National Park, Poland. *Wildl. Biol.*, 13:48-52.
- Klippel, W.E., Snyder, L.M. & Parmalee, P.W. (1987). Taphonomy and archaeologically recovered mammal bone from southeast Missouri. *Journal of Ethnobiology*, 7: 155-169.
- Koenigswald, W. von, Sander, P.M. & Walders, M. (1995). Jungpleistozäne Tierfahrten aus der Emscher-Niederterrasse von Bottrop-Welheim. *Münchener Geowiss. Abh. (A)*, 27: 5-50.
- Kolska Horwitz, L. (1990). The origin of partially digested bones recovered from archaeological contexts in Israel. *Paléorient*, 16: 97-106.
- Kowalewski, D. (2009). The anatomy of a wolf den site: a field report. *Electronic Green Journal*, 1: 1-11.
- Krasińska, M. & Krasiński. Z.A. (2002). Body mass and measurements of the European bison during postnatal development. *Acta Theriologica*, 47: 85-106.
- Kretzoi, M. (1989). Zur stratigraphischen stellung der fauna von Vertesszöllös und Petralona. *Ethnographisch-archäologische Zeitschrift*, 30: 451-463.
- Kühtreiber, T. & Kunst. K. (1995). Das Spätglazial in der Gamssulzenhöhle im Toten Gebirge (Oberösterreich)-Artefakte, Tierreste, Fundschichtbildung in Die Gamssulzenhöhle im Toten Gebirge. In (G. Rabeder & G. Withalm, eds.) *Mitteilungen der Kommission für Quartärforschung*.
- Lord, T.C., O' Connor, T.P., Siebrandt, D.C. & Jacobi, R.M. (2007). People and large carnivores as biostratigraphic agents in Lateglacial cave assemblages. *Journal of Quaternary Science*, 22: 681-694.
- Magoun, A.J. & Valkenburg., P. (2001). Caribou remains at kill sites and the role of scavengers in producing patterned distribution in bone. In (Gerlach, S.C. & Murray, M.S., eds.) *People and wildlife in northern*

- North America: essays in honor of R. Dale Guthrie. BAR, i.e. 944: 294-299.
- Martin, R. (1968). Les Mammifères fossiles du gisement quaternaire de Villereversure (Ain). Etude des Carnivores, des Cervidés et des Equidés. *Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon*, 27: 1-153.
- Mashkour, M. et al. (2009). Carnivores and their prey in the Wezmeh cave (Kermanshah, Iran): a Late Pleistocene refuge in the Zagros. *Int. J. Osteoarchaeol.*, 19: 678-694.
- McDonald, J.N. & Bartlett, C.S. Jr. (1983). An associated Musk Ox skeleton from Saltville, Virginia. *Journal of Vertebrate Paleontology*, 2: 453-470.
- Mech, L.D. & Merrill, S.B. (1998). Daily departure and return patterns of wolves, *Canis lupus*, from a den at 80°N latitude. *Canadian Field Naturalist*, 112: 515-517.
- Mech, L.D. & Packard, J.M. (1990). Possible use of wolf, *Canis lupus*, den over several centuries. *The Canadian Field-Naturalist*, 104: 484-485.
- Méroc, L. (1956.) *Cent ans de Préhistoire toulousaine*. Muséum Histoire naturelle de Toulouse, pp. 1-87.
- Miracle, P.T., Mauch Lenardic, J., & Brajkovic, D. (2010). Last glacial climates, "Refugia", and faunal change in Southeastern Europe: Mammalian assemblages from Veternica, Velika pecina, and Vindija caves (Croatia). *Quaternary International*, 212: 137-148.
- Morel, P. (1984). Découverte de restes d'un élan holocène à la Schratzenfluh, Flühi, LU. *Cavernes*, 28: 19-30.
- Okarma, H. (1995). The trophic ecology of wolves and their predatory role in ungulate communities of forest ecosystems in Europe. *Acta theriologica*, 40: 335-386.
- Pacher, M. & Döppes, D. (1997). Zwei Faunenelemente aus pleistozänen Höhlenfundstellen des Toten Gebirges: *Canis lupus* L. und *Gulo gulo* L. *Geologisch-Paläontologische Mitteilungen Innsbruck*, 22: 129-151.
- Paletta, C. (2005). *L'évolution des comportements de subsistance des hommes du Moustérien au Solutréen dans la région Poitou-Charentes (France)*. PhD., Muséum National d'Histoire Naturelle, Institut de Paléontologie Humaine.
- Peterson, R.O. (1977). Wolf ecology and prey relationships on Isle Royale. *Natl. Park Serv. Sci.*, Monogr. Ser. 11: 1-210.
- Pohar, V. (1981). Pleistocenska favna iz Jame pod Herkovimi pecmi (Pleistocene fauna of the Jama pod Herkovimi pecmi Cave). *Geologija*, 24: 241-284.
- Prucca, A. (2011). Tanières et sites de rendez vous: exploitation temporaire de sites d'habitat par *Canis lupus*. In (Brugal, J.P., Gardeisen, A. & Zucker, A., eds.) *Prédateurs dans tous leurs états; évolution, biodiversité, interactions, mythes, symboles*. XXXI rencontres internationales d'archéologie et d'histoire d'Antibes : 97-111.
- Romandini, M. (2011). *Analisi archeozoologica, tafonomica, paleontologica e spaziale dei livelli Uluzziani e tardo-Musteriani della Grotta di Fumane (VR). Variazioni e continua strategico-comportamentali umane in Italia Nord Orientale: i casi di Grotta del Col della Stria (VI) e Grotta del Rio Secco (PN)*. PhD., Università degli Studi di Ferrara.
- Sattler, R.A. (1997). Large mammals in Lower Rampart Cave 1, Alaska: interspecific utilization of an eastern Beringian cave. *Geoarchaeology*, 12: 657-688.
- Selva, N. (2004). *The role of scavenging in the predator community of Bialowieza Primeval Forest*. PhD., Universidad de Sevilla, Sevilla.
- Smietana, W. (2005). Selectivity of wolf predation on red deer in the Bieszczady Mountains, Poland. *Acta Theriologica*, 50 (2): 277-288.
- Smietana, W. & Klimek, A. (1993). Diet of wolves in the Bieszczady Mountains, Poland. *Acta Theriologica*, 38: 245-251.
- Soergel, W. (1922). *Jagd der Vorzeit*. Iena.
- Stehlin, H.G. (1933). Paléontologie. In (Dubois, A. & Stehlin, H.G., eds.) *La grotte de Cotencher, station moustérienne. Mémoires de la Société paléontologique suisse*, 52-53: 1-178.
- Stiner, M.C. (1991). The faunal remains from Grotta Guattari: a taphonomic perspective. *Current Anthropology*, 32: 103-138.
- Stiner, M.C. (2004). Comparative ecology and taphonomy of spotted hyenas, humans and wolves in Pleistocene Italy. *Revue de Paléobiologie*, 2322: 771-785.
- Stiner, M.C., Munro, D. & Sanz M. (2012). Carcass damage and digested bone from mountain lions (*Felis concolor*): implications for carcass persistence on landscapes as a function of prey age. *Journal of Archaeological Science*, 39: 896-907.
- Sutcliffe, A.J. (1970). Spotted hyaena: crusher, gnawer, digester and collector of bones. *Nature*, 227 (5263): 1110-1113.
- Suire, C. (1969). *Contribution à l'étude du genre Canis d'après les vestiges recueillis dans quelques gisements pléistocènes du Sud-Ouest de la France*. Thèse 3^{ème} cycle, Université de Bordeaux I.
- Theuerkauf, J., Rouys, S. & Jedrzejewski, W. (2003). Selection of den, rendezvous, and resting sites by wolves in the Bialowieza Forest, Poland. *Can. J. Zoology*, 81:163-167.
- Toskan, B. (2007). 11. Remains of large mammals from Divje babe I - Stratigraphy, taxonomy and biometry. In (Turk, I, ed.) *Divje Babe I. Upper Pleistocene Palaeolithic site in Slovenia, Opera Instituti Archaeologici Sloveniae*, 221-278.

- Trapp, J.R. (2004). *Wolf den site selection and characteristics in the Northern Rocky Mountains: a multi-scale analysis*. Master, Prescott College.
- Trapp, J.R., Beier, P., Mack, C., Parson, D.R. & Paquet, P.C. (2008). Wolf, *Canis lupus*, den site selection in the Rocky Mountains. *The Canadian Field Naturalist*, 122: 49-56.
- Turner, A. (1981). *The palaeoeconomy of British upper Pleistocene large predators and their prey*. PhD., Sheffield.
- Valensi, P. (1994). *Les Grands Mammifères de la grotte du Lazaret. Étude paléontologique et biostratigraphique des carnivores*. *Archéozoologie des grandes faunes*. Muséum National d'Histoire Naturelle, Paris.
- Webb, E. (1988). Interpretating the faunal debris found in Central European sites occupied by Neandertals. In (Webb, R.E., ed.) *Recent developments in environmental analysis in Old and New world archaeology*. BAR, 416: 79-104.
- 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.
- Yravedra, J., Lagos, L. & Barcena, F. (2011). A taphonomic study of wild wolf (*Canis lupus*) modification of horse bones in Northwestern Spain. *Journal of Taphonomy*, 9: 37-65.
- Zapfe, H. (1966). Lebensspuren. In (Ehrenberg, K., ed.) *Die Teufels - oder Fuchsenlucken bei Eggenburg (N.O.)*. *Österreichische Akademie der Wissenschaften*, pp. 109-122.
- Ziegler, R. (1996). Die Großsäuger aus der Frühwürmzeitlichen Fauna von der Villa Seckendorff in Stuttgart-Bad Cannstatt. *Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie)*, 237: 1-67.